# Conservation management for lowland breeding waders in the UK

LUCY ROSE MASON

Thesis submitted for the degree of Doctor of Philosophy by Publication at the
University of East Anglia
School of Biological Sciences
United Kingdom

2019

Supervisors:
Professor Jennifer A. Gill (University of East Anglia)
Dr Jennifer Smart (RSPB Centre for Conservation Science)

Funded by
RSPB Centre for Conservation Science
The Royal Society for the Protection of Birds
United Kingdom

# Abstract

Biodiversity loss is occurring globally at an alarming rate through the impacts of an unsustainably expanding human population, with changes in land-use practices, pollution, exploitation of natural resources and climate threatening species and ecological communities worldwide. Species range contractions and population declines as a result of these changes, combined with predicted future changes in climatic distributions, make managing their remaining suitable habitats even more important. Threatened birds, by acting as indicators of ecosystem health, can provide a basis on which conservation management can be designed and targeted at the site-level. Waders breeding in European lowland habitats are an example of a species-suite in which populations have declined dramatically, and where concurrent range contractions are now compounded by the impacts of climate change. Breeding success (nest and chick survival to fledging) is the main demographic parameter driving these declines, so conservation management focusses on enhancing productivity by restoring or maintaining suitable nesting habitat and high levels of nest and chick survival. Such management can be organised into a decision tree where each step indicates a research requirement or deployment method in the conservation toolkit. Through two case studies of wader species breeding in lowland habitats in the UK (Redshank *Tringa totanus* on saltmarsh, and Lapwing *Vanellus vanellus* on wet grassland), the types of management required and challenges faced are explored, while discussing the research underpinning each step, including the contributions of eight key publications. The issues and solutions presented in these case studies are widely applicable to other lowland wader species and habitats at similar European latitudes. The next step will be to apply this conservation management at the landscape-scale across the continent to ensure the provision of effective supranational ecological networks of well-managed sites able to promote ecosystem resilience in the face of global threats.

# Contents

**PUBLICATIONS**

**APPENDIX**

# List of publications

This thesis is based on the following published or submitted papers, which are referred to in the text by Roman numerals:

**I** Stephens, P.A., **Mason, L.R.**, Green, R.E., Gregory, R.D., Sauer, J.R., Alison, J., Aunins, A., Brotons, L., Butchart, S.H.M., Campedelli, T., Chodkiewicz, T., Chylarecki, P., Crowe, O., Elts, J., Escandell, V., Foppen, R.P.B., Heldbjerg, H., Herrando, S., Husby, M., Jiguet, F., Lehikoinen, A., Lindström, Å., Noble, D.G., Paquet, J.-Y., Reif, J., Sattler, T., Szép, T., Teufelbauer, N., Trautmann, S., van Strien, A.J., van Turnhout, C.A.M., Vorisek, P. & Willis, S.G. (2016) Consistent response of bird populations to climate change on two continents. *Science*, 352: 84-87.

**II** **Mason, L.R.**, Green, R.E., Stephens, P.A., Willis, S.G., Aunins, A., Brotons, L., Chodkiewicz, T., Chylarecki, P., Escandell, V., Foppen, R.P.B., Herrando, S., Husby, M., Jiguet, F., Kålås, J.A., Lindström, Å., Massimino, D., Moshøj, C., Nellis, R., Paquet J.-Y., Reif, J., Sirkiä, P.M., Szép, T., Tellini Florenzano, G., Teufelbauer, N., Trautmann, S., van Strien, A., van Turnhout, C.A.M., Voříšek, P. & Gregory R.D. (in review) Responses of bird populations to climate change on two continents vary with species' ecological traits but not with the direction of the change in climate suitability. Submitted to *Climatic Change*.

**III** **Malpas, L.R.**, Smart, J., Drewitt, A.L., Sharps, E. & Garbutt, A. (2013) Continued declines of Redshank *Tringa totanus* breeding on saltmarsh in Great Britain: is there a solution to this conservation problem? *Bird Study*, 60: 370-383.

**IV** Sharps, E., Smart, J., **Mason, L.R**., Jones, K., Skov, M.W., Garbutt, A. & Hiddink, J.G. (2017) Nest trampling and ground nesting birds: quantifying temporal and spatial overlap between cattle activity and breeding Redshank. *Ecology and Evolution*, 7, 6622–6633.

**V** **Mason, L.R.**, Feather, A., Godden, N., Vreugdenhil, C.C. & Smart, J. (2019) Are agri-environment schemes successful in delivering conservation grazing management on saltmarsh? *Journal of Applied Ecology*, 00: 1-13.

**VI** **Mason, L.R.** & Smart, J. (2015) Wader chick condition is not limited by resource availability on wader-friendly lowland wet grassland sites in the UK. *Wader Study*, 122: 193-200.

**VII** **Mason, L.R.**, Smart, J. & Drewitt, A.L. (2018) Tracking day and night provides insights into the relative importance of different wader chick predators. *Ibis*, 160: 71-88.

**VIII** **Malpas, L.R.**, Kennerley, R.J., Hirons, G.J.M., Sheldon, R.D., Ausden, M., Gilbert, J.C. & Smart, J. (2013) The use of predator-exclusion fencing as a management tool improves the breeding success of waders on lowland wet grassland. *Journal for Nature Conservation,* 21: 37-47.

*Note change of surname from Malpas to Mason in August 2013*

## Table of contributions

| | **I** | **II** | **III** | **IV** | **V** | **VI** | **VII** | **VIII** |
|---|---|---|---|---|---|---|---|---|
| Initial concept | PAS, REG, RDG, SGW | REG, **LRM**, RDG, PAS, SGW | JS, ALD | JS, **LRM**, ES | **LRM**, JS | JS, **LRM** | JS, **LRM** | GJMH, JCG, JS, MA, RDS, RJK |
| Study design | PAS, REG, RDG, SGW, **LRM** | REG, **LRM**, RDG, PAS, SGW | **LRM**, JS | ES, **LRM**, KJ, JS | **LRM** | **LRM**, JS | **LRM**, JS | GJMH, JCG, JS, MA, RDS, RJK, **LRM** |
| Data acquisition or collation | PAS, **LRM**, SGW, RDG, REG, AA, AJvS, ALe, ALi, CAMvT, DGN, FJ, HH, JA, JE, JR, JRS, JYP, LB, MH, NT, OC, PC, PV, RF, SB, SH, ST, TCa, TCh, TSa, TSz, VE | PAS, **LRM**, SGW, RDG, REG, AA, ALi, AJvS, CM, CAMvT, DM, FJ, GTF, JYP, JR, JAK, LB, MH, NT, PMS, PV, PC, RN, RF, SH, ST, TSz, TCh, VE | **LRM**, ES | ES, KJ | AF, NG, CV, **LRM** | **LRM** | **LRM** | RJK, **LRM** |
| Analysis | PAS, **LRM**, SGW | **LRM** | **LRM** | ES | **LRM** | **LRM** | **LRM** | **LRM** |
| Manuscript preparation | PAS, SGW, **LRM,** REG, RDG, AA, AJvS, ALe, ALi, CAMvT, DGN, FJ, HH, JA, JE, JR, JRS, JYP, LB, MH, NT, OC, PC, PV, RF, SB, SH, ST, TCa, TCh, TSa, TSz, VE | **LRM**, REG, PAS, SGW, RDG, AA, ALi, AJvS, CM, CAMvT, DM, FJ, GTF, JYP, JR, JAK, LB, MH, NT, PMS, PV, PC, RN, RF, SH, ST, TSz, TCh, VE | **LRM**, JS, AG, ALD, ES | ES, **LRM,** JS, AG, JGH, MWS, KJ | **LRM**, JS, AF, NG, CV | **LRM**, JS | **LRM**, JS, ALD | **LRM**, JS, GJMH, JCG, MA, RDS, RJK |

**Lucy R. Mason (LRM)**, Ainars Aunins (AA), Åke Lindström (ALi), Alastair Feather (AF), Aleksi Lehikoinen (ALe), Allan L. Drewitt (ALD), Angus Garbutt (AG), Arco J. van Strien (AJvS), Charlotte Moshøj (CM), Chris A. M. van Turnhout (CAMvT), Chris C. Vreugdenhil (CV), Dario Massimino (DM), David G. Noble (DGN), Elwyn Sharps (ES), Frédéric Jiguet (FJ), Graham J. M. Hirons (GJMH), Guido Tellini Florenzano (GTF), Henning Heldbjerg (HH), Jaanus Elts (JE), Jamie Alison (JA), Jan G. Hiddink (JGH), Jean-Yves Paquet (JYP), Jennifer Smart (JS), Jiri Reif (JR), Joanne C. Gilbert (JCG), John Atle Kålås (JAK), John R. Sauer (JRS), Kate Jones (KJ), Lluís Brotons (LB), Magne Husby (MH), Malcolm Ausden (MA), Martin W. Skov (MWS), Nick Godden (NG), Norbert Teufelbauer (NT), Olivia Crowe (OC), Päivi M. Sirkiä (PMS), Petr Vorisek (PV), Philip A. Stephens (PAS), Przemysław Chylarecki (PC), Renno Nellis (RN), Rhys E. Green (REG), Richard D. Gregory (RDG), Rob D. Sheldon (RDS), Rosalind J. Kennerley (RJK), Ruud P. B. Foppen (RF), Sergi Herrando (SH), Stephen G. Willis (SGW), Stuart H. M. Butchart (SB), Sven Trautmann (ST), Thomas Sattler (TSa), Tibor Szép (TSz), Tomasz Chodkiewicz (TCh), Tommaso Campedelli (TCa), Virginia Escandell (VE)

# List of figures and tables

## List of Figures

## List of Tables

# Critical Analysis

CLIMATE CHANGE

Consistent response of bird populations to climate change on two continents

1 Responses of bird populations to climate change on two continents vary with species' ecological traits but not with the direction of the change in climate suitability

5 Short title: Bird population responses to climate change

RESEARCH ARTICLE

Journal of Applied Ecology

Are agri-environment schemes successful in delivering conservation grazing management on saltmarsh?

Lucy R. Mason[1] | Alastair Feather[1] | Nick Godden[1] | Chris C. Vreugdenhil[1] | Jennifer Smart[1,2]

Bird Study (2013) 60, 370–383

Continued declines of Redshank *Tringa totanus* breeding on saltmarsh in Great Britain: is there a solution to this conservation problem?

LUCY R. MALPAS[1*], JENNIFER SMART[1], ALLAN DREWITT[2], ELWYN SHARPS[1,3,4] and ANGUS GARBUTT[3]

research paper Wader Study 122(3): 193–200. doi: 10.18194/ws.00017

Wader chick condition is not limited by resource availability on wader-friendly lowland wet grassland sites in the UK

Lucy R. Mason* & Jennifer Smart

*RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK*

ORIGINAL RESEARCH

WILEY Ecology and Evolution

Nest trampling and ground nesting birds: Quantifying temporal and spatial overlap between cattle activity and breeding redshank

Elwyn Sharps[1,2,3] | Jennifer Smart[3,4] | Lucy R. Mason[3] | Kate Jones[3,5] | Martin W. Skov[1] | Angus Garbutt[2] | Jan G. Hiddink[1]

IBIS international journal of avian science

Tracking day and night provides insights into the relative importance of different wader chick predators

LUCY R. MASON,[1*] JENNIFER SMART[1] & ALLAN L. DREWITT[2]

*[1]RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire SG19 2DL, UK*
*[2]Natural England, Eastbrook, Cambridge CB2 8DR, UK*

Author's personal copy

Journal for Nature Conservation

The use of predator-exclusion fencing as a management tool improves the breeding success of waders on lowland wet grassland

Lucy R. Malpas*, Rosalind J. Kennerley, Graham J.M. Hirons, Rob D. Sheldon, Malcolm Ausden, Joanne C. Gilbert, Jennifer Smart

## Conservation in a changing world

Biodiversity is being lost globally at an exceptional rate, with the Earth now undergoing a sixth mass extinction event unparalleled for 65 million years (Barnosky *et al.* 2011; Ceballos *et al.* 2015). This biodiversity loss – linked primarily to the global impacts of climate change, terrestrial and marine pollution, habitat loss and fragmentation, non-native invasive species and overexploitation of natural resources – stems ultimately from a large and exponentially increasing human population with unsustainable requirements for food, accommodation and energy (Secretariat of the Convention on Biological Diversity 2010; Ehrlich & Ehrlich 2013). The rate of loss is so profound that in the past 25 years two warnings to humanity, signed by over 20,000 scientists worldwide, have been published highlighting the global threats of highest concern to both biodiversity and human civilisation itself (Ripple *et al.* 2017); a clarion call for improved and globally-coordinated conservation measures.

Conserving biodiversity and dealing with global threats requires intervention at different spatial scales (Boyd *et al.* 2008). Through the Convention on Biological Diversity (CBD), multiple member states agreed to achieve 20 targets to address the underlying causes of biodiversity loss by 2020 (Aichi Biodiversity Targets; Secretariat of the Convention on Biological Diversity 2011). Although these targets are not yet being achieved (Butchart *et al.* 2010; Secretariat of the Convention on Biological Diversity 2010), they provide a guidance mechanism and incentive for individual governments to design and implement environmental and conservation policy at smaller spatial scales within countries. Such policy can then be applied through individual site or habitat protection, leading to a mosaic of different conservation management techniques deployed at different scales throughout the landscape, a necessary prerequisite if mass extinction is to be prevented (Boyd *et al.* 2008).

Conservation action can also be applied at different demographic and ecological scales, focussing on global, national or local populations within individual ecosystems, on whole taxa, suites of similar species or species individually. Birds, for example, can act as indicators of ecosystem health by existing at relatively high trophic levels, reacting quickly to changing environmental conditions and being highly sensitive to anthropogenic impacts (Browder *et al.* 2002; Gregory & van Strien 2010). This, and the ease with which they can often be monitored relative to other taxa, means that birds are regularly used as a focus for conservation of the ecosystems and habitats in which they reside, as well as often being of conservation concern in their own right.

## Lowland wader conservation management

European wading birds are a good example of a species-suite with specific requirements for conservation management at different spatial and demographic scales. Northern Lapwing *Vanellus vanellus*, Common Redshank *Tringa totanus*, Common Snipe *Gallinago gallinago*, Black-tailed Godwit *Limosa limosa*, Eurasian Oystercatcher *Haematopus ostralegus* and Eurasian Curlew *Numenius arquata* were once among the most common breeding birds in European lowland habitats (grasslands, arable crop land, inland marshes and saltmarshes), but have undergone substantial declines, losing 45% of their breeding populations on average between 1980 and 2015 (Figure 1; Lapwing -55%, Redshank -56%, Snipe = -50%, Black-tailed godwit -54%, Oystercatcher -16%, Curlew -41%; EBCC/BirdLife/RSPB/CSO 2017). As a result of these declines, five of these species are classified as Vulnerable to, or Endangered with, extinction in Europe (Lapwing, Redshank, Curlew, Black-tailed Godwit, Oystercatcher; BirdLife International 2015), and four are also classified as Near Threatened with extinction globally (Lapwing, Black-tailed Godwit, Oystercatcher, Curlew; BirdLife International 2018).

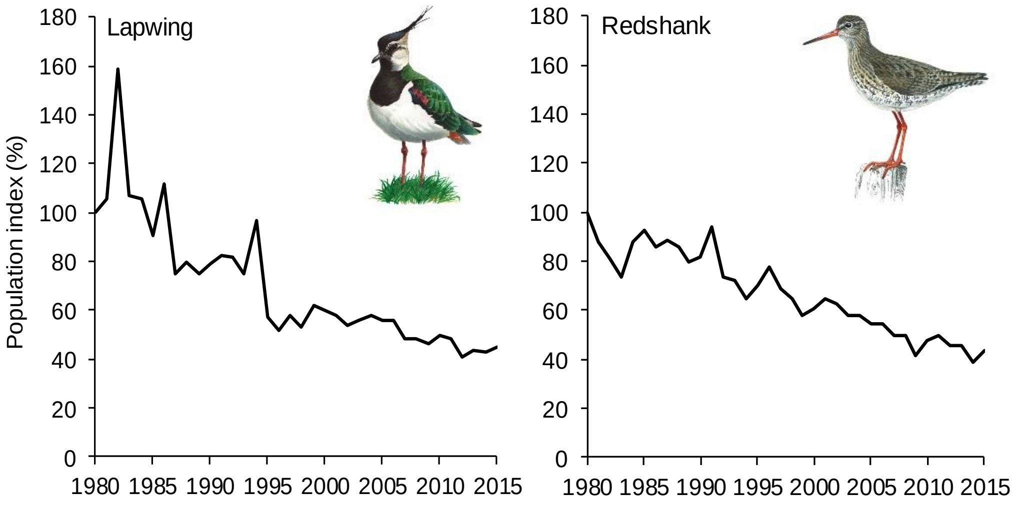


Figure 1. Annual population trends for Lapwing *Vanellus vanellus* and Redshank *Tringa totanus* in Europe for the period 1980-2015 redrawn from data published by the Pan-European Common Bird Monitoring Scheme (PECBMS; EBCC/BirdLife/RSPB/CSO 2017). Population indices were arbitrarily set to 100% in 1980. Wader images © Mike Langman rspb-images.com.

## Contribution of low productivity to wader population declines

There are three key demographic parameters that could contribute to the ongoing population declines of lowland-breeding waders: i) breeding success, namely the reproductive output of a population in terms of the number of young fledged per year (also referred to as ‘productivity’); ii) post-fledging juvenile mortality, the survival of young in the 1–2 years post-fledging; and iii) adult mortality, the number of adults surviving each year (e.g. Dempster 1975; Moss *et al.* 1982; Evans & Pienkowski 1984; Rockwood 2015). All three parameters drive population change by influencing the number of new recruits or existing breeders progressing into breeding populations in future years, thereby having a cumulative impact on population size in subsequent years through a feedback loop. In the case of population declines, where any of the three demographic parameters are lower than sufficient to balance the other two, a negative feedback loop can occur, where fewer breeding individuals results in fewer young produced leading to even fewer breeding individuals in subsequent years. In species which undergo post-breeding dispersal or migration, post-juvenile mortality and adult survival rates can be influenced by the range of conditions experienced in locations throughout the species’ range, including while breeding, on passage or in winter, with individuals from the same breeding population often experiencing different non-breeding conditions (e.g. Webster *et al.* 2002; Morrison *et al.* 2016). Breeding success is inherently linked to local breeding habitat conditions however (Morrison *et al.* 2016), although carry-over effects of conditions experienced elsewhere can also have an impact (e.g. Norris *et al.* 2004; Harrison *et al.* 2011).

A recent meta-analysis of European wader species’ population dynamics concluded that low breeding success is the demographic parameter primarily responsible for the recent dramatic population declines and for preventing population recovery, with rates of post-fledging juvenile and adult mortality having remained relatively stable, but with reproductive output becoming too low to counteract them (Roodbergen *et al.* 2012; Robinson *et al.* 2014). For lowland breeding waders, this low productivity could be a result of high nest mortality (not enough eggs hatching), high chick mortality (nests hatching but chicks not surviving long enough to fledge), or a combination of the two. Lowland wader nests, which typically contain up to four eggs in a shallow scrape on the ground, are particularly susceptible to failure, being at great risk from predation (MacDonald & Bolton 2008b), flooding (when placed in wet or regularly flooded habitats;

Green 1986; Posthumus *et al.* 2010), livestock trampling (Beintema & Müskens 1987), and destruction by farm machinery (for nests on arable crop or intensively managed land; Shrubb 1990; Sheldon *et al.* 2007; Exo *et al.* 2017). Similarly, wader chicks, which are precocial and leave the nest soon after hatching, are also susceptible to predation, death by agricultural machinery (e.g. mowing hay in the wader chick rearing period), or starvation and exposure as a result of insufficient food availability and poor body condition (Teunissen *et al.* 2008; Schekkerman *et al.* 2009; Kleijn *et al.* 2010; Exo *et al.* 2017). Although mechanisms to counter the threat of egg and chick predation have evolved, including adult anti-predator defence behaviours, chick hiding or escape behaviours, egg and chick crypsis, and the ability of females to make multiple nesting attempts after failure at the egg stage (e.g. Hale 1988; Shrubb 2007), the widespread population declines of wader species indicate that these mechanisms are not currently sufficient to counteract changing environmental and anthropogenic threats.

### Historical and contemporary drivers of low productivity in lowland waders

It is widely accepted that agricultural intensification, urbanisation and associated wetland drainage are the primary causes of European lowland farmland bird population declines, including waders, since the 1950s (e.g. Fuller *et al.* 1995; Donald *et al.* 2001; Donald *et al.* 2006). A change from traditional methods of farming to more intensive practices and mechanisation after the Second World War led to a reduction in the availability of suitable habitat for nesting and potentially an increase in nest and chick mortality in some remaining suitable habitats (Roodbergen *et al.* 2012; Kentie *et al.* 2015). Changes in crop planting methods from spring-sown to winter-sown varieties reduced the availability of short arable swards for nesting (as winter-sown varieties are already too tall and dense once early spring arrives; Sheldon 2002; Sheldon *et al.* 2004; Milsom 2005; Sheldon *et al.* 2007). An emphasis on food production and high yields led to increased fertiliser and pesticide inputs into agricultural land, both arable and pastoral, further reducing the availability of suitable nesting sward and invertebrate food supplies (Vickery *et al.* 2001). Mechanisation and more frequent mowing, ploughing and chemical applications compounded the issue by increasing direct nest and chick mortality in these already degraded conditions (Sheldon 2002; Sheldon *et al.* 2007). Wetland drainage, to facilitate mechanisation and increased production, resulted in soils that were less penetrable and with an invertebrate community more adapted to drier conditions (i.e. situated lower down the soil profile, particularly an issue for species such as Snipe, Curlew and

Oystercatcher which feed by probing for soil invertebrates near the surface; McCracken & Tallowin 2004; Smart *et al.* 2008).

There may also be a hidden cost to this agricultural intensification in the increased use of environmentally-persistent pesticides on farmland, which leach into wetland surface- and ground-water and may be partly responsible for a 75% reduction in invertebrate biomass (the main wader food source) across European habitats (Hallmann *et al.* 2017). Farmland pesticides also build up in higher trophic levels (e.g. Sánchez-Bayo; Pimentel & Edwards 1982; Kelly *et al.* 2007), potentially leading to hidden reductions in wader adult and chick body condition making them more susceptible to predation or environmental stochasticity. No studies have yet investigated the extent of these threats in affecting the breeding success (or survival) of wader species, largely because of the difficulties involved in such a study. The need for blood, feather or other biological samples, a specialist laboratory and skilled researchers to detect chemical build-up in individuals, a lack of historical data against which to compare modern levels and insufficient methods for linking this to body condition, breeding success or survival have so far precluded research of this kind. It is highly likely that waders are being affected in some way, however, given that similar effects have been linked to population declines in other insectivorous farmland birds (Benton *et al.* 2002; Hallmann *et al.* 2014).

As a result of the widespread changes in farming and land management practices, and the reduction in the amount and quality of remaining nesting habitats, many lowland wader populations have undergone severe range contractions in addition to population declines, with breeding populations now highly fragmented and restricted to small and increasingly isolated habitat patches (Henderson *et al.* 2002; Wilson *et al.* 2005; Balmer *et al.* 2013; Smart *et al.* 2014). Here they may experience Allee effects (positive density dependence) due to low population densities and, with ongoing agricultural intensification continuing in the background, they may be influenced by other more specific threats. For example, population growth may be inhibited because the smaller numbers of adults are less able to effectively deter nest and chick predators thus leading to lower productivity (Stephens & Sutherland 1999), particularly if fragmented sites (which often support a higher abundance of prey species than the wider countryside due to less-intensive management and/or protected status) act as ‘honeypots’ attracting in predators from the surrounding countryside (e.g. Chalfoun *et al.* 2002; Leigh *et al.* 2016). There may also be greater competition for nesting territories, nest sites and food in these small habitat patches, and high levels of natal philopatry and site-fidelity will make migration of breeding individuals between subpopulations unlikely, so if a population is failing at one site it is unlikely to be rescued by immigration or migration to another location (Sutherland 1997). Isolated populations are also more at risk from environmental and demographic stochasticity (Wilcox & Murphy 1985; Lawton 1994), with a higher potential for predation, disease or hunting to eradicate populations, and with the number, timing and ultimate success of breeding attempts highly dependent on annual environmental conditions such as the extent of flooding and spring temperature.

These habitat fragmentation effects can be further compounded by larger-scale global threats such as climate change, which may impact directly on breeding habitat suitability. In western Europe, climate change is already leading to reduced rainfall and increased evaporation in spring/summer (e.g. Jenkins *et al.* 2008; IPCC 2014) and thus the drying of lowland breeding wader habitats (such as wet grasslands and saltmarshes) during the breeding season, making them less suitable for wader adult and chick foraging (Thompson *et al.* 2009). Climatic change may also increase the frequency and magnitude of strong spring/summer winds and heavy rains (Easterling *et al.* 2000; IPCC 2014), which increase the likelihood of flooding, leading to nest and chick mortality and increasing the requirement for replacement clutches (Ratcliffe *et al.* 2005; van de Pol *et al.* 2010). Coastal wader breeding habitats such as saltmarshes are further at risk from climate-induced sea level rise exacerbated by coastal squeeze, where the natural succession of saltmarsh habitat inland is prevented by hard sea defences (Doody 2004; FitzGerald *et al.* 2008; Pontee 2013), making them less-suitable for wader breeding (Smart & Gill 2003; Hughes 2004; van de Pol *et al.* 2010; Clausen & Clausen 2014).

Many European and North American breeding bird species are now known to have undergone country- or state-level population changes matching the direction of change in the suitability of their climate (**I, II**). Those that have experienced an increase in climate suitability in their current range have also tended to undergo concurrent population increases, while those experiencing decreased climate suitability tend to show population declines (**I, II**). In wetland birds, including waders, the relationship between population trend and the trend in climate suitability is more strongly positive than in species breeding in any other habitat, indicating that populations of wetland birds may be tracking the changes in climate suitability more closely than any other group (both declining in response to declining suitability and increasing in response to increasing suitability; **II**). For wetland birds there are therefore particularly urgent implications for site management, with likely requirements for local actions to be effectively targeted through research (such as that presented in **III–VIII**).

In Western Europe, species' climate envelopes (the climatic conditions within a species' current geographical range) are generally predicted to move northwards (Huntley *et al.* 2007) which, twinned with the fact that climate change is already impacting on bird populations (**I**, **II**), has potentially large-scale repercussions for species and site conservation. Range contractions as a result of land-use changes and habitat loss, combined with observed and future changes in species' climatic distributions, make managing remaining suitable habitats to ensure population recovery within a species' climate suitable range even more important. Managing protected land appropriately to provide the conditions required by species of conservation concern can help counteract the adverse effects of climate change however (e.g. Clausen *et al.* 2013; Greenwood *et al.* 2016). For lowland breeding waders such management should focus on enhancing productivity by restoring or maintaining suitable nesting habitat and high levels of nest and chick survival.

### Managing lowland wader breeding sites

The protection and conservation management of small, isolated patches of habitat is unlikely to be sufficient to maintain viable populations of breeding waders so, in recent years, much emphasis has been placed on the necessity of implementing conservation management at landscape scales (Lawton *et al.* 2010). The chief aim of landscape-scale conservation is to create ecological networks, where sites are of sufficient quality to support source populations, and have sufficient ecological connections between them to enable individuals to disperse (Isaac *et al.* 2018). In theory this can be achieved by managing landscapes as mosaics by expanding, improving and linking existing sites, and providing zones of sympathetic land-use between them to allow individuals to disperse between habitat patches (Boyd *et al.* 2008; Lindenmayer *et al.* 2008; Eigenbrod *et al.* 2016).

The need for this connectivity is further emphasised by the threat of climate change, with landscape-scale conservation able to fulfil many of the principles guiding the conservation of biodiversity in a changing climate, namely: the need to conserve existing biodiversity; reduce threats to species not linked to climate; develop ecologically adaptable and varied landscapes; and establish ecological networks by which species can disperse (Hopkins *et al.* 2007; Eigenbrod *et al.* 2016). As climate change is already impacting on European and North America biodiversity (**I, II**), the need to develop and manage this landscape-scale connectivity is even more important.

Managing a site to provide suitable conditions for a species (or species-suites) of conservation concern requires multiple diagnosis, testing and delivery stages which can be organised into a decision tree (Figure 2). If, as in the case of lowland breeding waders, low productivity has been identified as the primary underlying demographic driver preventing population recovery, the first step towards managing habitats to halt or reverse population declines is to diagnose what conditions a species needs to breed successfully. For lowland waders this includes the conditions required to attract breeding pairs, encourage favourable levels of nest and chick survival, and to ensure sufficient food availability for foraging chicks and adults. Once the required conditions are identified, habitat management must be designed to deliver them, be this through changes in grazing practices or other sward management techniques, the provision of microhabitats to facilitate feeding, or the control or management of sources of mortality. Once designed, these management solutions must be trialled to ensure they are fit for purpose, are practical and economically viable to implement and deliver the required increase in productivity. Only after these three stages are accomplished successfully is conservation management likely to be effective.

Different habitats and their target wader species are currently at different stages on the conservation management decision tree (Figure 2). The following sections present two case studies concerning common, though rapidly declining, wader species and the research background behind their current location on the decision tree for their contrasting primary habitat types.

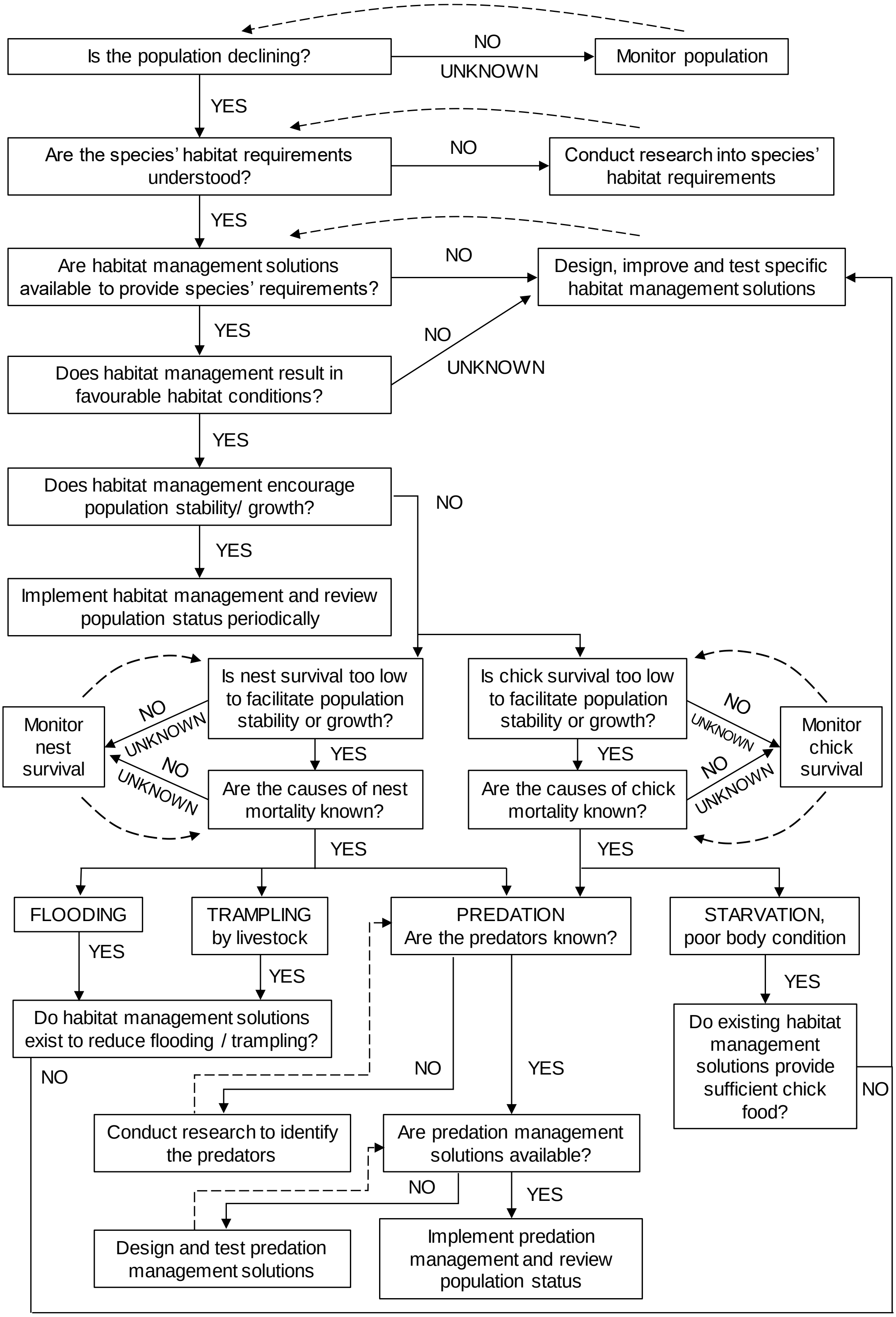


Figure 2. Decision tree for the stages involved in designing and implementing lowland breeding wader conservation management, assuming the target site or landscape already supports or has the potential to support breeding waders.

## Case study 1: Redshank breeding on saltmarsh in the UK

Over the past 30 years, research to understand the population dynamics and underlying drivers of change in saltmarsh-breeding Redshank populations means this system is now at a stage where habitat management solutions to address specific problems are being designed, improved, tested and ultimately implemented on a national scale. Publications **III**, **IV** and **V** have provided key contributions to this process, as highlighted in Figure 3. The following sections describe the background knowledge and research underpinning the steps prior to this stage on the conservation management decision tree.

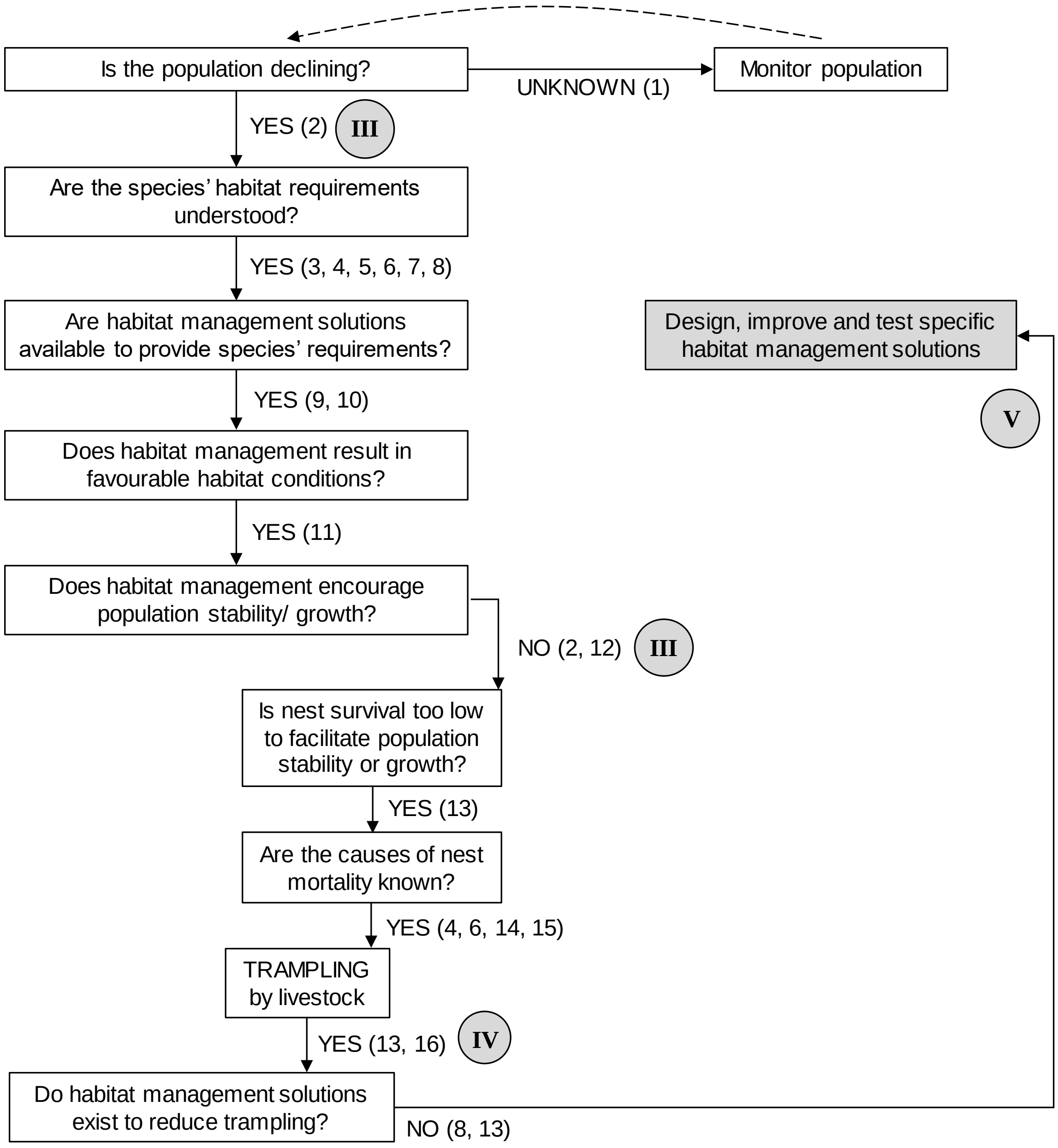


Figure 3. The current position of UK saltmarsh-breeding Redshank on the lowland wader conservation management decision tree (grey shaded box), the research steps leading up to this position and the location of influence of the research presented in publications **III, IV** and **V**. Numbers in parentheses refer to other key references in the evidence base underlying each research step: 1. Allport *et al.* (1986); 2. Brindley *et al.* (1998); 3. Green (1986); 4. Thompson (1987); 5. Hale (1988); 6. Smart (2005); 7. Smart *et al.* (2006); 8. Sharps *et al.* (2016); 9. Adnitt *et al.* (2007); 10. Doody (2008); 11. Norris *et al.* (1997); 12. Norris *et al.* (1998); 13. Sharps *et al.* (2015); 14. Yates (1982); 15. Green *et al.* (1984); 16. Jones (2014).

## Introducing saltmarsh

Saltmarshes are highly productive ecosystems supporting rich communities of halophytic plants, invertebrates and birds (Norris *et al.* 1998; Boorman 2003; Rickert *et al.* 2012) that cover ~5.5 million hectares of land surface globally (McOwen *et al.* 2017). As an intertidal habitat they form a transition between near-coastal marine habitats and coastal terrestrial habitats, situated above the mean high water mark (Burd 1989; Davidson *et al.* 1991). Through sediment accretion they typically form on a slope, with higher substrates closer to the landward edge (now often bounded by a sea wall), decreasing in a gradient down to the sea (Figure 4; Beeftink 1977). This forms a progression of zones of different levels of tidal inundation, with halophytic plant species with different degrees of salt tolerance forming distinct communities in each one (Figure 4; Adam 1981; Burd 1989; Rodwell 2000).The lowest ‘pioneer’ zone, closest to the sea, is inundated on almost every high tide and therefore supports the most salt-tolerant pioneer species such as glassworts *Salicornia spp.* and cord grasses *Spartina spp.*, which have the ability to rapidly colonise previously unvegetated mudflats. This is followed by the ‘low’ marsh zone, still frequently inundated but not on every tide, dominated primarily by saltmarsh grass *Puccinellia maritima* and sea purslane *Atriplex* (*Halimione) portulacoides*. The ‘mid’ and ‘upper’ marsh zones are found closer to the landward edge, supporting less salt-tolerant species due to their infrequent inundation on only the highest of spring tides. Grasses such as *P. maritima*, red fescue *Festuca rubra* and sea couch grass *Elytrigia atherica* typically dominate these zones, with the ‘mid’ marsh communities also often comprising the highest diversity of flowering plants such as sea lavenders *Limonium spp.*, sea aster *Aster tripolium*, sea arrow grass *Triglochin maritimum*, sea plantain *Plantago maritima* and scurvy grasses *Cochlearia spp.* (Figure 4; Burd 1989; Rodwell 2000).

Saltmarsh zones are not necessarily ordered contiguously, and their specific location and order on a particular marsh will depend on the tidal system, presence or absence of particular plant species, the creek system dynamics and patterns of historical and current management (Beeftink 1977). Many saltmarshes with defined creek systems exhibit ‘upper’ marsh vegetation in a narrow buffer around the creek edges, followed by ‘mid’ or ‘low’ marsh communities on the remainder of the marsh. This forms as water fills the creek systems first before over-topping them and flooding the marsh, depositing a narrow band of sediment along the creek edge which gradually builds up and becomes a raised levee (Figure 4; Adnitt *et al.* 2007). This raised band will drain more rapidly on receding tides, making it more suitable for ‘upper’ and ‘mid’ marsh plant species (Beeftink 1977; Packham & Willis 1997).

Saltmarshes provide important resources and habitat structures needed for bird breeding, wintering and migratory staging (Thyen *et al.* 2008), as well as important fish nursery grounds, human recreational opportunities and valuable ecosystem services in the form of tidal defence, water quality regulation and carbon storage (Boorman 2003; Gedan *et al.* 2009; Barbier *et al.* 2011; Jones *et al.* 2011; Davidson *et al.* 2017). They are also considered premium grazing land for livestock, with saltmarsh-raised meat reaching premium prices (Gedan *et al.* 2009; Jones *et al.* 2011).

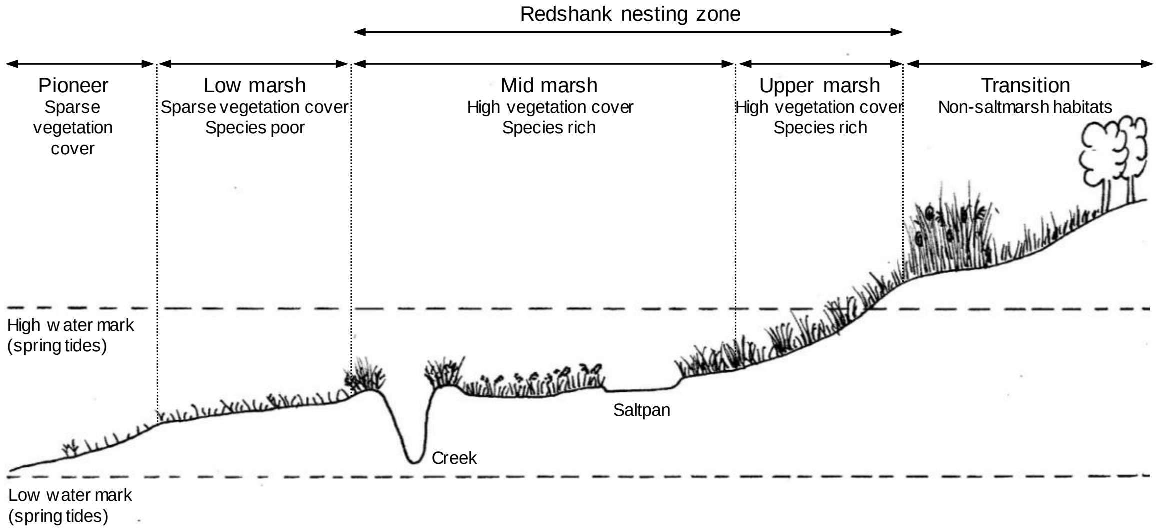


Figure 4. Cross-sectional representation of a typical saltmarsh from sea (left) to landward edge (right) showing the main vegetation zones and the zones typically used by nesting Redshank. Partially redrawn from Burd (1989).

In northwest Europe, which supports ~8% of global saltmarsh habitat (McOwen *et al.* 2017), saltmarshes are protected under the EU Habitats and Water Framework Directives (EC 1992; EC 2000; Doody 2008) but, despite their importance and protected status, their biodiversity value is declining (Garbutt *et al.* 2017). Land claim and drainage associated with conversion for development or intensive agriculture are key factors in saltmarsh loss globally (Gedan *et al.* 2009), with the rate of degradation now exacerbated by climate change, accelerated sea level rise and coastal squeeze (Boorman 1992; Doody 2004; Hughes 2004; FitzGerald *et al.* 2008; Clausen & Clausen 2014). In this process the upper marsh zones close to the sea wall become more frequently inundated and cannot naturally-progress inland due to the presence of hard sea defences, so gradually revert to lower zonal communities (Doody 2004; FitzGerald *et al.* 2008; Pontee 2013). Saltmarsh erosion, invasive species, pollution and changes in vegetation management are also important threats on a more local scale (Boorman 2003; Gedan *et al.* 2009).

### Saltmarsh Redshank population declines

Saltmarsh is the primary breeding habitat for Redshank in the UK, which supports over 18% of the northwest European breeding population (**III**; Piersma 1986; Batten *et al.* 1990; BirdLife International 2004b; BirdLife International 2004a). Around 45% of British breeding pairs are found on the coast (Brindley *et al.* 1998), with an even higher proportion found in saltmarsh habitats in England specifically (Table 1); the remainder breeding on lowland wet grassland or on upland 'in-bye' rough grassland. Redshank are short-distance migrants in the winter, dispersing from their breeding grounds to coastal estuaries (Hale 1988; Wernham *et al.* 2002). Like many waders, they show a high degree of natal philopatry and breeding site fidelity, with both females and males returning to the same sites year on year to breed (Thompson & Hale 1989). There is therefore likely to be very little movement of populations between breeding habitats.

National surveys of the British saltmarsh Redshank population identified a 23% decline in breeding pair abundance over 11 years, from 21,022 pairs in 1985 to 16,433 pairs in 1996 (Allport *et al.* 1986; Brindley *et al.* 1998). England followed by Wales then Scotland supported the highest populations of breeding pairs (14,136 pairs, 86%; 1,486 pairs, 9%; 811 pairs, 5% respectively), largely due to differences in the proportions of saltmarsh available in each country (71%, 15% and 14% respectively of the total 43,783 ha in Britain; Brindley *et al.* 1998). Declines were, however, most pronounced in Scotland and Wales, each experiencing average declines in breeding density of 13 pairs/km$^2$ (Brindley *et al.* 1998).

The concerning magnitude of these declines prompted a repeated survey in 2011, where a large sample of the original sites monitored in 1985 and 1996 were revisited (**III**). This survey identified that declines had continued at the same rate, with a total loss of 9,485 pairs between 1985 and 2011 at a rate of 1 pair/km$^2$ per year, representing an overall 53% decline in breeding density in 26 years (**III**). The position of Redshank towards the top of the trophic foodchain in saltmarsh ecosystems suggests they can be used as an indicator of saltmarsh ecosystem health (Furness & Greenwood 1993), so their dramatic population decline in this habitat is of great concern.

Table 1. Recent estimates of numbers and proportions of Redshank pairs breeding in each of their three main breeding habitats in England.

| Estimation method | Saltmarsh | Upland in-bye | Lowland wet grassland | Total (all habitats) |
|---|---|---|---|---|
| Method 1 [a] | 9,117 = **66%**<br>2016 [1] | 1,662 = **12%**<br>2016 [2] | 2,944 = **21%**<br>2011-2016 | 13,722<br>2011-2016 |
| Method 2 [b] | 9,117 = **75%**<br>2016 [1] | 1,662 = **14%**<br>2016 [2] | 1,354 = **11%**<br>estimated | 12,132<br>2014 [2] |

[a] Method 1: Saltmarsh estimate extrapolated to 2016 from the 2011 population estimate for English saltmarsh based on a decline of -2% of breeding pairs per year 1985-2011 reported in **III**. Upland population estimate from a survey in 2016 (Siriwardena *et al.* 2018). Lowland wet grassland estimate is from pairs recorded during RSPB Farm Advisory Focus Area (FAFA) surveys and annual survey data from RSPB Reserves 2011-2016 (likely to be an underestimate; RSPB, unpublished data). The total is the sum of saltmarsh (2016), upland (2016) and wet grassland (2011–2016) estimates. [b] Method 2: Saltmarsh and upland estimation methods the same as in Method 1. The total is an estimate of the total English population derived from British Breeding Bird Survey (BBS) data accounting for the BBS Redshank trend (Siriwardena *et al.* 2018). Lowland wet grassland population estimate is this total minus saltmarsh and upland (likely to be an underestimate). [1] **III**, [2] (Siriwardena *et al.* 2018)

## Redshank breeding habitat requirements

Redshank habitat requirements for breeding are now reasonably well understood (Figure 3). On saltmarsh, the peak nesting period for Redshank is from mid-April to the end of May, with pairs nesting semi-colonially (Hale 1988). Each male creates numerous defined shallow circular scrapes in tussocky vegetation, one of which the female selects to lay in, typically laying a 4-egg clutch over the course of a few days (Hale & Ashcroft 1983; Thompson 1987; Hale 1988). As the vegetation around the nest grows taller, the incubating female pulls it over the nest to form an overarching canopy, increasing nest crypsis (Figure 5; Hale 1988). Nests are typically found in vegetation averaging ~15 cm in height (Smart 2005; Smart *et al.* 2006; Sharps *et al.* 2016), although swards of mixed structure are preferred, with tussocks or patches of longer vegetation for nesting (≥ 15 cm) interspersed with shorter, more-open vegetation (< 15 cm; Milsom *et al.* 2000; Smart

2005; Smart *et al.* 2006). These surrounding shorter swards may facilitate increased predator detection, and provide suitable areas for chicks to feed effectively. Redshank exhibit less anti-predator defence behaviour than other species (e.g. Lapwing), instead incubating birds often ‘sit tight’ until predators are almost on top of them (Hale 1988). Incubation is shared equally between female and male, the latter usually incubating during the night (Hale 1988; Bulla *et al.* 2016). The male will remain in the vicinity of the nest to defend the nesting territory and provide an early warning system against predators or other sources of disturbance, although both adults often feed up to 1.5 km away from the nest when off-duty (Green 1986). Females will re-lay up to three times following failed nesting attempts at the egg stage (e.g. if are eggs are lost through predation, flooding, trampling or other causes), although usually not if their clutch hatches but the brood fails (Hale 1988).

On saltmarsh there is no evidence that females time their egg laying to correspond to intertidal periods to reduce the likelihood of flooding (Smart 2005), and nests can withstand flooding by the tide and continue to hatch as long as the eggs are not washed out the nest (in which case the adults will usually abandon it). To prevent this, denser, longer saltmarsh grasses and vegetation such as *F. rubra* , *P. maritima*, *E. atherica* and *A. portulacoides* may therefore provide the most suitable nesting locations, and are preferentially selected by Redshank where available (Sharps *et al.* 2016). This vegetation is most common in the ‘upper’ and ‘mid’ marsh zones closer to the landward saltmarsh edge, which also experience less-frequent tidal flooding (Figure 4; Burd 1989).

Nests hatch after ~29 days (Cramp & Simmons 1983) and the chicks are precocial and leave the nest within the first day after hatching. Both chicks and adults feed by gleaning invertebrates off the surface of shallow water, as well as off wet soil or vegetation, and require damp soils and a network of shallow pools where they feed along the edges (Green 1986). Invertebrate species included in their diet on UK saltmarshes include insects, small *Carcinus* crabs, *Corophium* shrimps and *Hydrobia* snails (Hale 1988). As with nesting, foraging Redshank show a preference for mosaics of short and longer vegetation patches (Green & Cadbury 1987) which facilitate feeding in the open, as well as denser vegetation to hide from predators. Broods can travel up to several hundred metres and as far as 2 km in the course of a day when feeding, the chicks often moving in a loose group guided both by their own feeding opportunities and by one or both parents who call continuously to maintain contact (Hale 1988). Fledging occurs after ~25 days (Hale 1988). When a predator is detected, the adults make warning calls to which the chicks typically respond by crouching to hide (when young), or running and hiding in patches of long vegetation (when older). Chick plumage colouration makes them incredibly cryptic when crouching and still.

Figure 5. Typical Redshank nest with 4 eggs (centre of image) in tall saltmarsh vegetation (photograph taken towards the end of May after the grass has grown tall).

### Habitat management

Traditionally, many western European saltmarshes are managed for economic gain by livestock grazing (cattle, sheep, horses; Dijkema 1990; Bouchard *et al.* 2003) or mowing of the upper vegetation zones (Exo *et al.* 2017). The number and density of nesting Redshank on a site is directly linked to the grazing intensity, with nesting densities (and therefore numbers of pairs) much higher on lightly grazed sites and lowest on those grazed heavily (**III**; Norris *et al.* 1997; Brindley *et al.* 1998; Norris *et al.* 1998). The UK national saltmarsh Redshank surveys identified grazing pressure as a primary correlate of the Redshank population decline, with breeding densities declining most markedly on sites experiencing increases in grazing intensity from ungrazed or light grazing to moderate or heavy grazing (Norris *et al.* 1998). These grazing management changes have been driven largely by agricultural intensification, with both increases in grazing intensity or abandonment of grazing on saltmarsh stemming from the requirement for higher yields and economic gain (e.g. Chatters 2004). Although other possible drivers of saltmarsh species declines exist, such as climate change, sea level rise and associated habitat change, grazing is one of the few factors that could be relatively easy to influence through direct conservation management on a national level, and which could act as a tool to mitigate the effects of larger-scale drivers of change (Clausen *et al.* 2013; Pearce-Higgins & Green 2014).

There are two mechanisms through which grazing management is likely to affect the breeding success of Redshank populations on saltmarsh. Indirectly, by influencing the suitability of the sward structure for nesting, heavy grazing may drive pairs to nest in shorter swards where rates of nest loss to predation and tidal flooding are higher (Sharps *et al.* 2015; Sharps *et al.* 2016). Directly, livestock grazing may also result in excessive nest losses to trampling within the ‘mid’ and ‘upper’ marsh zones (Figure 4; **IV**; Sharps *et al.* 2015).

### Grazing and sward structure

By influencing sward structure, grazing affects the suitability of the habitat for nesting, with different grazing intensities resulting in different sward heights, densities and degrees of heterogeneity (Figure 6). Heavy grazing at high intensity usually results in uniformly short swards which do not provide the necessary mosaic of sward heights required to attract breeding pairs or the resources and cover likely to increase nesting success (Hale 1988; Andresen *et al.* 1990; Norris *et al.* 1997; Milsom *et al.* 2000; Smart 2005). Contrastingly, grazing abandonment can lead to swards that are too long, rank and dense and provide few opportunities for nesting scrapes or feeding. Different stock types also influence the sward height and variability differently, with cattle stocked at low numbers producing the most varied sward structure due their feeding behaviour (ripping mouthfuls of grass rather than biting it, avoiding grass immediately around dung; Crofts & Jefferson 1999; Chatters 2004; Rook *et al.* 2004; Adnitt *et al.* 2007). Sheep and horses nibble and bite the vegetation so crop it shorter and are more likely to create uniform swards of short vegetation with very little height variation (Crofts & Jefferson 1999). These effects on sward structure can indirectly impact on Redshank breeding success, as swards that are too short and do not provide the necessary height variation often have higher rates of nest predation (Yates 1982; Sharps *et al.* 2015), and are also potentially more at risk of nest failure through tidal flooding (higher risk of eggs floating out of nests not covered by a sufficient canopy).

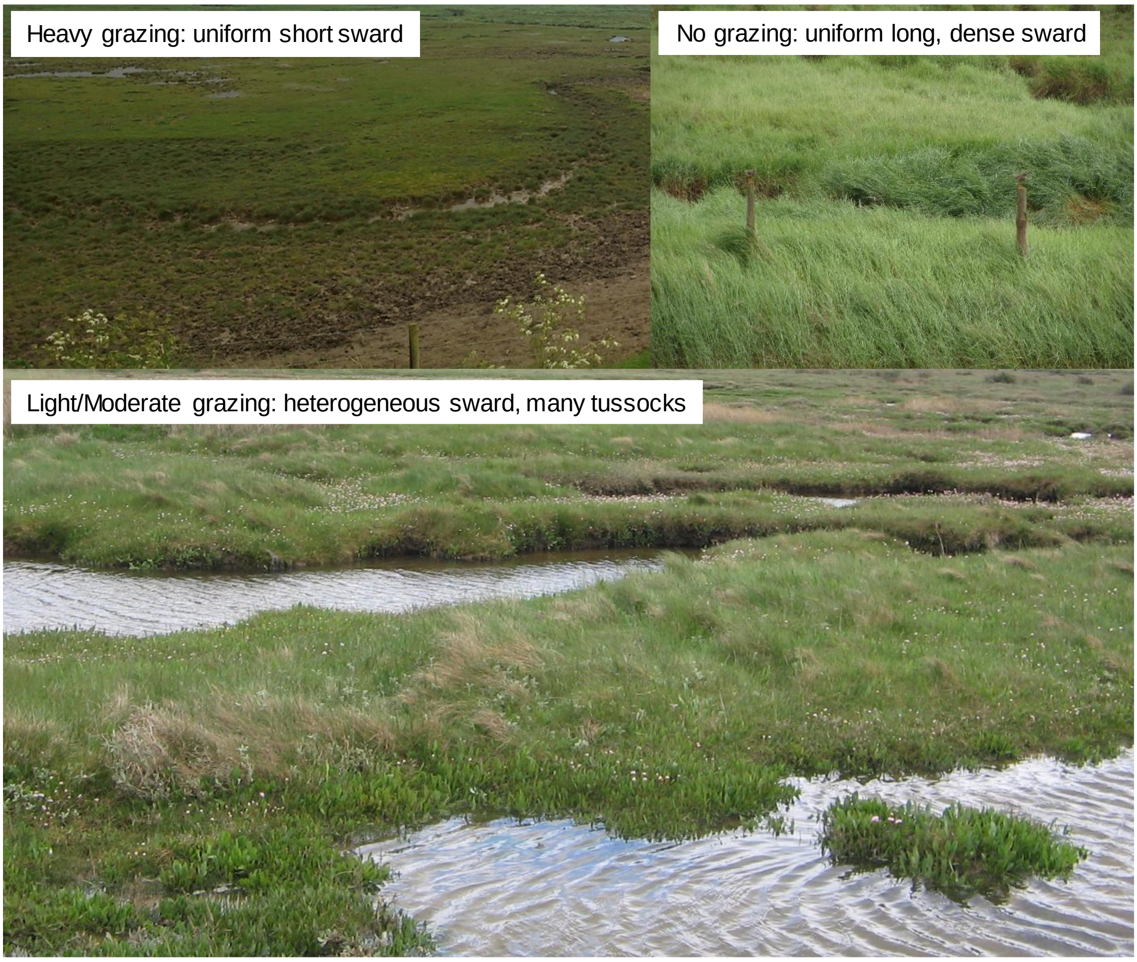


Figure 6. Saltmarsh sward structures in relation to grazing intensity. Upper images © Kate Jones.

Due to their requirements for fresh drinking water (usually situated at the landward edge of saltmarsh grazing areas) and timidity in venturing out into new locations, cattle, sheep and horses all typically remain within ~500 m of the sea wall or landward edge during early spring and summer (Table 2, Figure 7), only venturing further out when the grazing has been exhausted within this area (usually by late summer or early autumn; **IV**). Extremely low intensity grazing can therefore be as detrimental to the habitat as high intensity grazing or abandonment: small numbers of livestock have no need to graze far from the sea wall (as they never exhaust the available grazing here) and thus create a heavily-grazed band adjacent to it while the rest of the site remains effectively ungrazed. Therefore, under extremely low intensity grazing, no part of the habitat may receive the intermediate levels of grazing important for providing suitable Redshank nesting habitat structure.

Table 2. Distances travelled from the sea wall or landward edge (m) by three common saltmarsh livestock types. Shown is the mean distance across the whole grazing season (Mean; April–October), the mean maximum distance across the whole grazing season (Max$_{\text{season}}$) and the mean maximum distance during the Redshank nesting season only (Max$_{\text{early}}$; April–June).

| | Distance travelled (m) | | | | | |
|---|---|---|---|---|---|---|
| Stock type | Mean | 95% CI | Max$_{\text{season}}$ | 95%CI | Max$_{\text{early}}$ | 95%CI |
| Cattle | 113 | 88–138 | 280 | 184–376 | 162 | 96–230 |
| Horses | 109 | 45–173 | 149 | 0–302 | 23 | 0–69 |
| Sheep | 169 | 136–202 | 389 | 273–506 | 342 | 213–471 |

Distances were estimated from the centre of mapped polygons of livestock distribution recorded during four saltmarsh grazing survey visits conducted on 213 sites by the RSPB in 2013 (**V** unpublished data). The mean distance travelled (± 95% confidence intervals) was calculated by multiplying polygon centroid distances by the number of livestock contained within it (i.e. distance travelled per individual animal), averaging these individual animal distances across all visits to a site, then averaging across all sites. Mean maximum distances travelled (maximum from any visit to a site, averaged across all sites) across the whole grazing season (Max$_{\text{season}}$; April–October) and Redshank nesting season (Max$_{\text{early}}$: April–June) are also shown.

The consensus between saltmarsh conservation managers and researchers is that a mosaic or rotation of low (≤ 0.3) or moderate (≤ 0.7 Livestock Units per ha) grazing intensities by cattle during the summer months (April–October) is the most parsimonious option for maintaining, enhancing or restoring saltmarsh biodiversity overall (e.g. Doody 2007; Mandema *et al.* 2015; Rupprecht *et al.* 2015; van Klink *et al.* 2016; Davidson *et al.* 2017; Lagendijk *et al.* 2017), and should provide the habitat structures required by breeding Redshank (**V**; Norris *et al.* 1998; Milsom *et al.* 2000). This pattern of grazing is now recommended for saltmarsh conservation management in western Europe (Adnitt *et al.* 2007; Doody 2008). The profitability of grazing saltmarsh in this way is, however, lower than high-intensity farming due to the low intensity and restricted timings, so uptake incentives for land managers are often required. Taking the form of payments through Agri-Environment Schemes (AES) in Europe, these are a key mechanism by which conservation grazing of saltmarsh, as well as other sympathetic management practices, can be delivered at national levels (Batáry *et al.* 2015). Such targeted AES have been successful in delivering conservation management to benefit other wetland systems (e.g.

Schekkerman *et al.* 2008; Smart *et al.* 2014), but inadequate monitoring has made the overall assessment of AES effectiveness difficult (Kleijn & Sutherland 2003).

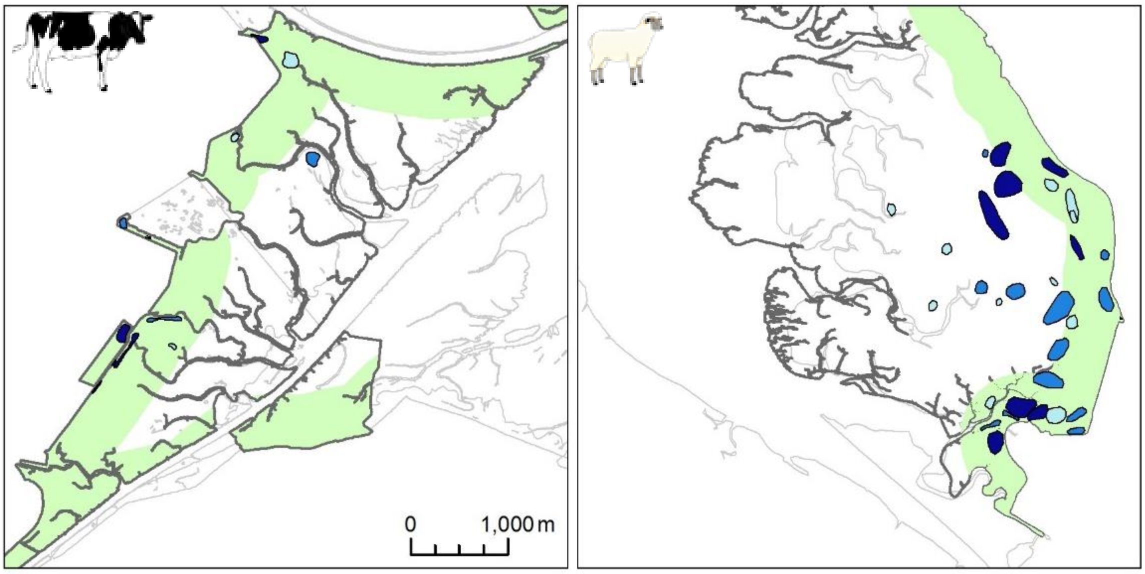


Figure 7. Examples of livestock distributions (blue polygons) within 500m of the sea wall on saltmarsh in early spring (April and May) within two UK regions surveyed in 2013 for **V** (left: saltmarsh in The Wash estuary, eastern England; right: saltmarsh in the Dee estuary, northwest England). The degree of polygon shading indicates the number of cattle (left) or sheep (right) represented; darker shading indicates larger numbers. Green shading indicates saltmarsh within 500m of the sea wall, dark grey lines indicate site outlines and pale grey lines indicate the extent of vegetated saltmarsh.

In the UK, AES have a strong emphasis on enhancing the landscape for wildlife conservation (Kleijn & Sutherland 2003) although the scheme specifics and their evolution over time varies between countries. In England, AES with specific saltmarsh management options in the form of ‘input-based’ systems (where payments are made based on agreed management being undertaken; Hanley *et al.* 2012) have existed since 1991, and their implementation relies on a list of management prescriptions associated with different payment options within each site’s AES agreement. These schemes, and similar management on nature reserves, had little effect on grazing pressure on English saltmarsh sites between 1996 and 2011 however (**III**) which, combined with continued declines of saltmarsh-breeding Redshank over this timescale, indicates that AES mechanisms are not delivering the necessary conservation outcomes in terms of grazing pressure or Redshank population stability in the wider countryside (**III**). Saltmarsh AES sites are also not delivering the recommended grazing management required to maintain and enhance saltmarsh biodiversity overall, and are no different from sites without AES, largely as a result of a lack of specificity and detail in the AES management prescriptions regarding grazing management (**V**). There is therefore a need to improve this delivery mechanism to ensure that saltmarsh management solutions for breeding Redshank are more-effectively implemented on a national scale.

### Grazing and nest trampling

Even on protected sites and nature reserves where conservation grazing recommendations are implemented, and where the habitat supports Redshank breeding, the number of breeding pairs is still declining (Figure 3, Figure 8; **III**). This implies that there may be other mechanisms at work in addition to the indirect impact of grazing on the habitat.

Grazing saltmarsh may influence nest survival directly, by causing excessive nest losses to trampling due to a substantial temporal and spatial overlap of livestock with nesting Redshank (**IV**; Yates 1982; Jones 2014; Sharps *et al.* 2015). The area within ~500 m of the sea wall or landward saltmarsh edge that is utilised by livestock during the early spring and summer also usually comprises the higher marsh vegetation communities (the ‘upper’ and ‘mid’ marsh zones) within which the majority of Redshank nest (Figure 4, Figure 7, Table 2; **IV**). This spatial overlap is further exacerbated by a temporal overlap between the peak in Redshank nesting and the time when livestock, particularly cattle, are introduced to the marsh after a period of no grazing during the winter (mid-April to late-May). This overlap in space and time may be particularly detrimental if the habitat and sward structure is otherwise suitable and attractive to nesting Redshank early in the breeding season (prior to grazing onset), as sites could then form an ecological trap whereby nesting pairs are attracted to nest but then experience high rates of nest loss and low resulting productivity (**IV**).

Removing this spatial and temporal overlap is likely to improve Redshank breeding success considerably, and relatively simple changes to saltmarsh grazing practices would be sufficient to achieve this (**IV**). Firstly, grazing could be delayed until mid-July to remove the temporal overlap with the peak nesting period, after which stock could be introduced at an increased grazing intensity than usually recommended for conservation grazing (i.e. if grazing from April-October) to maintain economic viability and ensure that a suitable sward structure is maintained. In theory this seems a simple change, however many graziers would struggle to find replacement grazing land during the intervening period (April – mid-July) which would make grazing untenable and could result in increased saltmarsh abandonment. Alternatively, a rotational system could be used, whereby areas of the saltmarsh are grazed in one year but left ungrazed during the Redshank breeding season the following year (Lagendijk *et al.* 2017). This could provide ungrazed refugia for nesting Redshank while maintaining the availability of grazing land. Using this method, graziers could potentially maintain economic income and herd size by grazing the entirety of their current herd on the grazed section from April onwards (i.e. at a higher grazing intensity than is recommended for conservation grazing early in the season), before moving half the herd into the ungrazed area from mid-July after the risk of Redshank nest trampling is passed. This would also act to maintain suitable sward structures for breeding Redshank in each area. Nest trampling may still occur within the grazed area when using this second rotational option, so the magnitude of the positive effect on Redshank breeding success and therefore population response is uncertain. This rotational option also requires fencing or otherwise-independent grazing compartments to provide multiple grazing areas within one site, which may be expensive. The adoption of these potential solutions within AES may require an initial testing phase aiming to provide evidence for a positive response of breeding Redshank to trial management.

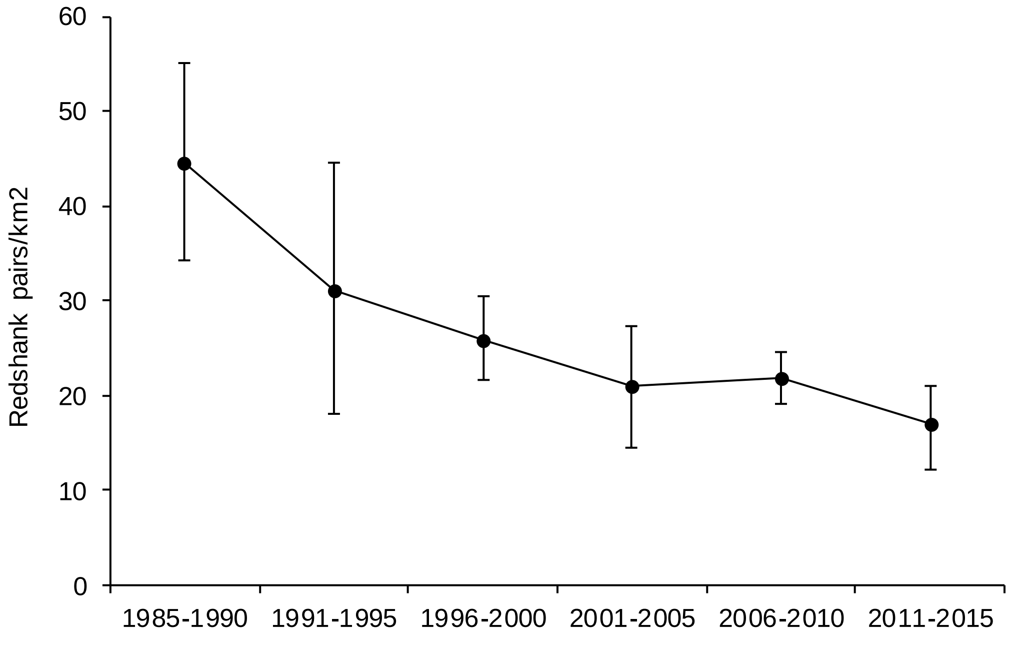


Figure 8. Five year mean Redshank breeding density (± 95% confidence intervals) recorded on saltmarsh at Frampton RSPB nature reserve, eastern England, between 1985 and 2015.

### Improving grazing on a national scale

The two mechanisms through which saltmarsh grazing is driving low Redshank breeding success – unsuitable sward structure and nest trampling – could both be addressed on a national scale through the more effective implementation of conservation grazing management delivered through AES. Emerging evidence suggests that saltmarshes in England are not being grazed at levels appropriate for achieving conservation aims in terms of stock types, grazing intensity, timing of grazing or resulting habitat structure however, and that saltmarsh specific AES have had little effect in encouraging this management (**V**). This may be due to insufficient detail regarding these aspects of grazing in the management prescriptions provided to landowners within AES agreements (**V**). As agreement-holders are required to follow these prescriptions strictly, but are not required to undertake any other management, it is perhaps not surprising that the lack of specificity has resulted in a lack of appropriate conservation grazing. Conversely, if prescription wording could be improved then on-site grazing management is also likely to improve, as better conservation management is often implemented where prescriptions are more specific and appropriate (**V**).

Another reason why saltmarsh AES management options are currently failing may be a lack of sufficient monitoring, auditing and inspection to ensure that agreement holders are following the prescribed management. Very few agreements are ever inspected: in 2013 when surveys of AES sites were conducted for **V**, the Rural Payment Agency in England inspected only 5% of new agreements within their first 5 years, and only 2.5% of agreements older than 5 years (RPA 2018). Agreement-holders are expected to keep 'adequate records' demonstrating compliance with management prescriptions in the event of these inspections (JNCC 2004), but there is no formal system (e.g. standardised central online repository) for doing so, nor is there detailed guidance on what 'adequate records' entail (Natural England 2013). An online annual submission system of evidence of management practices, including grazing, would be of great benefit and would most likely be possible at a relatively low cost.

Additionally, AES in England have so far primarily been input-based schemes, which have often been criticised for making payments for management actions rather than the delivery of desired outputs (e.g. Armsworth *et al.* 2012; Hanley *et al.* 2012). Input-based schemes have been favoured because of their lower transaction costs, but output-based (also known as 'results-based') schemes, by being more selective, may be more efficient in their allocation of financial resources and provide more flexible incentives to facilitate innovation by landowners and managers (Hasund 2013). Two results-based schemes – one targeting grassland breeding waders in Yorkshire, another targeting arable farmland birds in East Anglia – are currently being piloted in the UK (Natural England 2017a; Natural England 2017b), though none yet target saltmarsh habitats. Moving to a results-based scheme, perhaps where saltmarsh sward structural heterogeneity, botanical species richness (target species defined on a site-specific basis at the start of agreements) and Redshank breeding density (where Redshank are present; site-specific levels again pre-defined to encourage habitat management favouring the maintenance or increase in number of breeding pairs) as target ‘results’ may encourage more actual improvements in saltmarsh conservation status (Keenleyside *et al.* 2014).

If the above issues with AES design and implementation could be solved, and future schemes incorporate the conservation grazing recommendations and changes in timing and spatial pattern of grazing as described above, it is highly likely that saltmarsh breeding Redshank populations would respond in a positive way through resulting improvements in breeding success.

## Case study 2: Lapwing breeding on UK lowland wet grassland

© David Wootton (rspb-images.com) & Richard Mason

Research focussing on waders breeding on lowland wet grassland has progressed to the stage where the species' habitat requirements are well-understood, habitat management solutions have been designed to successfully meet these requirements, and sites implementing these management solutions are in good condition from a habitat perspective. Publications **VI**, **VII** and **VIII** have provided key contributions to this process, as highlighted in Figure 9. Wader populations are still declining in some of these well-managed habitats however, so in recent years research has focussed on identifying causes of low breeding success (poor nest and chick survival) and designing and testing solutions to address these issues. These solutions are now being implemented on protected sites and nature reserves in lowland areas of the UK with positive outcomes, and ongoing research is being conducted to test how to apply these solutions and others on a landscape scale outside of protected areas.

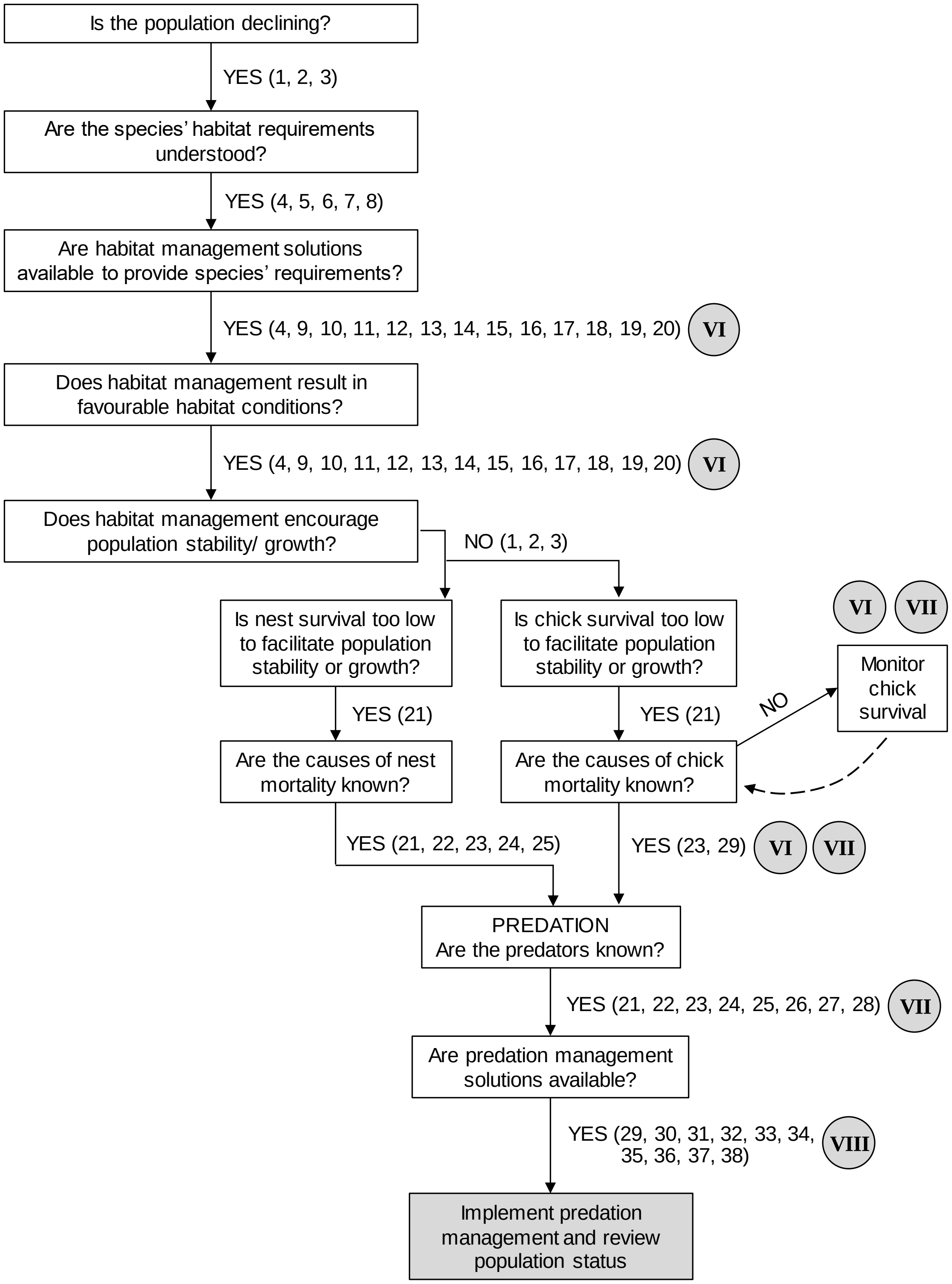

Is the population declining?
YES (1, 2, 3)
Are the species' habitat requirements understood?
YES (4, 5, 6, 7, 8)
Are habitat management solutions available to provide species' requirements?
YES (4, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20)
VI
Does habitat management result in favourable habitat conditions?
YES (4, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20)
VI
Does habitat management encourage population stability/ growth?
NO (1, 2, 3)
Is nest survival too low to facilitate population stability or growth?
Is chick survival too low to facilitate population stability or growth?
VI
VII
Monitor chick survival
YES (21)
YES (21)
NO
Are the causes of nest mortality known?
Are the causes of chick mortality known?
YES (21, 22, 23, 24, 25)
YES (23, 29)
VI
VII
PREDATION
Are the predators known?
YES (21, 22, 23, 24, 25, 26, 27, 28)
VII
Are predation management solutions available?
YES (29, 30, 31, 32, 33, 34, 35, 36, 37, 38)
VIII
Implement predation management and review population status

Figure 9. The current position of Lapwing breeding on UK lowland wet grassland on the lowland wader conservation management decision tree (grey shaded box), the research steps leading up to this position and the location of influence of the research presented in publications **VI**, **VII** and **VIII**. Numbers in parentheses refer to other key references in the evidence base underlying each research step: 1. Wilson *et al.* (2005); 2. Harris *et al.* (2017); 3. Hayhow *et al.* (2017); 4. Green (1986); 5. Milsom *et al.* (2000); 6. Eglington *et al.* (2008); 7. Durant *et al.* (2008a); 8. Smart *et al.* (2006); 9. Benstead *et al.* (1997); 10. Crofts and Jefferson (1999); 11. Vickery *et al.* (2001); 12. Ausden and Hirons (2002); 13. Milsom *et al.* (2002); 14. RSPB (2005); 15. Wilson *et al.* (2007); 16. Durant *et al.* (2008b); 17. Eglington *et al.* (2009b) 18. Eglington *et al.* (2010); 19. O'Brien and Wilson (2011); 20. Smart *et al.* (2014); 21. MacDonald and Bolton (2008b); 22. Jackson and Green (2000); 23. Bolton *et al.* (2007a); 24. Teunissen *et al.* (2008); 25. Ausden *et al.* (2009); 26. Bellebaum and Bock (2009); 27. Eglington *et al.* (2009a) 28. Schekkerman *et al.* (2009); 29. Isaksson *et al.* (2007); 30. Bolton *et al.* (2007b); 31. Rickenbach *et al.* (2011); 32. Laidlaw *et al.* (2013); 33. Laidlaw *et al.* (2015b); 34. Laidlaw *et al.* (2015a); 35. Laidlaw *et al.* (2016); 36. Leigh *et al.* (2016); 37. Mason *et al.* (2016); 38. Smart (2016).

## Introducing lowland wet grassland

Lowland wet grasslands, also known as coastal and floodplain grazing marsh or lowland meadows in the UK, are seasonally-flooded freshwater grasslands characterised by networks of drainage ditches, with the enclosed fields traditionally managed by grazing or for hay production (Ausden & Treweek 1995). Where free from inorganic fertiliser and pesticide inputs they can be of high biodiversity and nature conservation value, supporting a wide variety of plants, animals and invertebrates (Benstead *et al.* 1997), and are therefore often protected under national and international designations as Sites of Special Scientific Interest (SSSI), Special Areas of Conservation (SACs; EC Habitats Directive: EC 1992), Special Protection Areas (SPAs; EC Birds Directive: EC 2000), and as part of larger Ramsar sites (Ramsar Convention, 1971). They also provide important ecosystem services in the form of flood alleviation, groundwater recharging, improving and maintaining water quality, and as pasture land for food production (Posthumus *et al.* 2010; Rhymer *et al.* 2010; Fisher *et al.* 2011).

Due to agricultural intensification, 97% of unimproved lowland grassland in England and Wales was lost between the 1930s and 1980s, mainly through drainage and conversion to arable production (Williams & Hall 1987; UK Biodiversity Steering Group 1998). Much of that which has survived as pasture or meadows to the present day is now managed intensively, with controlled low water levels to allow mechanisation (e.g. grass reseeding and inorganic fertiliser application) and high grazing intensities to increase yield. These grasslands have also been further degraded by the regulation or canalisation of adjacent waterways for flood defence (often interrupting the seasonal flooding and functioning of the floodplain), and pollution from adjacent agricultural land (pesticide and nitrogen run-off; Benstead *et al.* 1999). These threats are likely to be exacerbated further by climate change, which is predicted to result in a reduction in spring surface water and aquifer recharging due to lower rainfall, and in sea level rise which may threaten many coastal sites (Nicholls *et al.* 1999; Thompson *et al.* 2009).

Lowland wet grassland is an important breeding and wintering habitat for many waders and wildfowl due to its provision of seasonally-wet soils and shallow surface flooding which provide opportunities for feeding on the grass itself (wintering wildfowl) and on the diverse soil, water and aerial invertebrate communities (breeding and wintering waders; Ausden & Treweek 1995). In the UK, typical breeding wader species supported by this habitat include Lapwing, Redshank, Snipe and Oystercatcher, with Black-tailed Godwit and Curlew also present on some sites. Lapwing is the species which has been most commonly studied in this habitat however, due to its abundance and ubiquitous nature relative to the other species, and the relative ease with which it can be monitored.

### Lapwing population declines

In the UK, Lapwing mainly breed in three habitats: lowland wet grassland, upland ‘in-bye’ rough grassland and arable farmland. There are few estimates for the proportion breeding in each habitat, but a survey of Lapwing in England and Wales in 1998 estimated that 39% of the population was supported by arable farmland, and 56% by grassland (across both the lowlands and uplands; Wilson *et al.* 2001). A more recent survey has estimated that in England, uplands account for 54% of the Lapwing population (Siriwardena *et al.* 2018), suggesting that lowland wet grassland and arable habitats now support around 46% of breeding pairs.

The lowland wet grassland population has been the most extensively studied to date, with population declines of 38% in England and Wales reported between 1982 and 2002 (Wilson *et al.* 2005). Lapwing show a high degree of natal philopatry and breeding site fidelity (Thompson *et al.* 1994) so, similar to Redshank, there is little movement of individuals between breeding habitats and sites. Lowland wet grassland specific population declines are therefore unlikely to be explained by emigration to other habitats, particularly as population declines and range contractions for the UK as a whole, and in upland and arable areas specifically, have been occurring over the same time period (25% reduction in UK breeding distribution 1986/72–2007/11, 63% UK population decline 1970–2014 and 43% decline 1995–2015, considerable declines on arable farmland 1981–1995, annual decline of 8.6% in UK uplands 2001–2010: Sheldon *et al.* 2004; Milsom 2005; Balmer *et al.* 2013; Smart *et al.* 2013; Harris *et al.* 2017; Hayhow *et al.* 2017).

### Lapwing breeding habitat requirements

On wet grassland, Lapwing nesting habitat requirements are well known (Figure 9). Lapwing in lowland UK typically begin nesting from late-March or early-April (later on more northerly sites), with April being the peak laying period. Pairs nest semi-colonially and show a preference for slightly raised bare ground or very short vegetation surrounded by homogenously short sward in close proximity to surface water (Green

1986; Milsom *et al.* 2000; Eglington *et al.* 2008). Field occupancy and nesting densities are highest on fields where the median vegetation height is 10–15 cm in mid-May (and typically lower than this in April before the rate of grass growth increases; Green 1986; Milsom *et al.* 2000; Durant *et al.* 2008a; Eglington *et al.* 2008), and where there is a higher degree of surface flooding (Milsom *et al.* 2000; Eglington *et al.* 2008). This open habitat may be selected to increase predator detection, with close proximity to tall landscape features or those that may harbour predators (e.g. trees, hedgerows, buildings, woodland) reducing the likelihood of site occupancy by breeding pairs (Milsom *et al.* 2000; MacDonald & Bolton 2008a; Bertholdt *et al.* 2016). Lapwing also show a preference for feeding in short grass more than other wader species (Green 1986; Ausden *et al.* 2003).

Males make multiple shallow nest scrapes, one of which the female chooses to lay eggs in after filling it with a thin layer of broken vegetation, typically with up to four eggs in the clutch laid over ~5 days (Figure 10). Incubation is initiated once the final egg is laid and lasts for ~26 days (egg laying and incubation period ~31 days in total, Galbraith 1988). Chicks are precocial and leave the nest within a day of hatching to feed on invertebrates gleaned off the surface of mud, water, livestock dung and short vegetation (Eglington *et al.* 2010), with the bulk of their diet comprising earthworms, ground beetles (carabids), rove beetles (staphylinids), *Aphodius* dung beetles, crane fly larvae (tipulids) and soldier fly larvae (stratiomyids; Beintema *et al.* 1991). As these are detected visually, shorter vegetation and bare ground is likely to facilitate prey detection and capture (Green 1986). The female remains in close proximity to the chicks, with broods remaining loosely together and often foraging around wet features (Eglington *et al.* 2010). Females will brood the chicks in inclement or very hot weather, and fledging usually occurs after 35–40 days (Cramp & Simmons 1983), although later after long periods of wet or cold weather when chicks cannot forage as efficiently (Eglington *et al.* 2010).

Nesting out in the open is a trade-off strategy between increased susceptibility of nests and chicks to predation, and increased visibility for the adults to facilitate early predator detection. To counter this, both nests and chicks are cryptically coloured, adults quickly leave the nest if predators are detected, and adults perform vocal and active anti-predator displays where predators or sources of disturbance are mobbed until they leave the area. This mobbing and alarming can both deter predators from hunting in the area and warn chicks to crouch and remain hidden until the threat has passed. Due to this anti-predator behaviour, Lapwing often breed more successfully when nesting at higher densities (when there are more adults to respond to predators), and also convey a benefit to other, less vocal wader species nesting in close proximity (e.g. Redshank; MacDonald & Bolton 2008a; Eglington *et al.* 2009a; Laidlaw *et al.* 2015b).

Figure 10. Typical Lapwing nest with 4 eggs surrounded by short vegetation.

### Habitat management

Habitat management on lowland wet grassland to benefit breeding Lapwing chiefly involves the manipulation of sward height, spring and summer water levels, and the availability of shallow-edged wet features to fulfil their nesting and chick rearing habitat requirements (Figure 9; **VI**).

### Sward structure

Lowland wet grassland swards are traditionally managed by livestock grazing or mowing for hay or silage (Green 1986; Ausden & Treweek 1995; Benstead *et al.* 1997). Mowing, which usually occurs once the majority of Lapwing nests have hatched, is the least preferred option for conservation management because allowing the grass to grow long enough for a hay crop may encourage Lapwing broods to leave in search of shorter swards, and catching and killing chicks in the machinery is a risk (Schekkerman *et al.* 2009). This method, though widely used on wet grasslands in continental Europe, is less common on lowland wet grassland in the UK and only used on sites dry enough to allow machinery access in summer (Ausden & Treweek 1995). Grazing by livestock (usually cattle, sheep or horses) is instead the most common sward management option, particularly on sites targeting breeding Lapwing (**VI**; Benstead *et al.* 1997; Crofts & Jefferson 1999; Durant *et al.* 2008b; Fisher *et al.* 2011). In a wet grassland grazing system, the vegetation height and structure in the peak nesting period (April–May) is influenced by spring weather conditions and grazing in the previous year, both by the farmed livestock and also often by wildfowl during the winter months (Vickery *et al.* 1997).

The requirement of Lapwing for well-grazed short swards for nesting, feeding and chick rearing involves a difficult trade-off because the grazing levels required to keep the sward low has direct disadvantages in terms of nest and chick trampling. The risk of trampling is dependent on the type and number of livestock, the field area and the length of time livestock are present in a field (Green 1986; Beintema & Müskens 1987). How soon the livestock are introduced in spring will also affect the trampling risk: starting grazing in mid-May (i.e. after the start of nest hatching) may reduce nest trampling rates and encourage higher hatching success (Green 1986). The length of time that livestock are present not only influences trampling rates but also affects the habitat condition, with grazing through the winter by heavy stock such as cattle and horses risking soil compaction and poaching, and hindering the growth of vegetation in subsequent years (Crofts & Jefferson 1999; Rook *et al.* 2004). In grasslands grazed with conservation targets in mind, livestock are therefore best removed overwinter. Stocking densities of <1 Livestock Unit per ha from mid-May to October (Beintema & Müskens 1987) have been found to limit trampling while creating the desired sward structure in the following spring, and these levels are now recommended on lowland wet grassland managed for breeding waders (RSPB 2005; **VI**).

Other wader species breed on lowland wet grassland alongside Lapwing and all require slightly different sward conditions (e.g. Redshank and Snipe require a mosaic of vegetation heights; Milsom *et al.* 2000; Coutts 2005; Tichit *et al.* 2005; Smart *et al.* 2006; Natural England 2011). A delicate balance is therefore needed when managing swards, and most sites where breeding waders (including Lapwing) are a conservation priority will account for these differences by managing swards to provide tussocks and patches of taller vegetation within larger swathes of short sward to benefit the entire species suite (RSPB 2005). Cattle, when stocked at low–moderate densities, produce the most varied sward structure due their feeding behaviour (Ausden & Treweek 1995; Crofts & Jefferson 1999; Rook *et al.* 2004) so are the stock type recommended for managing wet grasslands (Vickery *et al.* 2001). Cattle are also better suited to the wet and often muddy conditions present on wet grassland sites compared to sheep and horses which are susceptible to leg injury and infections in such environments (Ausden & Treweek 1995). Livestock grazing also potentially increases the food supply for Lapwing via invertebrates that specialise on dung (Beintema *et al.* 1991), although this will be limited and potentially incur a hidden cost through heavy pesticide loads when livestock are treated with systemic insecticides as is common in modern animal husbandry (McCracken & Foster 1993; Vickery *et al.* 2001).

In addition to grazing, targeted sward management during the post-breeding period (August–October) is often used to limit the growth of invasive species to improve the grazing conditions and maintain a grass-dominated sward (RSPB 2005; **VI**). In particular, soft rush *Juncus effusus* is controlled through ‘topping’ where the tops of rush tussocks are mown with machinery, and thistles *Cirsium* spp. are controlled through targeted systemic herbicide application.

### Water and wet features

Equally as important as sward structure on wet grassland managed for breeding waders is the control of water levels and the provision of varied surface topography so that standing water and muddy shallow-edged wet features are available throughout the spring and summer (RSPB 2005; **VI**). This is primarily because the presence of shallow surface water and degree of soil saturation (affecting its penetrability) strongly influences the abundance and availability of invertebrate food (Green 1986; Ausden *et al.* 2003; Smart *et al.* 2008). Wet features support a higher invertebrate biomass than the surrounding sward (Eglington *et al.* 2010), in turn attracting higher densities of nesting

Lapwing which strongly aggregate around wet features (where their chicks will forage; Green 1986; Milsom *et al.* 2002; Ausden *et al.* 2003; Eglington *et al.* 2010), and thus potentially encouraging increased predator deterrence and improved breeding success (MacDonald & Bolton 2008a).

Spring and summer flooding can delay nesting or cause nest failure however (Green 1986), so water management can involve a trade-off between preventing extensive flooding just before or once Lapwing nesting has begun, and maintaining a sufficient water resource to ensure the availability of wet features into mid-summer, even in hot, dry weather (Eglington 2008; Eglington *et al.* 2008; Eglington *et al.* 2009b; Eglington *et al.* 2010). This is a challenging prospect and not always possible when sites were originally designed as flood- or wash-lands for major rivers and are hence likely to flood periodically (Ratcliffe *et al.* 2005), or are surrounded by drained arable land so have a limited water resource. Typically, water is trapped within a site using a system of sluices and wind-pumps throughout the winter, so that ditch water levels are high (i.e. above or level with the field surface) at the start of the wader breeding season (Burgess & Hirons 1990). Sluices can then be opened or closed to further trap or release water depending on the level of evaporation and rainfall experienced throughout the spring and summer (RSPB 2005).

How water moves through the soil is determined by its structure and type, so the soil underlying a lowland wet grassland site strongly influences the extent and type of within-field water management techniques required to maintain surface water flooding (Crofts & Jefferson 1999). Peat soils, typically underlying wet grasslands which were historically drained from even wetter marshland and fen, are more permeable due to their higher organic content and therefore have a high hydraulic conductivity, allowing greater lateral movement of water into the field from ditch edges (Armstrong 1993; Armstrong & Rose 1999). In such soils, maintaining high water levels in the surrounding ditches is often sufficient to maintain within-field wetness.

In contrast, wet grasslands formed on clay soils or soils which have undergone compaction through historical agricultural operations with heavy machinery (both of which are more common than virgin peat), are relatively impermeable and have low hydraulic conductivity, preventing lateral water movement (Armstrong 1993; Armstrong & Rose 1999). In these cases, maintaining high water levels in ditches is insufficient to keep fields wet, so more creative methods of conveying water into field centres from ditch edges are required. One method is to implement extensive shallow surface flooding (Crofts & Jefferson 1999), but this often evaporates rapidly and is less conducive to vegetation growth and livestock production. There are also inherent disadvantages to wader breeding through this method (i.e. high potential for nest flooding), and prolonged extensive flooding can impact on the availability of soil invertebrates whose community structure and abundance are strongly dependent on the degree of soil saturation (Ausden *et al.* 2001; Erber *et al.* 2002; Plum & Filser 2005).

A practical alternative, and one which is now commonly used on lowland wet grassland managed for breeding waders, is the use of shallow features to introduce localised rather than extensive flooding (Joiner 2002; Milsom *et al.* 2002). This involves the artificial creation, restoration or repurposing of surface topography and drainage channels known as footdrains, rills or grips (depending on geographic location). These may be relics of old marsh creek systems, particularly on wet grassland that was historically reclaimed from fen or saltmarsh through the construction of enclosure banks (Milsom *et al.* 2002), or old field drains initially installed to facilitate in-field drainage for agriculture. They are typically shallow-edged sloping channels ~2–3 m wide and ~50 cm deep which connect to ditch edges such that they fill and introduce within-field localised flooding when ditch water levels are high (Burgess & Hirons 1990; RSPB 2005; Eglington *et al.* 2009b). Installing localised flooding and wet features in this way is the primary method by which arable land can be reverted back to wet grassland for breeding waders following agricultural production, and has positive impacts on chick condition later in the season (Eglington *et al.* 2008; Eglington *et al.* 2009b). Once installed, linear features need to be kept free of vegetation and be maintained to ensure the persistence of shallow muddy edges, otherwise the benefits to breeding waders may decline and result in a reduction in nesting density (RSPB reserve managers *pers. comm.*).

### Applying solutions on a landscape scale

The extensive nature of habitat management to optimise sward structure and water availability on lowland wet grassland for breeding Lapwing makes it less profitable relative to high-intensity livestock rearing, silage production or conversion to arable farming (Crofts & Jefferson 1999). There are therefore two main methods by which such conservation management can be implemented on sites and in the wider landscape: i) through site protection, both by statutory designations which permit recommended management but prevent potentially damaging alternatives (largely as Sites of Special

Scientific Interest, SSSIs in the UK) and by managing sites as nature reserves where recommendations can be directly implemented; and ii) through uptake incentives to private landowners in the form of AES.

In the UK, targeted habitat management on nature reserves has proven successful at creating suitable habitat conditions to attract breeding Lapwing, particularly when used in combination with AES aimed at enhancing habitat conditions for this species (Ausden & Hirons 2002; O'Brien & Wilson 2011; Smart *et al.* 2014). When these methods are used in conjunction, habitat management is also successful at providing conditions in which local numbers of breeding Lapwing can be maintained or increased (Ausden & Hirons 2002; Wilson *et al.* 2007). AES and the habitat management they demand are improving over time through the uptake and integration of new research findings, with evidence that newer AES schemes are better at encouraging more positive population change in Lapwing (Smart *et al.* 2014). Similar schemes also promote comparable positive effects in continental Europe if they account for existing hydrology and former farming history (Kahlert *et al.* 2007), and where hydrological management forms part of the management prescribed (Kleijn & vanZuijlen 2004; Breeuwer *et al.* 2009).

Breeding Lapwing populations continue to decline in the wider countryside and on nature reserves despite suitable habitat conditions, however, indicating that successful habitat management through site protection and AES alone are not delivering the necessary improvements in breeding success across the landscape (Figure 9). On well-managed sites (i.e. protected sites and nature reserves), Lapwing chicks are able to maintain good body condition, indicating that here the habitat management is delivering conditions suitable for providing sufficient and available invertebrate food (**VI**). Other drivers of low productivity must therefore be influencing Lapwing populations, even on these otherwise well-managed sites.

### Additional causes of low productivity

Demographic modelling incorporating best estimates of Lapwing survival rates has indicated that, to balance annual adult mortality and maintain population stability, Lapwing populations must achieve a level of productivity between 0.6 and 0.8 chicks fledged per pair (MacDonald & Bolton 2008b). Productivity is influenced by two main parameters – hatching success (nest survival from laying to hatching) and fledging success (chick survival from hatching to fledging) – so understanding the mechanisms behind these parameters, and their relative contributions to limited productivity are a key requirement for Lapwing conservation management (Figure 9).

### Nest survival

Lapwing nest survival rates exceeding 50% per year are likely to be sustainable and result in the minimal productivity range required for population stability if annual chick survival rates (from hatching to fledging) are around 25% (MacDonald & Bolton 2008b). Few sites achieve even this level of nest survival however (MacDonald & Bolton 2008b). Identifying and reversing the causes of nest failure have therefore been a major priority for lowland wet grassland Lapwing conservation in recent years, with many studies using intensive nest monitoring techniques to determine the causes of low nest survival (Figure 9).

Lapwing nests on lowland wet grassland, by being out in the open in short vegetation, are easy to monitor relative to those of other wader species. Nests are located by identifying incubating adults from a vantage point (usually a vehicle or raised bank) and then marked in the field so they can be relocated rapidly on subsequent visits. A cane or numbered flag is often used for this, placed far enough away from the nest to prevent trampling by livestock and avoid attracting predators (e.g. 20 paces), relative to a prominent landscape feature or compass direction (Galbraith 1987; Green 2004). Nests can then be relocated on the ground by walking to the marker point and pacing the required distance in the necessary direction. Once found, nests are usually assigned a unique identifier number or code for quick reference and the location is marked on a map. Egg biometric measurements including mass, length and breadth (to approximate egg volume) can be used to estimate hatch dates for the clutch using published equations because the weight of an egg decreases relative to its volume over time as the chick develops and water is lost (Green 1984; Galbraith & Green 1985; Green 2004). Individual eggs can also be labelled with the nest identifier and egg number using a black permanent marker (hard to distinguish against natural egg colouration; Figure 10), which is useful when deducing causes of nest failure when individual eggs are found far from the nest location. Marking nests in this way has no effect on nest predation rates (Galbraith 1987; Fletcher *et al.* 2005; Ibáñez-álamo *et al.* 2012; Zámečník *et al.* 2018).

Monitoring nests periodically after marking (ideally every 2–3 days) can then provide an indication of nest survival and the relative importance of different causes of nest failure on a site (Bolton *et al.* 2007b). If the presence of an incubating adult cannot be confirmed from a distance, the nest can be relocated on the ground and its status assessed (Green 1986; Green 2004). Warm intact eggs are indicative of continuing incubation, while an empty nest with tiny fragments of eggshell in the lining are indicative of hatching (as is finding newly-hatched chicks; Green 2004). Hatch date estimates from egg biometrics are also useful when determining if hatching is likely to have occurred (Green 1984; Galbraith & Green 1985). Cold intact eggs indicate abandonment however, and if the nest cup is sitting in or under water and eggs are cold then flooding is the likely cause of failure. Eggs crushed in the nest cup surrounded by crushed vegetation, hoof prints and other signs of livestock are likely signs of trampling, while an empty nest with no shell fragments in the lining, partially eaten eggs or large fragments of eggshell in the vicinity of the nest cup are indicative of predation (Green *et al.* 1987).

The total number of days for which marked nests survived (i.e. the cumulative number of days for which nests were exposed to causes of failure, termed ‘exposure days’), and the number of nests that failed, can be used to calculate a measure of nest survival using the methods described by Mayfield (1961) and Mayfield (1975). Here, the daily survival rate (DSR) of nests is calculated as 1 – DFR, where DFR is the daily failure rate of nests calculated as the number of nests that failed divided by the total exposure days. Hatching success, the proportion of nests predicted to have survived to hatch, is then the DSR raised to the power of 31 days (the length of the Lapwing laying and incubation period; Galbraith 1988). It is this metric that must reach or exceed 50% to allow population stability given reasonable levels of chick survival (MacDonald & Bolton 2008b).

Multiple studies and regular monitoring on lowland wet grassland sites using the above nest monitoring methods have identified predation as the primary cause of Lapwing nest failure, accounting for over 50% of clutch failure in the majority of studies (MacDonald & Bolton 2008b; Teunissen *et al.* 2008; Ausden *et al.* 2009; Figure 9). This is now a key factor compounding the declines of lowland waders as they become confined to an ever decreasing number of isolated suitable breeding sites. Potential egg predators present on lowland wet grassland in the UK fall into two main groups: avian species such as corvids (Carrion Crow *Corvus corone*, Jackdaw *C. monedula*, Rook *C. frugilegus*, Magpie *Pica pica*, Raven *C. corax*) and gulls (Common Gull *Larus canus*, Black-headed Gull *L. ridibundus*, Herring Gull *L. argentatus*, Lesser Black-backed Gull *L. fuscus*); and mammalian species such as Red Foxes *Vulpes vulpes*, European Badger *Meles meles*, small mustelids (Stoat *Mustela erminea*, Weasel *M. nivalis*, American Mink *Neovison*

*vison*), Otter *Lutra lutra* and Hedgehog *Erinaceus europaeus*. There are three main methods of identifying which predators are responsible for nest predation and quantifying their relative contributions to Lapwing nest failure: i) the examination of nest remains, ii) the recording of the timing of predation events, and iii) the use of nest cameras (Green 2004; MacDonald & Bolton 2008b).

Eggshell remains at predated nests can be used to assess the likely predator groups involved (Green 1986; Green *et al.* 1987; Green 2004; MacDonald & Bolton 2008b). Cleanly broken edges and single puncture marks may be indicative of an avian predator (particularly corvids), while crushing damage to fragment edges in a band ~5 mm wide and paired tooth puncture marks are indicative of a mammal. The distance between incisor toothmarks can also be used to deduce the identity of the mammal species in some cases (Green *et al.* 1987). Whole eggs found further away from the nest location and buried in earth or vegetation with or without paired puncture marks may also be indicative of mammalian predation, as mammals often cache eggs to use as a later food source. However, avian predators can cause shell crushing when predating eggs, and mammals may not crush edges or leave bite marks, so this method is highly subjective and unreliable. Different predators also differ in their tendency to leave evidence of predation at the nest, so basing inference of predator importance on predation signs alone is likely to be biased (Green *et al.* 1987).

A more reliable and quantitative method for studies at lower latitudes (where periods of darkness occur in the summer) is to determine the timing of nest predation, as the two main egg predator groups are active at different times: avian predators being active only during the day, mammalian predators chiefly active at night with a small amount of daytime activity only. The timing of predation can be determined by inserting a temperature logger into the base of the nest: during incubation the temperature is recorded as near constant, while after a predation event (when the incubating adult abandons the nest) there is a sharp drop in temperature followed by large daily ambient fluctuations (Green 2004; Bolton *et al.* 2007b; Teunissen *et al.* 2008; Eglington *et al.* 2009a; Laidlaw *et al.* 2015b). The timing of the predation event can then be determined by plotting temperature against date and time. Nocturnal predation events can be reliably attributed to mammalian predators, while diurnal predation is more likely to be avian or potentially also mammalian. Studies using this method have found that on lowland wet grassland it is nocturnal predation, i.e. by mammals, that is responsible for 70–90% of all nest predation events (Bolton *et al.* 2007b; Teunissen *et al.* 2008; Bellebaum & Bock 2009; Eglington *et al.* 2009a).

It is not possible to identify the mammal species involved using temperature loggers however. For this, remotely operated infrared nest cameras are required to capture footage of predation events as they occur (Green 2004; Bolton *et al.* 2007a; Teunissen *et al.* 2008). A typical design in the UK is a compact miniature camera on a short stake placed ~1 m from the nest cup and connected with a cable to a battery and recording box hidden in the vegetation or buried further away (~5 m) to prevent attracting predators (Figure 11; Bolton *et al.* 2007a). These cameras use a video motion detection system to record images when activity above a pre-set activity threshold occurs within a specified part of the nest image (to avoid excessive triggering on movement of the incubating birds; Bolton *et al.* 2007a; MacDonald & Bolton 2008b). By using these cameras, the relative contribution of mammalian predators in influencing Lapwing nest survival has been further confirmed and the key species identified as Red Fox (Figure 11); although Badgers, small mustelids and Hedgehogs also contribute to predation on specific sites (Jackson & Green 2000; Teunissen *et al.* 2008; Ausden *et al.* 2009).

Figure 11. Lapwing nest monitoring with an infra-red motion-sensing camera (left) and a resulting image of nocturnal predation by a Red Fox (right). Images © RSPB.

### Chick survival

Lapwing chick survival rates are dependent on two interrelated sources of mortality: i) predation, and ii) other ‘natural’ mortality i.e. starvation and poor body condition or exposure to extreme conditions, usually a result of low food availability, with chicks in poor condition also potentially more susceptible to predation (Sharpe *et al.* 2009). In many cases, Lapwing productivity is still lower than the target 0.6–0.8 chicks per pair even when nest survival exceeds 50% (MacDonald & Bolton 2008b), indicating that low chick survival (hatching to fledging) as a result of either or both of these sources of mortality may be at play. Studying Lapwing chick survival is much more difficult than studying nests however, and involves intensive marking and tracking techniques (Green 2004). Marking is usually done by ringing each chick with a unique combination of permanent colour rings and/or coded leg flags, or by using temporary leg flags made from electrical tape placed over a permanent metal ring (Figure 12; **VI**, **VII**). Tracking is done using radio tags which are first glued to gauze with permanent adhesive before being attached to the chick's back next to the synsacrum and over the pelvic girdle with latex adhesive (Figure 12; **VI, VII**; Hönisch *et al.* 2008; Teunissen *et al.* 2008; Schekkerman *et al.* 2009). Chick down is folded over the glued gauze to aid adhesion and the tag is often coloured with a dark permanent marker if not already covered with dark plastic potting to limit detection by predators. Most tracking studies use manual telemetry to monitor chick movements, aid the relocation of chicks in the field and detect if chicks are alive (indicated by fluctuating amplitude and pitch of the radio tag signal as chicks move around) or dead (signal static or lost).

Site managers and policymakers are often concerned that low food availability may be leading to low chick survival even on protected sites implementing targeted sward and water management for breeding Lapwing. However, using marking and manual tracking as described above to aid brood relocation and chick identification on 15 lowland wet grassland sites across the UK, **VI** demonstrates that Lapwing chicks achieved greater indices of body condition than expected for their age (Beintema 1994), and achieved growth rates similar to those of larger samples of chicks studied during the past four decades in the UK and Netherlands (Beintema & Visser 1989; Sharpe *et al.* 2009; Eglington *et al.* 2010). These results suggest that food availability is unlikely to be limiting chick survival on well-managed lowland wet grassland sites, and instead the focus should be placed on other causes of chick mortality (**VI**).

Figure 12. Lapwing chick monitoring using radio tags (left), temporary legs flags (centre) and permanent colour rings (right). Central image © Rosalind Kennerley.

If chick condition and 'natural' mortality are not the main causes of low Lapwing chick survival then it must be predation that is preventing the attainment of required levels of productivity for population stability. Studies using manual chick tracking to monitor Lapwing chicks until death and then track their remains to infer the predators involved have implicated birds of prey as the most important chick predators (Junker *et al.* 2004; Schoppenhorst 2004; Junker *et al.* 2006; Teunissen *et al.* 2008; Schekkerman *et al.* 2009). The results of this method are not supported by trials in which chick survival and productivity increase following mammalian predator removal or exclusion however (Bolton *et al.* 2007b; Schifferli *et al.* 2009; Rickenbach *et al.* 2011). For example, Schifferli *et al.* (2009) report an increase in productivity from 0.4 to a maximum of 1.26 chicks fledged per pair between years with and without electric fences to exclude nocturnal mammalian predators, while Rickenbach *et al.* (2011) also report an increase in cumulative chick survival from hatching to fledging from 0.0 to 0.24 between unfenced and fenced areas, with nocturnal predation driving chick survival outside fences. This effect is further demonstrated by **VIII**, where productivity increased significantly in years when fences were used to exclude large mammalian predators (foxes and badgers). The results of these studies indicate that nocturnal mammalian predation is more important than the manual telemetry of chick remains alone indicates. The source of this disparity could be that the likelihood of finding predated remains through manual telemetry is dependent on the type of predator involved (Schaub 2009): avian-predated remains may be easier to find because they are often plucked close to the site of predation or taken to high locations where tag signals can be more easily detected, hence the bias towards this predator type (Figure 13; **VII**).

**VII** describes the results of a study where this uncertainty was reduced by using Automatic Radio Tracking Stations (ARTS) to add additional information, namely the timing of predation events. ARTS constantly recorded signals from radio-tagged Lapwing chicks and enabled the time of their predation to be identified to within 10 minutes. As with the use of temperature loggers in Lapwing nests, this allowed the classification of predation events to either nocturnal (mammalian) or diurnal (likely avian, but potentially mammalian) predators. When combined with traditional manual telemetry and inference from predated remains, this revealed that chick predation rates on the 15 lowland wet grassland sites monitored 2009–2013 were as high as 87% overall (**VII**). Diurnal predation was the most common, but nocturnal predation was more intensive, with chicks more likely to be predated per hour at night (**VII**). Mammalian predation accounted for 10% more predation events than avian predation, reflecting the high nocturnal predation rate and the partial contribution of mammals to predation during the day (**VII**). Red Foxes were the principal mammalian predators and were the only predator group that statistically influenced chick predation probability: where fox activity was high, the probability that a chick would survive 30 days in the field was < 2% (**VII**).

**VII** also shows that chick predation was less likely at the start of the breeding season than at the end, meaning that if predation management could be targeted in late March and early April to encourage successful early nesting attempts then early-hatched chicks may be more likely to fledge, and may also be more likely to recruit to future breeding populations if hatching early confers other benefits, such as greater likelihoods of surviving to breed in future years (Gill *et al.* 2014). **VII** also found that the proportion of chicks predated by three main predator groups (foxes, small mustelids, raptors) were directly related to the activity of those predators on a site, so predator activity monitoring could indicate which of these groups to focus on when managing predation (**VII**).

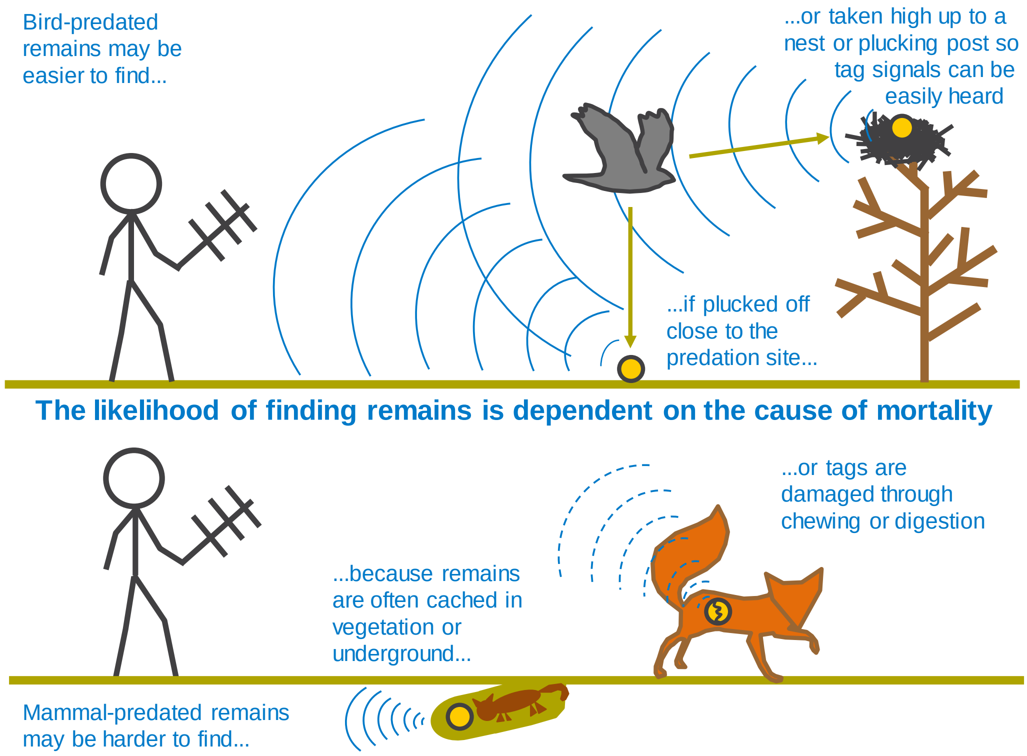


Figure 13. Manually tracking radio-tagged chick remains can help determine the ID of the chick predator, but this approach may be biased because those predated by avian predators are easier to find (**VII**).

## Managing predation

Now that the predators involved in Lapwing nest and chick predation in lowland UK are known, targeted predation management solutions can be used to limit their impact (Figure 9). Predation can be micro-managed on a site-specific basis by intensive methods requiring significant resources and time allocation but with high, and often immediate, gains in terms of nest and chick survival. Alternatively, less intensive landscape-scale methods of managing predation can be employed at a potentially reduced cost. Positive impacts on Lapwing productivity from this latter approach are likely to be less immediate, but such applications may be a more sustainable method of reducing Lapwing predation on a national level.

### Intensive site-level solutions

The first predation management method to be trialled on lowland UK nature reserves for the protection of Lapwing nests and chicks was the lethal control of Red Foxes and Carrion Crows, both species implicated in limiting nest survival. This method mimics the type of management regularly carried out in the countryside surrounding lowland wet grassland sites by gamekeepers and farmers raising and releasing gamebirds. On reserves, lethal fox control (shooting) is conducted before the wader breeding season (late winter–early spring) from a vehicle or high-seat at night by trained marksmen (Bolton *et al.* 2007b). This control is aimed at reducing the abundance of foxes during the peak Lapwing nesting and chick rearing periods, rather than reducing the fox population year-round (Bolton *et al.* 2007b). Crows are trapped and dispatched during the wader breeding season (March–June) with Larsen cage traps (GWCT 2014), which use a decoy adult crow to attract other territorial birds (Bolton *et al.* 2007b; Ausden *et al.* 2009). Larson traps are effective for catching and controlling breeding pairs of crows nesting in close proximity to wader breeding areas which are the individuals most often implicated in wader nest predation (RSPB unpublished data). Crow nests are also occasionally destroyed during the construction or incubation stage for the same reason if trapping is ineffective.

The success of these lethal control methods in reducing Lapwing nest predation varies between sites in relation to predator density: only sites with higher starting densities of predators experience positive impacts on nest survival (Bolton *et al.* 2007b). This is because reducing the numbers of foxes and crows is difficult, as vacant fox territories are rapidly recolonised by individuals immigrating from the surrounding countryside, and the removal of territorial crows results in an influx of non-territorial crows (Bolton *et al.* 2007b; Ausden *et al.* 2009). Removing top predators (such as foxes) from the predator-prey system may also encourage mesopredator release, where predation pressures from predator species in lower trophic levels (e.g. small mustelids) increase once they are themselves relieved from direct predation or prey competition (Latham 1952; Crooks & Soulé 1999; Malpas 2009; Ritchie & Johnson 2009; Ellis-Felege *et al.* 2012). Lethal control methods are also time-consuming, highly skilled and involve difficult animal welfare topics (Smith *et al.* 2011). The development of more-successful, less controversial methods of predation management was therefore needed.

An alternative to lethal control is to non-lethally exclude predators from individual nests or from areas where waders breed through the use of nest exclosures (Isaksson *et al.* 2007) or predator-exclusion fencing (Figure 14; **VIII**). The former are usually large cages placed over each nest through which the adults can move to feed and access the nest for incubation, but through which large predators cannot penetrate. Nest exclosures can successfully increase hatching success in small wader populations (Murphy *et al.* 2003a; Isaksson *et al.* 2007; Pauliny *et al.* 2008), but are impractical for sites with large numbers of nests, have no effect on chick survival (Smith *et al.* 2011), and are unsuitable for species that rely on nest crypsis (where nest exclosures result in high levels of adult mortality; Murphy *et al.* 2003b; Isaksson *et al.* 2007; Smith *et al.* 2011).

Figure 14. Nest exclosures (left) and electric fencing (right) can be used to exclude large mammalian predators from individual nests or areas where waders breed. Images © Jennifer Smart (left) and Graham White (right).

In contrast, predator-exclusion fencing is often more practical for large localised wader populations because it can be used to enclose larger areas (**VIII;** Mayer & Ryan 1991; LaGrange *et al.* 1995; Jackson 2001; Rickenbach *et al.* 2011). Such fencing is specifically designed to deter large mammalian predators in two ways – by presenting a physical barrier and by modifying behaviour through the use of unpleasant stimuli such as a small electric shock (Poole & McKillop 2002) – and has improved wader breeding success in arable and mixed farmland habitats in continental Europe (Schifferli *et al.* 2009; Rickenbach *et al.* 2011). Trialling this method on lowland wet grassland sites across the UK resulted in significant increases in Lapwing nest survival and productivity inside fences and in years when fences were operational, in both cases greatly exceeding the minimum levels required for population stability (**VIII**).

Both lethal control and exclusion methods primarily target large mammalian predator species responsible for the majority of Lapwing nest predation and chick predation. Raptors are also important in limiting chick survival however (**VII**), and this may be the case particularly on sites where raptor abundance is high, or where raptor predation pressure increases as a result of the removal or exclusion of large mammalian predators. This compensatory increase in raptor predation has occurred on at least one UK nature reserve employing mammalian predator-exclusion fencing with resultantly high Lapwing nesting densities within the fenced area (**VIII**; Mason *et al.* in prep). On this site, rates of nest survival are very high (87% on average; RSPB unpublished data), and most nests hatch synchronously after the first attempt, hence chick abundance peaks in a single pulse in late-April and early-May. This in turn has attracted predation from Red Kite *Milvus milvus* pairs nesting in the vicinity, with an average of 0.6 kite strikes per hour across the breeding season and 70% of identifiable prey items being wader chicks (Figure 15). In 2015, a diversionary feeding trial was instigated, where small animal carcasses (largely defrosted frozen rats and poultry chicks) were provided at feeding stations on the ground in a short pulse during the peak Lapwing chick rearing period in the attempt to divert kites (Mason *et al.* in prep). Food was provided for two years (2015 and 2016), with baseline and post-feeding years (2014 and 2017) before and after for comparison. Preliminary results indicate that diversionary feeding in this way successfully reduced the predatory strike rate of target kite pairs from an average 0.6 strikes per hour in non-feeding years to 0.2 strikes per hour when feeding, and resulted in an increase in Lapwing productivity from 0.45 in non-feeding years to 1.02 in feeding years; well above the range required for a stable population (Figure 15; MacDonald & Bolton 2008b; Mason *et al.* in prep).

Diversionary feeding has also been used successfully in other predator-prey systems, including the reduction of predation by breeding Hen Harriers *Circus cyaneus* on the economically valuable Red Grouse *Lagopus lagopus* on moorland (Redpath *et al.* 2001; New *et al.* 2012), and predation by breeding Kestrels *Falco tinnunculus* on beach-nesting colonies of Little Terns *Sterna albifrons* (Smart & Amar 2018). It has also been proposed for the management of predation by breeding Common Buzzards *Buteo buteo* on gamebirds (Pheasant *Phasianus colchicus*, Red-legged Partridge *Alectoris rufa*) in lowland farmland (Rooney *et al.* 2014). This method could therefore become a valuable addition to the lowland wet grassland predator management toolkit in future.

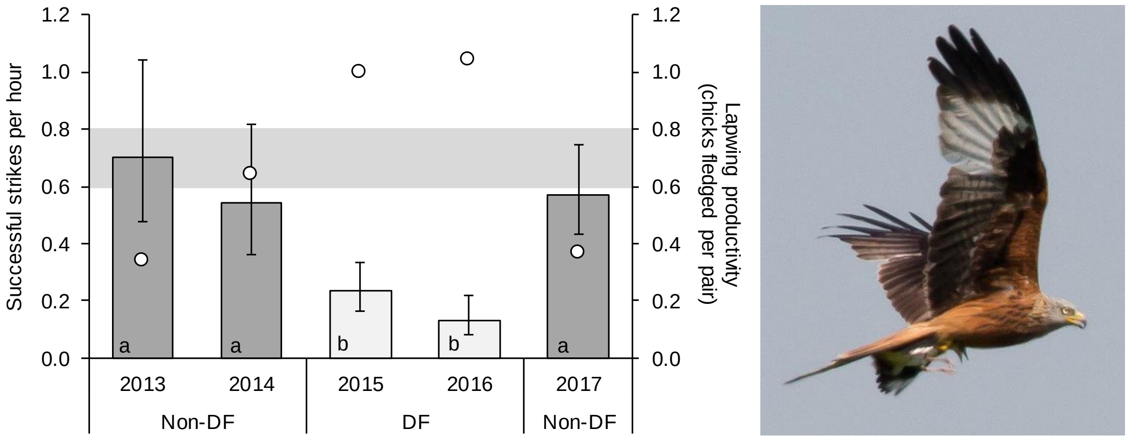


Figure 15. Annual average red kite predatory strike rates (bars, ± 95% confidence intervals) within a wader breeding area surrounded by a predator-exclusion fence compared with annual site-level lapwing productivity (points) on an RSPB nature reserve in years with (pale bars) and without (dark bars) red kite diversionary feeding. The horizontal shaded area indicates the range of productivity required for a stable lapwing population (MacDonald & Bolton 2008b). Figure reproduced from Mason *et al.* (in prep). Red kite with lapwing chick image © Roger Wyatt.

## Landscape-scale predation management

The high-intensity micro-management approaches to predation management described above have their place in maximising Lapwing productivity at the site-scale when habitat management to provide suitable breeding conditions is insufficient to improve breeding success. However, these methods are unsuitable for protecting larger areas where densities of Lapwing or other wader species are low and pairs are spread widely. They are also likely to result in compensatory predation from other predators not targeted by the technique in use (as in the case with Red Kites and exclusion fencing above), or in mesopredator release (Latham 1952; Crooks & Soulé 1999; Ritchie & Johnson 2009; Ellis-Felege *et al.* 2012). A situation could therefore arise whereby removing one source of predation results in having to remove another, and so on, in the hopeless quest to eliminate all predators from the system. A much more sustainable approach may be to focus on returning wet grassland to a more naturally-functioning state through habitat management which provides alternative prey sources or diverts predators away from wader breeding areas.

Lapwing nest predation rates are often lowest when they nest at higher densities and in large numbers away from field edges (MacDonald & Bolton 2008a), so manipulating the habitat to encourage this behaviour could be a step towards reducing predation in a less-intensive way. Testing this on a nature reserve by increasing sward height around field edges and increasing the number of wet features at the centre to make edges less favourable and centres more attractive was unsuccessful in reducing the impacts of predators on Lapwing nests however (Bodey *et al.* 2010; Smart 2016). This is most likely because foxes, as the main target predators, hunt over large areas so field-scale manipulation is insufficient to produce effects (Smart 2016).

A more effective approach could be the provision of habitats that support small mammals to divert predators away from wader breeding areas. Small mammals are the main prey of foxes and many avian predators because they are available all year round, while Lapwing and other waders provide only a temporary spring and summer food source (Laidlaw *et al.* 2013). On wet grasslands, small mammals are most abundant in patches of taller vegetation on drier ground, usually present as verges outside of fields along tracks, railways and rivers (Laidlaw *et al.* 2013). Research on reserves has indicated that Lapwing nest predation rates are lower closer to these taller vegetation patches, and that targeted management and provision of these features could result in a ~20% reduction in nest predation overall, although only in areas with high lapwing nest density close to field edges (Laidlaw *et al.* 2015b; Laidlaw *et al.* 2016). These effects are also present in the wider-countryside, indicating that the provision of small mammal corridors and verges around wader breeding fields could form part of a viable landscape–scale predation management solution (Laidlaw *et al.* 2015a; Smart 2016).

One method by which small mammal corridors, and other more-intensive predation management methods, could be deployed throughout the landscape is through AES, forming a connecting buffer around and between nature reserves. Up until recently, AES habitat management for breeding waders in the UK has only targeted sward structure and water levels to encourage Lapwing nesting however, and doesn’t convey any positive impacts on predation pressure (Leigh *et al.* 2016). Instead, Lapwing nest predation rates on reserve fields are actually higher when surrounded by AES farmland compared to commercial farmland, suggesting that predator activity is attracted to the more amenable conditions and prey availability on both AES and reserve sites (Leigh *et al.* 2016). The deployment of AES around reserves does have the potential to increase the contiguous habitat area available for wader breeding however, and thus the potential for population increase, so if options for predation management were made available within them they might provide an effective landscape-scale delivery mechanism.

Further research is currently underway to assess the effectiveness of integrating both intensive predation management approaches such as exclusion fencing temporally-targeted to increase early nest and chick survival (**VIII**), and landscape-scale approaches in the form of long vegetation, and therefore small mammal prey, provision. Funding for electric predator exclusion fencing is now available for breeding wader conservation through the new Countryside Stewardship AES scheme in England (Natural England 2016). Modelling different scenarios of deploying these measures in the wider countryside under limited resource availability could also indicate where they would have the biggest positive impact and be the next step in lowland Lapwing conservation management (Mason *et al.* 2016).

## Wider implications for wader conservation

The issues and conservation management solutions presented here for Redshank and Lapwing in the UK are widely relevant to similar lowland areas and other wader species at these latitudes in Western Europe (Roodbergen *et al.* 2012). Saltmarsh throughout Western Europe supports breeding Lapwing and Oystercatcher as well as Redshank, while lowland wet grassland supports Redshank, Black-tailed Godwit, Oystercatcher, Snipe, Curlew, Baltic Dunlin *Calidris alpina schinzii* and Ruff *Calidris pugnax* in addition to Lapwing (Leyrer *et al.* 2018). Across Europe, all are undergoing population declines driven by low breeding success stemming from the same threats – the loss, degradation and fragmentation of breeding habitats, and high rates of nest and chick loss due to agricultural activities and predation – and most require similar or complementary habitat conditions to breed successfully (Roodbergen *et al.* 2012; Leyrer *et al.* 2018).

Wader populations and their associated habitats span international borders, and much of the evidence-base supporting UK lowland wader conservation stems from studies conducted in other European countries – e.g. the Netherlands: Beintema and Müskens (1987), Teunissen *et al.* (2008), Breeuwer *et al.* (2009); France: Tichit *et al.* (2005), Durant *et al.* (2008a); Germany: Andresen *et al.* (1990), Bellebaum and Bock (2009), Exo *et al.* (2017); Denmark: Kahlert *et al.* (2007); Sweden: Isaksson *et al.* (2007); Switzerland: Rickenbach *et al.* (2011). The recovery and maintenance of European breeding wader populations is therefore unlikely to be achievable without scaling-up the deployment of conservation measures from targeted management at the individual site-scale to the landscape-scale, with the aim of delivering coherent and resilient ecological networks of suitable habitat (Hopkins *et al.* 2007; Boyd *et al.* 2008; Isaac *et al.* 2018; Leyrer *et al.* 2018). The increasing impacts of climate change (**I**, **II**), particularly the northwards movement of species' climate envelopes (Huntley *et al.* 2007), highlight the need to target these management actions in areas likely to have suitable conditions for waders in the future (e.g. sufficient water levels and appropriate grazing), as well as focussing on habitat conditions and habitat management within their current distribution.

Conservation at the landscape-scale requires more suitable breeding sites of larger size that are better managed and inter-connected to enhance species' resilience to demographic, genetic and environmental stochasticity (Lawton *et al.* 2010; Isaac *et al.* 2018). Within Europe, a potential approach to the structuring of ecological networks for breeding waders is one which focusses on the interplay between wetland nature reserves or protected sites where suitable habitat and predation management is in place, and surrounding farmland managed sympathetically by AES (Smart 2016; Leyrer *et al.* 2018). This mosaic of coordinated management could encourage a return to wilder conditions (Benton *et al.* 2003), supporting abundant small mammal prey for predators and thus reducing their reliance on waders during the breeding season. This could subsequently lead to lower nest and chick predation, facilitating population growth and encouraging nesting densities to increase to a point where anti-predator defence further reduces predation rates over larger areas. This approach is recommended by the new European Multi-species Action Plan for breeding wader species (Leyrer *et al.* 2018), which should help to ensure its delivery and shape the future of European breeding wader conservation going forward.

The main demographic parameter influencing wader populations is currently breeding success, but the influence of post-fledging juvenile and adult survival should not be ignored (Roodbergen *et al.* 2012). If survival and body condition during the non-breeding season declines, then focussing on maximising breeding success alone is unlikely to facilitate population stability or recovery. It is therefore important that coordinated conservation action is implemented on the staging and wintering grounds of lowland wader species – where hunting as well as habitat degradation may be key issues (Madsen & Fox 1995; Camphuysen *et al.* 1996; Duriez *et al.* 2012; Jiguet *et al.* 2012) – in addition to their breeding habitats. This will require international action, particularly through multilateral environmental agreements, such as the Convention on the Conservation of Migratory Species of Wild Animals (CMS) and the African-Eurasian Migratory Waterbird Agreement (AEWA), to ensure connectedness of site protection throughout the flyway.

## Critique of approaches used in publications I–VIII

### Study design: spatial and temporal scale

The issue of spatial and temporal scale and how these influence our perception and management of natural systems is central to the study of ecology, population biology and ecosystem science (Levin 1992). Different ecological processes act at different spatial and temporal scales (Azaele *et al.* 2015), meaning that biodiversity change may also differ in direction or magnitude depending on the scale at which it is monitored (Keil *et al.* 2011). The aims of conservation and the provision of ecosystem services are also scale-specific, with different goals concerning global, national, regional or site-level populations (Hein *et al.* 2006). Ecological threats often act at large spatial and temporal scales (e.g. over decades for large ecosystems), but most variables can only be measured at a fine-enough resolution to detect effects in small areas and over short time periods. The difficulty is then in translating the patterns defined at these small scales to what is happening at the larger scale (Schneider 2001).

The scope and conservation relevance of a study is therefore highly dependent on its ability to translate from small to large scale, regulated by its ‘extent’ and ‘grain’: extent being the size of the area being sampled, the grain being the size of the sampling units within this extent (Wiens 1989). The extent influences the number of different landscape features and threat types that are detectable (larger extents resulting in a greater variation in features and threats included), while the grain influences the ability to distinguish between patches and threats within these features (the smaller the sampling unit the fewer patches or threats that are averaged out during sampling; Wiens 1989). The spatial scale at which conservation studies are conducted is therefore highly important in determining their relevance to the population under study and the applicability of results for conservation intervention.

Publications **I–VIII** were conducted at different spatial scales, with the extent and grain of study chosen to best represent the scale at which populations were likely to be impacted by the threats under study, and the scale at which conservation interventions would most likely be necessary. **I** and **II** were conducted at the continental scale across a whole taxonomic group and multiple decades, because this is the scale at which global climate change is predicted to have the largest and most consistent impact. It was however necessary to account for regional variation in the magnitude and direction of the relationship between species population trends and the trend in the suitability of their climate, as these could differ depending on local climatic conditions and drivers of population change. By conducting these studies at such a large scale, it was possible to diagnose the extent of climate impacts and draw conclusions across an international meta-population of birds for a multi-species level threat, thus producing outputs with the potential to influence international environmental policy. Only at this level are interventions to adapt to and reduce the impacts of climate change likely to be successfully implemented.

In contrast, **III–VIII** were conducted at the national or regional level with the aim of influencing conservation policy and management implementation at a national scale. Although all these studies focussed on a national extent, the survey grain and temporal scale differed to maximise the applicability of results, as well as to fit within constraints of equipment, fieldworker and financial availability. **III** and **V** involved the national survey of saltmarsh for breeding Redshank or grazing management practices conducted within a restricted time period in one year, focussing on a representative proportion of the saltmarsh present in Great Britain or England and with discrete sites as sampling units. In **III**, this allowed the estimation of national population size and breeding density when average results across all sites were scaled to the total national area of saltmarsh they represented, while in **V** it allowed representative conclusions to be drawn about regional and national saltmarsh management. Diagnosing national-scale trends and patterns of habitat management in this way have more impact on influencing national government policies and generic environmental management initiatives designed for national implementation. **IV**, **VI**, **VII** and **VIII** were based on the meta-analysis of site-level studies conducted over multiple years (different years at different sites), to make the most efficient use of available equipment, staff time and resources. This also allowed more intensive studies of ecological impacts on specific variables such as nest and chick survival, informing detailed site- or habitat-specific conservation management.

### Study design: data complexity

Conducting studies at different spatial and temporal scales also conveys different benefits in terms of the level of detail inherent in the data. At the continental scale, only relatively ‘simple’ data is practical to collect within a reasonable timeframe. This broadbrush data is also best suited for comparisons between multiple species and geographical areas over long time periods, where excessive variation inherent in detailed data over this same scale could mask true overarching threats and population responses. For example, in both **I** and **II** the classification of species to one of four broad habitat categories was necessary to detect differences in responses to climate change between habitats. Classification based on more habitat categories, although more accurate in terms of species preferences, would have incorporated too much variation into the analysis and increased the difficulty of comparing species with very different fine-scale habitat associations between continents where habitat and community structures differ.

Data collected at multiple sites with the aim of detecting national trends or representing management conditions can be more-detailed, although must still be relatively simple if collected within a short time window (e.g. breeding season or grazing season as in the case of **III** or **V**). In **III** and **V**, data collection within one year only was necessary to prevent the need to account for inter-annual variation in analyses. Intensive data collection of very detailed data on autecology or habitat conditions as in **IV**, **VI**, **VII** and **VIII** was necessary to examine complex issues, and possible due to the small number of sites covered in each year.

### Study design: data collation or collection

**I**, **II**, **VI** and **VIII** made use of existing datasets collected through annual country or site monitoring schemes that required compilation and variable creation to ensure the data was fit for purpose to answer the research questions of interest. Contrastingly, data collection to answer specific research questions was designed in advance prior to fieldwork for **III, IV, V** and **VII**. There are positives and negatives to both approaches.

With existing datasets the data availability is known, removing a source of uncertainty as the variation that could occur during collection has already occurred and can be assessed prior to study design. Such datasets are often already available electronically and processed to ensure reliability in some way (as in the case of European and North American bird trends in **I** and **II**), and time is saved if variables already exist that can be quickly used to parameterise analyses. Using existing datasets also encourages the use of flexible study design around what is available, the identification of useful and interesting research questions and how the existing data could be used to answer them (as was the case for **VI** which made use of data collected through fieldwork designed initially for **VII**).

The negatives of using existing data are that it may not be collated into a single place, held by single individuals or organisations, or be in an easily comparable format. For **VIII** data were held by multiple sources (largely individual nature reserves) and a great deal of time was spent requesting, collating and combining datasets prior to analysis. Existing data may also not have been collected in the same way using the same methods, introducing compatibility issues and the need to control for this in more complex analyses. In **VIII** some sites were able to collect nest survival data inside and outside predator exclusion fences in the same year (allowing inside vs. outside comparisons) while for others only effects before versus after fence construction could be compared, hence the need for a two-part analysis. In **I** and **II** all countries (Europe) or states (North America) used the same or similar methods to conduct bird surveys, and the same methods were used to generate country- or state-level population size and trend estimates, so this issue was not present.

Figure 16. Fieldwork was conducted by the author (LRM) to collect data underpinning **III**, **VI** and **VII**. For **III** this involved breeding Redshank and saltmarsh vegetation surveys on 13 sites around the coast of eastern England (Lincolnshire, Norfolk, Suffolk and Essex) during the spring of 2011 (left). For **VI** and **VII** this involved intensive monitoring of wader nests, chick ringing and radio tagging, radio tracking, monitoring chick survival and predator activity surveys on four sites in 2010 and one site in 2012 in Norfolk (centre and right). LRM also provided training in fieldwork methods and managed fieldworkers collecting data for **III**, **IV**, **V**, **VI** and **VII**.

It is often necessary to collect new data for a specific project however, particularly if existing data is not at a suitable scale or level of detail to answer the research question of interest. Designing data collection from the outset can provide greater flexibility and efficiency, and ensure that only those variables that are needed to answer the specific question(s) are examined. Collecting data during the course of fieldwork projects also allows managers to plan how to collate and store that data so that it is all available in the same location once fieldwork has ended. The format the data takes can also be planned in advance to ultimately ensure efficient analysis. **III, IV, V** and **VII** all used this method, whereby the required data was assessed prior to fieldwork, fieldwork was designed and conducted to collect that data in the most robust and efficient way, after which it was entered in a consistent electronic format and stored in a central database to allow relatively rapid analysis at the end (Figure 16).

Collecting data as you go can introduce variation that is difficult to predict however, particularly if studying multiple sites or years where conditions may differ. Data collection approaches may therefore need to be adapted part-way through to fit the circumstances, and there is a greater risk that staffing, funding or equipment failure issues mean that it is not possible to collect all the data required. In these situations improvisation is often needed, and the ability to manage expectations of which outputs are likely given the circumstances.

### Analysis: inference approach

There are two main approaches used to assess the importance of a variable in affecting the species or system of interest in ecological research: the more-traditional hypothesis-testing method (used in **II**, **III**, **IV**, **VI** and **VIII**) and the newer Information Theoretic (IT) approach (used in **I**, **II**, **V** and **VII**). Hypothesis-testing focusses on the level of support available in the data to reject the null hypothesis (that the variable of interest has no effect on the system) in which case the alternative hypothesis (that the variable does have an effect) is accepted. Usually a test statistic is generated from the relationship of interest, the magnitude of which is assessed relative to the degrees of freedom in the analysis (the number of estimable parameters) and used to generate a ‘p-value’ (the probability that the null hypothesis is ‘true’). When p-values are less than an arbitrary cut-off value (usually $\alpha = 0.05$, 5%) there is considered to be sufficient evidence to reject the null hypothesis in favour of the alternative hypothesis, i.e. sufficient evidence to conclude that the variable of interest does have an effect; ‘sufficient evidence’ in this case being a < 5% probability of encountering that result by chance, given the sample size and variation. IT methods are instead based on Akaike's information criterion (AIC), or other indicators of model fit, which are used to compare and rank multiple models each containing different combinations of plausible predictor variables to estimate which best approximates the 'true' model, i.e. the processes (of those measured) most likely to underlie the ecological phenomenon studied (Anderson & Burnham 2002; Burnham & Anderson 2002; Burnham & Anderson 2004; Burnham *et al.* 2011; Grueber *et al.* 2011; Richards *et al.* 2011; Symonds & Moussalli 2011).

There is still much debate in the scientific community regarding the reliability of p-values and hypothesis-testing relative to IT methods, whether p-values are still a valid analytical tool for modern ecologists, and whether IT approaches are actually appropriate or helpful (e.g. the recent forum in Ecology 95(3): Aho *et al.* 2014; Barber & Ogle 2014; Burnham & Anderson 2014; de Valpine 2014; Ellison *et al.* 2014; Lavine 2014; Murtaugh 2014a; Murtaugh 2014b; Spanos 2014; Stanton-Geddes *et al.* 2014). Although there is no consensus, it seems that there is no right or wrong approach and that both are valid depending on the circumstance in question. In fact, for nested general linear models (used regularly throughout publications **I**–**VIII**), p-values and differences in AIC are based on identical statistical information and are therefore mathematically interchangeable (Ellison *et al.* 2014).

Hypothesis-testing is generally most appropriate where specific hypotheses are being tested, where determining if effects differ is of principle interest or where it is important to provide a result that is more-easily understandable by conservation practitioners and government officials. Hypothesis-testing has been used as a method for a long time so is understandable by more people. For these reasons, it was considered the best method to use for inference in **III**, **IV**, **VI**, **VIII** and parts of **II**. IT methods by contrast are most useful when there are a range of variables of interest that may interact within a system to affect the outcome or species of interest, and the principle aim is to understand which are the most important and to account for their relative contributions. This approach is therefore best suited to larger ecological studies where no one variable is hypothesised to be more important than another, therefore making it ideal for use in **I**, parts of **II**, **V** and **VII**.

# References

Adam, P. (1981) The vegetation of British saltmarshes. *New Phytologist,* 88: 143-196.

Adnitt, C., Brew, D., Cottle, R., Hardwick, M., John, S., Leggett, D., McNulty, S., Meakins, N. & Staniland, R. (2007) *Saltmarsh management manual*. Environment Agency, DEFRA, Bristol, UK.

Aho, K., Derryberry, D. & Peterson, T. (2014) Model selection for ecologists: the worldviews of AIC and BIC. *Ecology,* 95: 631-636.

Allport, G., O'Brien, M. & Cadbury, C.J. (1986) *Survey of Redshank and other breeding birds on saltmarshes in Britain 1985*. Nature Conservancy Council, Peterborough.

Anderson, D.R. & Burnham, K.P. (2002) Avoiding pitfalls when using Information-Theoretic methods. *The Journal of Wildlife Management,* 66: 912-918.

Andresen, H., Bakker, J.P., Brongers, M., Heydemann, B. & Irmler, U. (1990) Long-term changes of salt marsh communities by cattle grazing. *Vegetatio,* 89: 137-148.

Armstrong, A. & Rose, S. (1999) Ditch water levels manages for environmental aims: effects on field soil water regimes. *Hydrology and Earth System Sciences,* 3: 385-394.

Armstrong, A.C. (1993) Modelling the response of in-field water tables to ditch levels imposed for ecological aims: a theoretical analysis. *Agriculture, Ecosystems & Environment,* 43: 345-351.

Armsworth, P.R., Acs, S., Dallimer, M., Gaston, K.J., Hanley, N. & Wilson, P. (2012) The cost of policy simplification in conservation incentive programs. *Ecology Letters,* 15: 406-414.

Ausden, M., Bolton, M., Butcher, N., Hoccom, D.G., Smart, J. & Williams, G. (2009) Predation of breeding waders on lowland wet grassland - is it a problem? *British wildlife,* October 2009: 29-38.

Ausden, M. & Hirons, G.J.M. (2002) Grassland nature reserves for breeding wading birds in England and the implications for the ESA agri-environment scheme. *Biological Conservation,* 106: 279-291.

Ausden, M., Rowlands, A., Sutherland, W.J. & James, R. (2003) Diet of breeding Lapwing *Vanellus vanellus* and Redshank *Tringa totanus* on coastal grazing marsh and implications for habitat management. *Bird Study,* 50: 285-293.

Ausden, M., Sutherland, W.J. & James, R. (2001) The effects of flooding lowland wet grassland on soil macroinvertebrate prey of breeding wading birds. *Journal of Applied Ecology,* 38: 320-338.

Ausden, M. & Treweek, J. (1995) Grasslands. In *Managing habitats for conservation* (eds W.J. Sutherland & D.A. Hill), pp. 197–229. Cambridge University Press, Cambridge.

Azaele, S., Maritan, A., Cornell, S.J., Suweis, S., Banavar, J.R., Gabriel, D. & Kunin, W.E. (2015) Towards a unified descriptive theory for spatial ecology: predicting biodiversity patterns across spatial scales. *Methods in Ecology and Evolution,* 6: 324-332.

Balmer, D.E., Gillings, S., Caffrey, B.J., Swann, R.L., Downie, I.S. & Fuller, R.J. (2013) *Bird Atlas 2007-11: the breeding and wintering birds of Britain and Ireland*. BTO Books, Thetford.

Barber, J.J. & Ogle, K. (2014) To P or not to P? *Ecology,* 95: 621-626.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. & Silliman, B.R. (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs,* 81: 169-193.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L. & Maguire, K.C. (2011) Has the Earth's sixth mass extinction already arrived? *Nature,* 471: 51.

Batáry, P., Dicks, L.V., Kleijn, D. & Sutherland, W.J. (2015) The role of agri-environment schemes in conservation and environmental management. *Conservation Biology,* 29: 1006-1016.

Batten, L.A., Bibby, C.A., Clement, P., Elliott, G.D. & Porter, R.F. (1990) *Red Data Birds in Britain*. Poyser, London.

Beeftink, W. (1977) Salt-marshes. In *The Coastline* (ed. R.S.K. Barnes), pp. 93-121. John Wiley and Sons, London.

Beintema, A.J. (1994) Condition indices for wader chicks derived from bodyweight and bill-length. *Bird Study,* 41: 68-75.

Beintema, A.J. & Müskens, G.J.D.M. (1987) Nesting success of birds breeding in Dutch agricultural grasslands. *Journal of Applied Ecology,* 24: 743-758.

Beintema, A.J., Thissen, J.B., Tensen, D. & Visser, G.H. (1991) Feeding ecology of Charadriiform chicks in agricultural grassland. *Ardea,* 79: 31-43.

Beintema, A.J. & Visser, G.H. (1989) The effect of weather on time budgets and development of chicks of meadow birds. *Ardea,* 77: 181-192.

Bellebaum, J. & Bock, C. (2009) Influence of ground predators and water levels on Lapwing *Vanellus vanellus* breeding success in two continental wetlands. *Journal of Ornithology,* 150: 221-230.

Benstead, P., Drake, M., Jose, P., Mountford, O., Newbold, C. & Treweek, J. (1997) *The wet grassland guide: Managing floodplain and coastal wet grasslands for wildlife*. The Royal Society for the Protection of Birds, Sandy, Bedfordshire.

Benstead, P.J., Jose, P.V., Joyce, C.B. & Wade, P.M. (1999) *European wet grassland: Guidelines for management and restoration*. The Royal Society for the Protection of Birds, Sandy, UK.

Benton, T.G., Bryant, D.M., Cole, L. & Crick, H.Q. (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology,* 39: 673-687.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution,* 18: 182-188.

Bertholdt, N.P., Gill, J.A., Laidlaw, R.A. & Smart, J. (2016) Landscape effects on nest site selection and nest success of Northern Lapwing *Vanellus vanellus* in lowland wet grasslands. *Bird Study,* 64: 30-36.

BirdLife International (2004a) *Birds in Europe: population estimates, trends and conservation status*. BirdLife International, Cambridge.

BirdLife International (2004b) *Birds in the European Union: a status assessment*. BirdLife International, Wageningen, The Netherlands.

BirdLife International (2015) *European Red List of birds*. Office for Official Publications of the European Communities, Luxembourg.

BirdLife International (2018) IUCN Red List for birds. Downloaded from http://www.birdlife.org on 23/07/2018.

Bodey, T.W., Smart, J., Smart, M.A. & Gregory, R.D. (2010) Reducing the impacts of predation on ground-nesting waders: A new landscape-scale solution? *Aspects of Applied Biology,* 100: 167-174.

Bolton, M., Butcher, N., Sharpe, F., Stevens, D. & Fisher, G. (2007a) Remote monitoring of nests using digital camera technology. *Journal of Field Ornithology,* 78: 213-220.

Bolton, M., Tyler, G., Smith, K. & Bamford, R. (2007b) The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *Journal of Applied Ecology,* 44: 534-544.

Boorman, L.A. (1992) The environmental consequences of climatic change on British salt marsh vegetation. *Wetlands Ecology and Management,* 2: 11-21.

Boorman, L.A. (2003) *Saltmarsh review: An overview of coastal saltmarshes, their dynamic and sensitivity characteristics for conservation and management. JNCC Report, No. 334*. JNCC, Peterborough.

Bouchard, V., Tessier, M., Digaire, F., Vivier, J.-P., Valery, L., Gloaguen, J.-C. & Lefeuvre, J.-C. (2003) Sheep grazing as a management tool in Western European saltmarshes. *Comptes Rendus Biologies,* 326: S148-S157.

Boyd, C., Brooks, T.M., Butchart, S.H., Edgar, G.J., Da Fonseca, G.A., Hawkins, F., Hoffmann, M., Sechrest, W., Stuart, S.N. & Van Dijk, P.P. (2008) Spatial scale and the conservation of threatened species. *Conservation Letters,* 1: 37-43.

Breeuwer, A., Berendse, F., Willems, F., Foppen, R., Teunissen, W., Schekkerman, H. & Goedhart, P. (2009) Do meadow birds profit from agri-environment schemes in Dutch agricultural landscapes? *Biological Conservation,* 142: 2949-2953.

Brindley, E., Norris, K., Cook, T., Babbs, S., Brown, C.F., Massey, P., Thompson, R. & Yaxley, R. (1998) The abundance and conservation status of redshank *Tringa totanus* nesting on saltmarshes in Great Britain. *Biological Conservation,* 86: 289-297.

Browder, S.F., Johnson, D.H. & Ball, I. (2002) Assemblages of breeding birds as indicators of grassland condition. *Ecological Indicators,* 2: 257-270.

Bulla, M., Valcu, M., Dokter, A.M., Dondua, A.G., Kosztolányi, A., Rutten, A.L., Helm, B., Sandercock, B.K., Casler, B. & Ens, B.J. (2016) Unexpected diversity in socially synchronized rhythms of shorebirds. *Nature,* 540: 109.

Burd, F. (1989) *The saltmarsh survey of Great Britain*. Nature Conservancy Council, Peterborough, UK.

Burgess, N.D. & Hirons, G.J. (1990) *Techniques of hydrological management at coastal lagoons and lowland wet grasslands on RSPB Reserves*. RSPB Management Case Study, RSPB.

Burnham, K. & Anderson, D. (2014) P values are only an index to evidence: 20th- vs. 21st-century statistical science. *Ecology,* 95: 627-630.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multi-model inference: A practical information-theoretic approach*. Springer-Verlag, Berlin.

Burnham, K.P. & Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods Research,* 33: 261-304.

Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology,* 65: 23-35.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.-C. & Watson, R. (2010) Global biodiversity: Indicators of recent declines. *Science,* 328: 1164-1168.

Camphuysen, C., Ens, B., Heg, D., Hulscher, J., Van der Meer, J. & Smit, C. (1996) Oystercatcher *Haematopus ostralegus* winter mortality in The Netherlands: the effect of severe weather and food supply. *Ardea,* 84: 469-492.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015) Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances,* 1: e1400253.

Chalfoun, A.D., Thompson, F.R. & Ratnaswamy, M.J. (2002) Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology,* 16: 306-318.

Chatters, C. (2004) Grazing domestic animals on British saltmarshes. *British wildlife,* 15: 392-400.

Clausen, K.K. & Clausen, P. (2014) Forecasting future drowning of coastal waterbird habitats reveals a major conservation concern. *Biological Conservation,* 171: 177-185.

Clausen, K.K., Stjernholm, M. & Clausen, P. (2013) Grazing management can counteract the impacts of climate change-induced sea level rise on salt marsh-dependent waterbirds. *Journal of Applied Ecology,* 50: 528-537.

Coutts, K.A. (2005) Balancing conflicting management requirements for breeding waders on lowland wet grassland. Unpublished MSc thesis, University of East Anglia.

Cramp, S. & Simmons, K.E.L. (1983) *Handbook of the Birds of Europe, the Middle East and North Africa: The birds of the Western Palearctic. Vol. III: Waders to Gulls*. Oxford University Press, Oxford.

Crofts, A. & Jefferson, R.G. (1999) *The lowland grassland management handbook,* 2nd edn. Natural England, Peterborough, UK.

Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature,* 400: 563-566.

Davidson, K.E., Fowler, M.S., Skov, M.W., Doerr, S.H., Beaumont, N. & Griffin, J.N. (2017) Livestock grazing alters multiple ecosystem properties and services in salt marshes: a meta-analysis. *Journal of Applied Ecology,* 54: 1395-1405.

Davidson, N.C., Laffoley, D., Doody, J.P., Way, L.S., Gordon, J., Key, R., Pienkwoski, M.W., Mitchell, R. & Duff, K.L. (1991) *Nature conservation and estuaries in Great Britain*. Nature Conservancy Council (JNCC), Peterborough.

de Valpine, P. (2014) The common sense of P values. *Ecology,* 95: 617-621.

Dempster, J. (1975) *Animal population ecology*. Academic Press, London.

Dijkema, K.S. (1990) Salt and brackish marshes around the Baltic Sea and adjacent parts of the North Sea: Their vegetation and management. *Biological Conservation,* 51: 191-209.

Donald, P.F., Green, R.E. & Heath, M.F. (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London, Series B: Biological Sciences,* 268: 25-29.

Donald, P.F., Sanderson, F.J., Burfield, I.J. & van Bommel, F.P.J. (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990-2000. *Agriculture Ecosystems & Environment,* 116: 189-196.

Doody, J.P. (2004) 'Coastal Squeeze' - an historical perspective. *Journal of Coastal Conservation,* 10: 129-138.

Doody, J.P. (2007) *Saltmarsh conservation, management and restoration*. Springer Science & Business Media.

Doody, J.P. (2008) *Management of Natura 2000 habitats: 1330 Atlantic salt meadows (Glauco-Puccinellietalia maritimae)*. European Commission.

Durant, D., Tichit, M., Fritz, H. & Kernéïs, E. (2008a) Field occupancy by breeding lapwings *Vanellus vanellus* and redshanks *Tringa totanus* in agricultural wet grasslands. *Agriculture, Ecosystems & Environment,* 128: 146-150.

Durant, D., Tichit, M., Kernéïs, E. & Fritz, H. (2008b) Management of agricultural wet grassland for breeding waders: Integrating ecological and livestock system perspectives - a review. *Biodiversity and Conservation,* 17: 2275-2295.

Duriez, O., Ens, B.J., Choquet, R., Pradel, R. & Klaassen, M. (2012) Comparing the seasonal survival of resident and migratory oystercatchers: carry-over effects of habitat quality and weather conditions. *Oikos,* 121: 862-873.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000) Climate extremes: observations, modeling, and impacts. *Science,* 289: 2068-2074.

EBCC/BirdLife/RSPB/CSO (2017) Trends of common birds in Europe, 2017 update. http://ebcc.birdlife.cz/trends-of-common-birds-in-europe-2017-update/ accessed Dec 2017.

EC (1992) Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Communities,* No. L 206: 7-50.

EC (2000) Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. *Official Journal of the European Communities,* No. L 327: 1-72.

Eglington, S.E., Gill, J.A., Smart, M.A., Sutherland, W.J., Watkinson, A.R. & Bolton, M. (2009a) Habitat management and patterns of predation of Northern Lapwings on wet grasslands: The influence of linear habitat structures at different spatial scales. *Biological Conservation,* 142: 314-324.

Eglington, S.M. (2008) Managing water levels on wet grasslands for breeding waders; the use of shallow wet features. PhD Thesis, University of East Anglia.

Eglington, S.M., Bolton, M., Smart, M.A., Sutherland, W.J., Watkinson, A.R. & Gill, J.A. (2010) Managing water levels on wet grasslands to improve foraging conditions for breeding northern lapwing *Vanellus vanellus*. *Journal of Applied Ecology,* 47: 451-458.

Eglington, S.M., Gill, J.A., Bolton, M. & Smart, M.A. (2009b) Reversion of arable land to wet grassland for breeding waders. *Conservation Land Management,* 7: 5-9.

Eglington, S.M., Gill, J.A., Bolton, M., Smart, M.A., Sutherland, W.J. & Watkinson, A.R. (2008) Restoration of wet features for breeding waders on lowland wet grassland. *Journal of Applied Ecology,* 45: 305-314.

Ehrlich, P.R. & Ehrlich, A.H. (2013) Can a collapse of global civilization be avoided? *Proceedings of the Royal Society of London, Series B: Biological Sciences,* 280: 20122845.

Eigenbrod, F., Adams, W., Hill, C., Macgregor, N., Osborne, P., Clarke, D., Sandbrook, L., Hodge, I., Steyl, I., Thompson, A., van Dijk, N. & Watmough, G. (2016) *A review of large-scale conservation in England, Scotland and Wales*.

Ellis-Felege, S.N., Conroy, M.J., Palmer, W.E. & Carroll, J.P. (2012) Predator reduction results in compensatory shifts in losses of avian ground nests. *Journal of Applied Ecology,* 49: 661-669.

Ellison, A.M., Gotelli, N.J., Inouye, B.D. & Strong, D.R. (2014) P values, hypothesis testing, and model selection: it's déjà vu all over again. *Ecology,* 95: 609-610.

Erber, C.P., Felix-Henningsen, P., Handke, K., Kundel, W. & Schreiber, K.-F. (2002) Management of moist grassland in a fresh-water marsh of the Weser river: Effects on soil, vegetation, and fauna. In *Wetlands in Central Europe* (eds G. Broll, W. Merbach & E.-M. Pfeiffer), pp. 71-98. Springer, Berlin, Germany.

Evans, P. & Pienkowski, M. (1984) Population dynamics of shorebirds. In *Shorebirds: Breeding behaviour and populations* (eds J. Burger & B.L. Olla), pp. 83-123. Springer, Boston, USA.

Exo, K.-M., Wellbrock, A.H., Sondermann, J. & Maier, M. (2017) Assessing the impact of mowing on Common Redshanks Tringa totanus breeding on saltmarshes: lessons for conservation management. *Bird Conservation International*: 1-14.

Fisher, B., Bradbury, R., Andrews, J., Ausden, M., Bentham-Green, S., White, S. & Gill, J. (2011) Impacts of species-led conservation on ecosystem services of wetlands: understanding co-benefits and tradeoffs. *Biodiversity and Conservation,* 20: 2461-2481.

FitzGerald, D.M., Fenster, M.S., Argow, B.A. & Buynevich, I.V. (2008) Coastal impacts due to sea-level rise. *Annual Review of Earth and Planetary Sciences,* 36: 601-647.

Fletcher, K., Warren, P. & Baines, D. (2005) Impact of nest visits by human observers on hatching success in Lapwings *Vanellus vanellus*: A field experiment. *Bird Study,* 52: 221-223.

Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R. & Carter, N. (1995) Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology,* 9: 1425-1441.

Furness, R.W. & Greenwood, J.J.D. (1993) *Birds as monitors of environmental change*. Chapman and Hall, London.

Galbraith, H. (1987) Marking and visiting lapwing *Vanellus vanellus* nests does not affect clutch survival. *Bird Study,* 34: 137-138.

Galbraith, H. (1988) Effects of agriculture on the breeding ecology of Lapwings *Vanellus vanellus. Journal of Applied Ecology,* 25: 487-503.

Galbraith, H. & Green, R.E. (1985) The prediction of hatching dates of Lapwing clutches. *Wader Study Group Bulletin,* 43: 16-18.

Garbutt, A., de Groot, A., Smit, C. & Pétillon, J. (2017) European salt marshes: ecology and conservation in a changing world. *Journal of Coastal Conservation,* 21: 405-408.

Gedan, K.B., Silliman, B.R. & Bertness, M.D. (2009) Centuries of human-driven change in salt marsh ecosystems. *Annual Review of Marine Science,* 1: 117–141.

Gill, J.A., Alves, J.A., Sutherland, W.J., Appleton, G.F., Potts, P.M. & Gunnarsson, T.G. (2014) Why is timing of bird migration advancing when individuals are not? *Proceedings of the Royal Society of London, Series B: Biological Sciences,* 281: 20132161.

Green, R.E. (1984) Nomograms for estimating the stage of incubation of wader eggs in the field. *Wader Study Group Bulletin,* 42: 36-39.

Green, R.E. (1986) *The management of lowland wet grassland for breeding waders*. Chief Scientist's Directorate, No 626. Nature Conservancy Council, Peterborough.

Green, R.E. (2004) Breeding biology. In *Bird ecology and conservation: A handbook of techniques* (eds W.J. Sutherland, I. Newton & R.E. Green), pp. 57-83. Oxford University Press, Oxford.

Green, R.E. & Cadbury, C.J. (1987) Breeding waders of Lowland Wet Grassland. *RSPB Conservation Review,* 1: 10-13.

Green, R.E., Collins, D. & Johnson, T. (1984) *An intensive survey of breeding redshank on the Wash, 1984.* RSPB, Sandy.

Green, R.E., Hawell, J. & Johnson, T.H. (1987) Identification of predators of wader eggs from egg remains. *Bird Study,* 34: 87-91.

Greenwood, O., Mossman, H.L., Suggitt, A.J., Curtis, R.J. & Maclean, I.M. (2016) Using *in situ* management to conserve biodiversity under climate change. *Journal of Applied Ecology,* 53: 885-894.

Gregory, R.D. & van Strien, A. (2010) Wild bird indicators: using composite population trends of birds as measures of environmental health. *Ornithological Science,* 9: 3-22.

Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011) Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology,* 24: 699-711.

GWCT (2014) *Hints for using Larsen traps*. Game & Wildlife Conservation Trust, Fordingbridge, UK.

Hale, W.G. (1988) *The redshank*. Shire Publications Ltd, Aylesbury, UK.

Hale, W.G. & Ashcroft, R.P. (1983) Studies of the courtship behaviour of the Redshank *Tringa totanus*. *Ibis,* 125: 3-23.

Hallmann, C.A., Foppen, R.P., van Turnhout, C.A., de Kroon, H. & Jongejans, E. (2014) Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature,* 511: 341.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D. & de Kroon, H. (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE,* 12: e0185809.

Hanley, N., Banerjee, S., Lennox, G.D. & Armsworth, P.R. (2012) How should we incentivize private landowners to ‘produce’ more biodiversity? *Oxford Review of Economic Policy,* 28: 93-113.

Harris, S.J., Massimino, D., Gillings, S., Eaton, M.A., Noble, D.G., Balmer, D.E., Procter, D. & Pearce-Higgins, J.W. (2017) *The Breeding Bird Survey 2016*. British Trust for Ornithology, Thetford.

Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. (2011) Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology,* 80: 4-18.

Hasund, K.P. (2013) Indicator-based agri-environmental payments: A payment-by-result model for public goods with a Swedish application. *Land use policy,* 30: 223-233.

Hayhow, D., Bond, A., Douse, A., Eaton, M., Frost, T., Grice, P., Hall, C., Harris, S., Havery, S., Hearn, R., Noble, D., Oppel, S., Williams, J., Win, I. & Wotton, S. (2017) *The state of the UK’s birds 2016*. The RSPB, BTO, WWT, DAERA, JNCC, NE, NRW and SNH, Sandy, Bedfordshire.

Hein, L., Van Koppen, K., De Groot, R.S. & Van Ierland, E.C. (2006) Spatial scales, stakeholders and the valuation of ecosystem services. *Ecological Economics,* 57: 209-228.

Henderson, I.G., Wilson, A.M., Steele, D. & Vickery, J.A. (2002) Population estimates, trends and habitat associations of breeding Lapwing *Vanellus vanellus*, Curlew *Numenius arquata* and Snipe *Gallinago gallinago* in Northern Ireland in 1999. *Bird Study,* 49: 17-25.

Hönisch, B., Artmeyer, C., Melter, J. & Tüllinghoff, R. (2008) Telemetrische Untersuchungen an Küken vom Großen Brachvogel Numenius arquata und Kiebitz *Vanellus vanellus* im EU-Vogel-schutzgebiet Düsterdieker Niederung [In German with English summary]. *Vogelwarte,* 46: 39-48.

Hopkins, J., Allison, H., Walmsley, C., Gaywood, M. & Thurgate, G. (2007) *Conserving biodiversity in a changing climate: guidance on building capacity to adapt*. DEFRA, London.

Hughes, R.G. (2004) Climate change and loss of saltmarshes: consequences for birds. *Ibis,* 146: 21-28.

Huntley, B., Green, R.E., Collingham, Y.C. & Willis, S.G. (2007) *A climatic atlas of European breeding birds*. Durham University, The RSPB and Lynx Edicions, Barcelona.

Ibáñez-álamo, J.D., Sanllorente, O. & Soler, M. (2012) The impact of researcher disturbance on nest predation rates: a meta-analysis. *Ibis,* 154: 5-14.

IPCC (2014) *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switzerland.

Isaac, N., Brotherton, P., Bullock, J., Gregory, R.D., Boehning-Gaese, K., Connor, B., Crick, H.Q., Freckleton, R.P., Gill, J. & Hails, R. (2018) Defining and delivering resilient ecological networks: nature conservation in England. *Journal of Applied Ecology*.

Isaksson, D., Wallander, J. & Larsson, M. (2007) Managing predation on ground-nesting birds: The effectiveness of nest exclosures. *Biological Conservation,* 136: 136-142.

Jackson, D.B. (2001) Experimental removal of introduced hedgehogs improves wader nest success in the Western Isles, Scotland. *Journal of Applied Ecology,* 38: 802-812.

Jackson, D.B. & Green, R.E. (2000) The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (Charadrii) on machair in South Uist, Scotland. *Biological Conservation,* 93: 333-348.

Jenkins, G.J., Perry, M.C. & Prior, M.J. (2008) *The climate of the United Kingdom and recent trends*. Met Office Hadley Centre, Exeter, UK.

Jiguet, F., Godet, L. & Devictor, V. (2012) Hunting and the fate of French breeding waterbirds. *Bird Study,* 59: 474-482.

JNCC (2004) *Common Standards Monitoring Guidance for Saltmarsh Habitats*.

Joiner, C. (2002) Management of wet grassland for breeding waders: are wet features important for the Northern Lapwing, *Vanellus vanellus*? Unpublished MSc thesis, University of East Anglia.

Jones, K. (2014) Do optimal cattle grazing densities on saltmarsh habitat present breeding Redshank with an ecological trap? A study of nest trampling rates by cattle on The Wash, East Anglia. Unpublished MSc thesis, University of Reading.

Jones, L., Angus, S., Cooper, A., Doody, P., Everard, M., Garbutt, A., Gilchrist, P., Hansom, J., Nicholls, R., Pye, K., Ravenscroft, N., Rees, S., Rhind, P. & Whitehouse, A. (2011) Coastal Margins. In *UK National Ecosystem Assessment Technical Report*, pp. 411-615. UNEP-WCMC, Cambridge.

Junker, S., Düttmann, H. & Ehrnsberger, R. (2006) Schlupferfolg und Kükenmortalität beim Kiebitz (*Vanellus vanellus*) auf unterschiedlich gemanagten Grünlandflächen in der Stollhammer Wisch (Landkreis Wesermarsch, Niedersachsen) [In German with an English abstract]. *Osnabrücker Naturwissenschaftliche Mitteilungen,* 32: 111-122.

Junker, S., Krawczynski, R., Ehrnsberger, R. & Düttmann, H. (2004) Habitat use and chick mortality of radio-tagged Lapwings *Vanellus vanellus* and Black-tailed Godwits *Limosa limosa* in the Stollhammer Wisch, Lower Saxony. *Wader Study Group Bulletin,* 103: 14.

Kahlert, J., Clausen, P., Hounisen, J.P. & Petersen, I.K. (2007) Response of breeding waders to agri-environment schemes may be obscured by effects of existing hydrology and farming history. *Journal of Ornithology,* 148: 287-293.

Keenleyside, C., Radley, G., Tucker, G., Underwood, E., Hart, K., Allen, B. & Menadue, H. (2014) *Results-based payments for biodiversity guidance handbook: Designing and implementing results-based agri-environment schemes 2014-2020*. Prepared for the European Commission, DG Environment, Contract ENV.B.2/ETU/2013/0046, Institute for European Environmental Policy, London.

Keil, P., Biesmeijer, J.C., Barendregt, A., Reemer, M. & Kunin, W.E. (2011) Biodiversity change is scale-dependent: an example from Dutch and UK hoverflies (Diptera, Syrphidae). *Ecography,* 34: 392-401.

Kelly, B.C., Ikonomou, M.G., Blair, J.D., Morin, A.E. & Gobas, F.A. (2007) Food web–specific biomagnification of persistent organic pollutants. *Science,* 317: 236-239.

Kentie, R., Both, C., Hooijmeijer, J.C. & Piersma, T. (2015) Management of modern agricultural landscapes increases nest predation rates in Black-tailed Godwits *Limosa limosa*. *Ibis,* 157: 614-625.

Kleijn, D., Schekkerman, H., Dimmers, W.J., Van Kats, R.J., Melman, D. & Teunissen, W.A. (2010) Adverse effects of agricultural intensification and climate change on breeding habitat quality of Black-tailed Godwits *Limosa l. limosa* in the Netherlands. *Ibis,* 152: 475-486.

Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology,* 40: 947-969.

Kleijn, D. & vanZuijlen, G.J.C. (2004) The conservation effects of meadow bird agreements on farmland in Zeeland, The Netherlands, in the period 1989-1995. *Biological Conservation,* 117: 443-451.

Lagendijk, D.D.G., Howison, R.A., Esselink, P., Ubels, R. & Smit, C. (2017) Rotation grazing as a conservation management tool: Vegetation changes after six years of application in a salt marsh ecosystem. *Agriculture, Ecosystems & Environment,* 246: 361-366.

LaGrange, T.G., Hansen, J.L., Andrews, R.D., Hancock, A.W. & Kienzler, J.M. (1995) Electric fence predator exclosure to enhance duck nesting: A long-term case study in Iowa. *Wildlife Society Bulletin,* 23: 261-266.

Laidlaw, R.A., Gill, J.A. & Smart, J. (2015a) *Reducing the impacts of predation on breeding waders using landscape-scale habitat management. Defra Research Report on Project LM0301*. RSPB and University of East Anglia.

Laidlaw, R.A., Smart, J., Smart, M.A. & Gill, J.A. (2013) Managing a food web: impacts on small mammals of managing grasslands for breeding waders. *Animal Conservation,* 16: 207-215.

Laidlaw, R.A., Smart, J., Smart, M.A. & Gill, J.A. (2015b) The influence of landscape features on nest predation rates of grassland-breeding waders. *Ibis,* 157: 700-712.

Laidlaw, R.A., Smart, J., Smart, M.A. & Gill, J.A. (2016) Scenarios of habitat management options to reduce predator impacts on nesting waders. *Journal of Applied Ecology,* 54: 1219-1229.

Latham, R.M. (1952) The fox as a factor in the control of weasel populations. *The Journal of Wildlife Management,* 16: 516-517.

Lavine, M. (2014) Comment on Murtaugh. *Ecology,* 95: 642-645.

Lawton, J., Brotherton, P., Brown, V., Elphick, C., Fitter, A., Forshaw, J., Haddow, R., Hilborne, S., Leafe, R. & Mace, G. (2010) Making space for nature: A review of England's wildlife sites and ecological network. *Report to DEFRA*.

Lawton, J.H. (1994) Population dynamic principles. *Philosophical Transactions of the Royal Society of London Series B,* 344: 61-68.

Leigh, S., Smart, J. & Gill, J. (2016) Impacts of grassland management on wader nest predation rates in adjacent nature reserves. *Animal Conservation*.

Levin, S.A. (1992) The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. *Ecology,* 73: 1943-1967.

Leyrer, J., Brown, D., Gerritsen, G., Hötker, H. & Ottvall R. (compilers) (2018) *International multi-species action plan for the conservation of breeding waders in wet grassland habitats in Europe (2018-2028). Report of Action A13 under the framework of Project LIFE EuroSAP (LIFE14 PRE/UK/002)*. NABU, RSPB, VBN and SOF.

Lindenmayer, D., Hobbs, R.J., Montague-Drake, R., Alexandra, J., Bennett, A., Burgman, M., Cale, P., Calhoun, A., Cramer, V. & Cullen, P. (2008) A checklist for ecological management of landscapes for conservation. *Ecology Letters,* 11: 78-91.

MacDonald, M.A. & Bolton, M. (2008a) Predation of Lapwing *Vanellus vanellus* nests on lowland wet grassland in England and Wales: Effects of nest density, habitat and predator abundance. *Journal of Ornithology,* 149: 555-563.

MacDonald, M.A. & Bolton, M. (2008b) Predation on wader nests in Europe. *Ibis,* 150: 54-73.

Madsen, J. & Fox, A.D. (1995) Impacts of hunting disturbance on waterbirds-a review. *Wildlife Biology,* 1: 193-207.

Malpas, L. (2009) Breeding waders of lowland wet grassland and their predators: monitoring techniques, predator impacts and mesopredator-release interactions. Unpublished MSc thesis, University of Reading.

Mandema, F.S., Tinbergen, J.M., Ens, B.J., Koffijberg, K., Dijkema, K.S. & Bakker, J.P. (2015) Moderate livestock grazing of salt, and brackish marshes benefits breeding birds along the mainland coast of the Wadden Sea. *The Wilson Journal of Ornithology,* 127: 467-476.

Mason, L.R., Feather, A., Gill, J.A., Hoodless, A.N., Laidlaw, R.A. & Smart, J. (2016) *Reducing predation of breeding waders using landscape scale habitat management – adding value by informing agri-environment deployment. Defra Research Report on Extension to Project LM0301*. RSPB and University of East Anglia.

Mason, L.R., Green, R.E., Hirons, G., Skinner, A., Peault, S., Upcott, E., Wells, E., Wilding, D., Drewitt, A. & Smart, J. (in prep) Reducing red kite *Milvus milvus* predation of lowland wader chicks by diversionary feeding.

Mayer, P.M. & Ryan, M.R. (1991) Electric fences reduce mammalian predation on Piping Plover nests and chicks. *Wildlife Society Bulletin,* 19: 59-63.

Mayfield, H. (1961) Nesting success calculated from exposure. *Wilson Bulletin,* 73: 255-261.

Mayfield, H. (1975) Suggestions for calculating nest success. *Wilson Bulletin,* 87: 456-466.

McCracken, D. & Foster, G.N. (1993) The effect of ivermectin on the invertebrate fauna associated with cow dung. *Environmental Toxicology and Chemistry,* 12: 73-84.

McCracken, D. & Tallowin, J. (2004) Swards and structure: the interactions between farming practices and bird food resources in lowland grasslands. *Ibis,* 146: 108-114.

McOwen, C.J., Weatherdon, L.V., Bochove, J.-W.V., Sullivan, E., Blyth, S., Zockler, C., Stanwell-Smith, D., Kingston, N., Martin, C.S., Spalding, M. & Fletcher, S. (2017) A global map of saltmarshes. *Biodiversity Data Journal*: e11764.

Milsom, T., Hart, J., Parkin, W. & Peel, S. (2002) Management of coastal grazing marshes for breeding waders: the importance of surface topography and wetness. *Biological Conservation,* 103: 199-207.

Milsom, T.P. (2005) Decline of Northern Lapwing *Vanellus vanellus* breeding on arable farmland in relation to loss of spring tillage. *Bird Study,* 52: 297-306.

Milsom, T.P., Langton, S.D., Parkin, W.K., Peel, S., Bishop, J.D., Hart, J.D. & Moore, N.P. (2000) Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. *Journal of Applied Ecology,* 37: 706-727.

Morrison, C.A., Robinson, R.A., Butler, S.J., Clark, J.A. & Gill, J.A. (2016) Demographic drivers of decline and recovery in an Afro-Palaearctic migratory bird population. *Proceedings of the Royal Society of London, Series B: Biological Sciences,* 283: 20161387.

Moss, R., Watson, A. & Ollason, J. (1982) *Animal population dynamics*. Chapman and Hall, London.

Murphy, R.K., Greenwood, R.J., Ivan, J.S. & Smith, K.A. (2003a) Predator exclusion methods for managing endangered shorebirds: Are two barriers better than one? *Waterbirds,* 26: 156-159.

Murphy, R.K., Michaud, I.M.G., Prescott, D.R.C., Ivan, J.S., Anderson, B.J. & French-Pombier, M.L. (2003b) Predation on adult Piping Plovers at predator exclosure cages. *Waterbirds,* 26: 150-155.

Murtaugh, P.A. (2014a) In defense of P values. *Ecology,* 95: 611-617.

Murtaugh, P.A. (2014b) Rejoinder. *Ecology,* 95: 651-653.

Natural England (2011) *Illustrated guide to managing lowland wet grassland for snipe*. Natural England.

Natural England (2013) *Higher Level Stewardship: Environmental Stewardship handbook. Fourth Edition*. Natural England, UK.

Natural England (2016) *Countryside Stewardship: Higher tier options, supplements and capital items. Revised September 2017,* 3rd edn. Forestry Commission, DEFRA, Natural England, UK.

Natural England (2017a) *Results based agri-environment payment scheme (RBAPS). Arable pilot: Norfolk/Suffolk*. Available from https://www.gov.uk/government/publications/results-based-agri-environment-payment-scheme-rbaps-pilot-study-in-england accessed Sept 2018.

Natural England (2017b) *Results based agri-environment payment scheme (RBAPS). Grassland pilot: Wensleydale, Yorkshire Dales*. Available from https://www.gov.uk/government/publications/results-based-agri-environment-payment-scheme-rbaps-pilot-study-in-england accessed Sept 2018.

New, L.F., Buckland, S.T., Redpath, S. & Matthiopoulos, J. (2012) Modelling the impact of hen harrier management measures on a red grouse population in the UK. *Oikos,* 121: 1061-1072.

Nicholls, R.J., Hoozemans, F.M.J. & Marchand, M. (1999) Increasing flood risk and wetland losses due to global sea-level rise:regional and global analyses. *Global Environmental Change,* 9: 69-87.

Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W. & Ratcliffe, L.M. (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences,* 271: 59-64.

Norris, K., Brindley, E., Cook, T., Babbs, S., Forster Brown, C. & Yaxley, R. (1998) Is the density of redshank *Tringa totanus* nesting on saltmarshes in Great Britain declining due to changes in grazing management? *Journal of Applied Ecology,* 35: 621-634.

Norris, K., Cook, T., O'Dowd, B. & Durdin, C. (1997) The density of redshank *Tringa totanus* breeding on the salt-marshes of the Wash in relation to habitat and its grazing management. *Journal of Applied Ecology,* 34: 999-1013.

O'Brien, M. & Wilson, J. (2011) Population changes of breeding waders on farmland in relation to agri-environmental management. *Bird Study,* 58: 399-408.

Packham, J.R. & Willis, A.J. (1997) *Ecology of dunes, salt marsh and shingle*. Chapman and Hall, London.

Pauliny, A., Larsson, M. & Blomqvist, D. (2008) Nest predation management: Effects on reproductive success in endangered shorebirds. *The Journal of Wildlife Management,* 72: 1579-1583.

Pearce-Higgins, J.W. & Green, R.E. (2014) *Birds and climate change: impacts and conservation responses*. Cambridge University Press, Cambridge.

Piersma, T. (1986) Breeding waders in Europe. *Wader Study Group Bulletin,* 48: 92-93.

Pimentel, D. & Edwards, C.A. (1982) Pesticides and ecosystems. *Bioscience,* 32: 595-600.

Plum, N.M. & Filser, J. (2005) Floods and drought: response of earthworms and potworms (Oligochaeta: Lumbricidae, Enchytraeidae) to hydrological extremes in wet grassland. *Pedobiologia,* 49: 443-453.

Pontee, N. (2013) Defining coastal squeeze: A discussion. *Ocean & Coastal Management,* 84: 204-207.

Poole, D.W. & McKillop, I.G. (2002) Effectiveness of two types of electric fence for excluding the Red Fox (*Vulpes vulpes*). *Mammal Review,* 32: 51-57.

Posthumus, H., Rouquette, J., Morris, J., Gowing, D. & Hess, T. (2010) A framework for the assessment of ecosystem goods and services; a case study on lowland floodplains in England. *Ecological Economics,* 69: 1510-1523.

Ratcliffe, N., Schmitt, S.A. & Whiffen, M. (2005) Sink or swim? Viability of a godwit population in relation to flooding. *Journal of Applied Ecology,* 42: 834-843.

Redpath, S., Thirgood, S. & Leckie, F.M. (2001) Does supplementary feeding reduce predation of red grouse by hen harriers? *Journal of Applied Ecology,* 38: 1157-1168.

Rhymer, C.M., Robinson, R.A., Smart, J. & Whittingham, M.J. (2010) Can ecosystem services be integrated with conservation? A case study of breeding waders on grassland. *Ibis,* 152: 698-712.

Richards, S.A., Whittingham, M.J. & Stephens, P.A. (2011) Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology,* 65: 77-89.

Rickenbach, O., Grüebler, M.U., Schaub, M., Koller, A., Naef-Daenzer, B. & Schifferli, L. (2011) Exclusion of ground predators improves Northern Lapwing *Vanellus vanellus* chick survival. *Ibis,* 153: 531-542.

Rickert, C., Fichtner, A., Van Klink, R. & Bakker, J. (2012) α-and β-diversity in moth communities in salt marshes is driven by grazing management. *Biological Conservation,* 146: 24-31.

Ripple, W.J., Wolf, C., Newsome, T.M., Galetti, M., Alamgir, M., Crist, E., Mahmoud, M.I., Laurance, W.F. & 15364 scientist signatories from 184 countries (2017) World scientists' warning to humanity: A second notice. *Bioscience,* 67: 1026-1028.

Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters,* 12: 982-998.

Robinson, R.A., Morrison, C.A. & Baillie, S.R. (2014) Integrating demographic data: towards a framework for monitoring wildlife populations at large spatial scales. *Methods in Ecology and Evolution,* 5: 1361-1372.

Rockwood, L.L. (2015) *Introduction to population ecology*. Wiley Blackwell, Oxford, UK.

Rodwell, J.S. (2000) *British plant communities. Volume 5: Maritime communities and vegetation of open habitats*. Cambridge University Press, Cambridge.

Roodbergen, M., van der Werf, B. & Hötker, H. (2012) Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: review and meta-analysis. *Journal of Ornithology,* 153: 53-74.

Rook, A., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M., Parente, G. & Mills, J. (2004) Matching type of livestock to desired biodiversity outcomes in pastures – a review. *Biological Conservation,* 119: 137-150.

Rooney, E., Reid, N. & Montgomery, W.I. (2014) Supplementary feeding increases Common Buzzard *Buteo buteo* productivity but only in poor-quality habitat. *Ibis,* 157: 181-185.

RPA (2018) Countryside Stewardship and Environmental Stewardship inspection. https://www.gov.uk/guidance/environmental-stewardship-site-inspection-and-what-impact-it-has-on-your-agreement accessed April 2018.

RSPB (2005) *Wet grassland practical manual: breeding waders*. RSPB (The Royal Society for the Protection of Birds), Cumbria.

Rupprecht, F., Wanner, A., Stock, M. & Jensen, K. (2015) Succession in salt marshes – large-scale and long-term patterns after abandonment of grazing and drainage. *Applied Vegetation Science,* 18: 86-98.

Sánchez-Bayo, F. Impacts of agricultural pesticides on terrestrial ecosystems. *Ecological impacts of toxic chemicals,* 2011: 63-87.

Schaub, M. (2009) Evaluation of bias, precision and accuracy of mortality cause proportion estimators from ring recovery data. In *Modeling demographic processes in marked populations* (eds D.L. Thompson, E.G. Cooch & M.J. Conroy), pp. 1081-1097. Springer, New York.

Schekkerman, H., Teunissen, W. & Oosterveld, E. (2008) The effect of ‘mosaic management’ on the demography of black-tailed godwit *Limosa limosa* on farmland. *Journal of Applied Ecology,* 45: 1067–1075.

Schekkerman, H., Teunissen, W. & Oosterveld, E. (2009) Mortality of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* chicks in wet grasslands: Influence of predation and agriculture. *Journal of Ornithology,* 150: 133-145.

Schifferli, L., Rickenbach, O., Koller, K. & Grüebler, M. (2009) Massnahmen zur Förderung des Kiebitzes *Vanellus vanellus* im Wauwilermoos (Kanton Luzern): Schutz der Nester vor Landwirtschaft und Prädation [In German with an English summary: Nest protection from agriculture and predation to improve nest and chick survival of the Northern Lapwing *Vanellus vanellus* in Swiss farmland]. *Ornithologische Beobachter,* 106: 311-326.

Schneider, D.C. (2001) The Rise of the concept of scale in ecology: The concept of scale is evolving from verbal expression to quantitative expression. *Bioscience,* 51: 545-553.

Schoppenhorst, A. (2004) Breeding success and clutch loss of grassland birds in the wet grassland area of the Bremer Becken – initial results of the breeding season 2002. *Wader Study Group Bulletin,* 103: 15.

Secretariat of the Convention on Biological Diversity (2010) *Global Biodiversity Outlook 3*. Montreal.

Secretariat of the Convention on Biological Diversity (2011) *Strategic Plan for Biodiversity 2011–2020 and the Aichi Targets*. Montreal.

Sharpe, F., Bolton, M., Sheldon, R. & Ratcliffe, N. (2009) Effects of color banding, radio tagging, and repeated handling on the condition and survival of Lapwing chicks and consequences for estimates of breeding productivity. *Journal of Field Ornithology,* 80: 101-110.

Sharps, E., Garbutt, A., Hiddink, J.G., Smart, J. & Skov, M.W. (2016) Light grazing of saltmarshes increases the availability of nest sites for Common Redshank *Tringa totanus*, but reduces their quality. *Agriculture, Ecosystems & Environment,* 221: 71-78.

Sharps, E., Smart, J., Skov, M.W., Garbutt, A. & Hiddink, J.G. (2015) Light grazing of saltmarshes is a direct and indirect cause of nest failure in Common Redshank *Tringa totanus*. *Ibis,* 157: 234-249.

Sheldon, R. (2002) Factors affecting the distribution, abundance and chick survival of the Lapwing (*Vanellus vanellus*). PhD thesis, Harper Adams University College and RSPB.

Sheldon, R., Bolton, M., Gillings, S. & Wilson, A. (2004) Conservation management of Lapwing *Vanellus vanellus* on lowland arable farmland in the UK. *Ibis,* 146, Suppl. 2: 41-49.

Sheldon, R.D., Chaney, K. & Tyler, G.A. (2007) Factors affecting nest survival of Northern Lapwings *Vanellus vanellus* in arable farmland: an agri-environment scheme prescription can enhance nest survival. *Bird Study,* 54: 168-175.

Shrubb, M. (1990) Effects of agricultural change on nesting lapwings Vanellus vanellus in England and Wales. *Bird Study,* 37: 115-127.

Shrubb, M. (2007) *The Lapwing*. T&AD Poyser, London.

Siriwardena, G., Conway, G., Stanbury, A. & Eaton, M. (2018) *Breeding waders of english upland farmland (BWEUF): survey and data analysis for breeding waders on in-bye land. Report to Natural England*. BTO, RSPB, Thetford.

Smart, J. (2005) Strategies of sea-level rise mitigation for breeding redshank. PhD Thesis, University of East Anglia.

Smart, J. (2016) A question of scale – from nature reserves to landscape-scale conservation. *Wader Study,* 123: 81-83.

Smart, J. & Amar, A. (2018) Diversionary feeding as a means of reducing raptor predation at seabird breeding colonies. *Journal for Nature Conservation,* 46: 48-55.

Smart, J., Amar, A., O'Brien, M., Grice, P. & Smith, K. (2008) Changing land management of lowland wet grasslands of the UK: impacts on snipe abundance and habitat quality. *Animal Conservation,* 11: 339-351.

Smart, J., Bolton, M., Hunter, F., Quayle, H., Thomas, G. & Gregory, R.D. (2013) Managing uplands for biodiversity: Do agri-environment schemes deliver benefits for breeding lapwing *Vanellus vanellus*? *Journal of Applied Ecology,* 50: 794-804.

Smart, J. & Gill, J.A. (2003) Climate change and the potential impact on breeding waders in the UK. *Wader Study Group Bulletin,* 100: 80-85.

Smart, J., Gill, J.A., Sutherland, W.J. & Watkinson, A.R. (2006) Grassland-breeding waders: Identifying key habitat requirements for management. *Journal of Applied Ecology,* 43: 454-463.

Smart, J., Wotton, S.R., Dillon, I.A., Cooke, A.I., Diack, I., Drewitt, A.L., Grice, P.V. & Gregory, R.D. (2014) Synergies between site protection and agri-environment schemes for the conservation of waders on lowland wet grasslands. *Ibis,* 156: 576-590.

Smith, R.K., Pullin, A.S., Stewart, G.B. & Sutherland, W.J. (2011) Is nest predator exclusion an effective strategy for enhancing bird populations? *Biological Conservation,* 144: 1-10.

Spanos, A. (2014) Recurring controversies about P values and confidence intervals revisited. *Ecology,* 95: 645-651.

Stanton-Geddes, J., de Freitas, C.G. & de Sales Dambros, C. (2014) In defense of P values: comment on the statistical methods actually used by ecologists. *Ecology,* 95: 637-642.

Stephens, P.A. & Sutherland, W.J. (1999) Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology & Evolution,* 14: 401-405.

Sutherland, W.J. (1997) *From individual behaviour to population ecology*. Oxford University Press, Oxford.

Symonds, M.R. & Moussalli, A. (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology,* 65: 13-21.

Teunissen, W., Schekkerman, H., Willems, F. & Majoor, F. (2008) Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis,* 150: 74-85.

Thompson, J., Gavin, H., Refsgaard, A., Sørenson, H.R. & Gowing, D. (2009) Modelling the hydrological impacts of climate change on UK lowland wet grassland. *Wetlands Ecology and Management,* 17: 503-523.

Thompson, P.S. (1987) Further studies on the breeding biology of Redshank (*Tringa totanus* L.). PhD thesis, Liverpool Polytechnic.

Thompson, P.S., Baines, D., Coulson, J.C. & Longrigg, G. (1994) Age at first breeding, philopatry and breeding site-fidelity in the Lapwing *Vanellus vanellus*. *Ibis,* 136: 474-484.

Thompson, P.S. & Hale, W.G. (1989) Breeding site fidelity and natal philopatry in the Redshank *Tringa totanus*. *Ibis,* 131: 214-224.

Thyen, S., Exo, K.-M., Marencic, H., Oberdiek, N., Smart, J. & Stock, M. (2008) The role of coastal saltmarshes in the annual life-cycle of waders: outcomes of a workshop held in November 2004, Papenburg, Germany. *Wader Study Group Bulletin,* 115: 98-101.

Tichit, M., Renault, O. & Potter, T. (2005) Grazing regime as a tool to assess positive side effects of livestock farming systems on wading birds. *Livestock Production Science,* 96: 109-117.

UK Biodiversity Steering Group (1998) Lowland meadows. In *Tranche 2 Action Plans: Volume 1 - Vertebrates and Vascular Plants* (ed. UK Biodiversity Steering Group), pp. 31-36. English Nature, Peterborough.

van de Pol, M., Ens, B.J., Heg, D., Brouwer, L., Krol, J., Maier, M., Exo, K.M., Oosterbeek, K., Lok, T., Eising, C.M. & Koffijberg, K. (2010) Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *Journal of Applied Ecology,* 47: 720-730.

van Klink, R., Nolte, S., Mandema, F.S., Lagendijk, D.G., WallisDeVries, M.F., Bakker, J.P., Esselink, P. & Smit, C. (2016) Effects of grazing management on biodiversity across trophic levels – The importance of livestock species and stocking density in salt marshes. *Agriculture, Ecosystems & Environment,* 235: 329-339.

Vickery, J., Sutherland, W., O'brien, M., Watkinson, A. & Yallop, A. (1997) Managing coastal grazing marshes for breeding waders and over wintering geese: Is there a conflict? *Biological Conservation,* 79: 23-34.

Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J. & Brown, V.K. (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology,* 38: 647-664.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S. & Holmes, R.T. (2002) Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution,* 17: 76-83.

Wernham, C.V., Toms, M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R. (2002) *The Migration Atlas: movements of the birds of Britain and Ireland*. Poyser, London.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology,* 3: 385-397.

Wilcox, B.A. & Murphy, D.D. (1985) Conservation strategy: the effects of fragmentation on extinction. *The American Naturalist,* 125: 879-887.

Williams, G. & Hall, M. (1987) The loss of coastal grazing marshes in South and East England, with special reference to East Essex, England. *Biological Conservation,* 39: 243-253.

Wilson, A., Vickery, J. & Pendlebury, C. (2007) Agri-environment schemes as a tool for reversing declining populations of grassland waders: Mixed benefits from Environmentally Sensitive Areas in England. *Biological Conservation,* 136: 128-135.

Wilson, A.M., Vickery, J.A. & Browne, S.J. (2001) Numbers and distrubition of Northern Lapwings *Vanellus vanellus* breeding in England and Wales in 1998. *Bird Study,* 48: 2-17.

Wilson, A.M., Vickery, J.A., Langston, R.H.W., Smallshire, D., Wotton, S. & Vanhinsbergh, D. (2005) Changes in the numbers of breeding waders on lowland wet grasslands in England and Wales between 1982 and 2002. *Bird Study,* 52: 55-69.

Yates, B.J. (1982) A population biology of breeding redshanks (*Tringa totanus* L.). PhD thesis, Liverpool Polytechnic.

Zámečník, V., Kubelka, V. & Šálek, M. (2018) Visible marking of wader nests to avoid damage by farmers does not increase nest predation. *Bird Conservation International,* 28: 293-301.

# Common Abbreviations

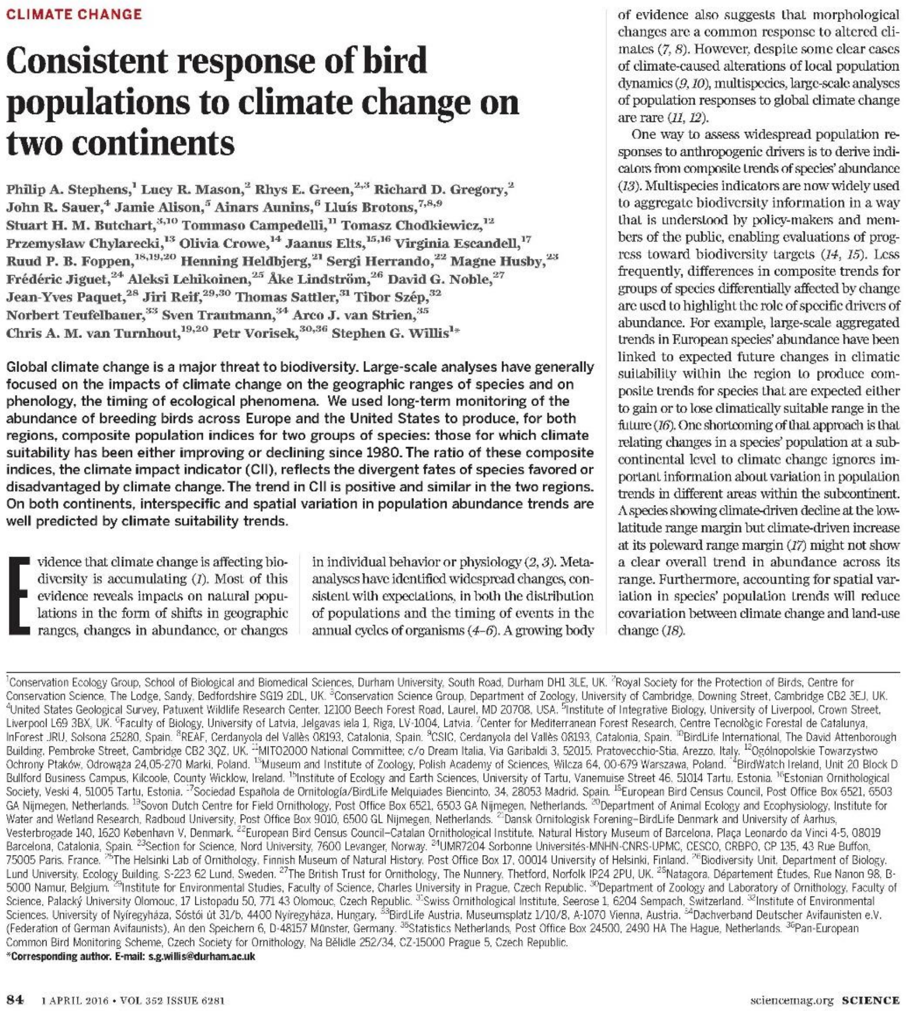
| | |
|---|---|
| AES | Agri-Environment Scheme |
| RSPB | The Royal Society for the Protection of Birds |

# PAPER I

# Consistent response of bird populations to climate change on two continents

Stephens, P.A., **Mason, L.R.**, Green, R.E., Gregory, R.D., Sauer, J.R., Alison, J., Aunins, A., Brotons, L., Butchart, S.H.M., Campedelli, T., Chodkiewicz, T., Chylarecki, P., Crowe, O., Elts, J., Escandell, V., Foppen, R.P.B., Heldbjerg, H., Herrando, S., Husby, M., Jiguet, F., Lehikoinen, A., Lindström, Å., Noble, D.G., Paquet, J.-Y., Reif, J., Sattler, T., Szép, T., Teufelbauer, N., Trautmann, S., van Strien, A.J., van Turnhout, C.A.M., Vorisek, P. & Willis, S.G.

*Science* (2016), **352**: 84–87. http://doi.org/10.1126/science.aac4858



CLIMATE CHANGE

## Consistent response of bird populations to climate change on two continents

**Philip A. Stephens,[1] Lucy R. Mason,[2] Rhys E. Green,[2,3] Richard D. Gregory,[2] John R. Sauer,[4] Jamie Alison,[5] Ainars Aunins,[6] Lluís Brotons,[7,8,9] Stuart H. M. Butchart,[3,10] Tommaso Campedelli,[11] Tomasz Chodkiewicz,[12] Przemysław Chylarecki,[13] Olivia Crowe,[14] Jaanus Elts,[15,16] Virginia Escandell,[17] Ruud P. B. Foppen,[18,19,20] Henning Heldbjerg,[21] Sergi Herrando,[22] Magne Husby,[23] Frédéric Jiguet,[24] Aleksi Lehikoinen,[25] Åke Lindström,[26] David G. Noble,[27] Jean-Yves Paquet,[28] Jiri Reif,[29,30] Thomas Sattler,[31] Tibor Szép,[32] Norbert Teufelbauer,[33] Sven Trautmann,[34] Arco J. van Strien,[35] Chris A. M. van Turnhout,[19,20] Petr Vorisek,[30,36] Stephen G. Willis[1]***

Global climate change is a major threat to biodiversity. Large-scale analyses have generally focused on the impacts of climate change on the geographic ranges of species and on phenology, the timing of ecological phenomena. We used long-term monitoring of the abundance of breeding birds across Europe and the United States to produce, for both regions, composite population indices for two groups of species: those for which climate suitability has been either improving or declining since 1980. The ratio of these composite indices, the climate impact indicator (CII), reflects the divergent fates of species favored or disadvantaged by climate change. The trend in CII is positive and similar in the two regions. On both continents, interspecific and spatial variation in population abundance trends are well predicted by climate suitability trends.

Evidence that climate change is affecting biodiversity is accumulating (*1*). Most of this evidence reveals impacts on natural populations in the form of shifts in geographic ranges, changes in abundance, or changes in individual behavior or physiology (*2*, *3*). Meta-analyses have identified widespread changes, consistent with expectations, in both the distribution of populations and the timing of events in the annual cycles of organisms (*4*–*6*). A growing body of evidence also suggests that morphological changes are a common response to altered climates (*7*, *8*). However, despite some clear cases of climate-caused alterations of local population dynamics (*9*, *10*), multispecies, large-scale analyses of population responses to global climate change are rare (*11*, *12*).

One way to assess widespread population responses to anthropogenic drivers is to derive indicators from composite trends of species' abundance (*13*). Multispecies indicators are now widely used to aggregate biodiversity information in a way that is understood by policy-makers and members of the public, enabling evaluations of progress toward biodiversity targets (*14*, *15*). Less frequently, differences in composite trends for groups of species differentially affected by change are used to highlight the role of specific drivers of abundance. For example, large-scale aggregated trends in European species' abundance have been linked to expected future changes in climatic suitability within the region to produce composite trends for species that are expected either to gain or to lose climatically suitable range in the future (*16*). One shortcoming of that approach is that relating changes in a species' population at a subcontinental level to climate change ignores important information about variation in population trends in different areas within the subcontinent. A species showing climate-driven decline at the low-latitude range margin but climate-driven increase at its poleward range margin (*17*) might not show a clear overall trend in abundance across its range. Furthermore, accounting for spatial variation in species' population trends will reduce covariation between climate change and land-use change (*18*).

---

[1]Conservation Ecology Group, School of Biological and Biomedical Sciences, Durham University, South Road, Durham DH1 3LE, UK. [2]Royal Society for the Protection of Birds, Centre for Conservation Science, The Lodge, Sandy, Bedfordshire SG19 2DL, UK. [3]Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK. [4]United States Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708, USA. [5]Institute of Integrative Biology, University of Liverpool, Crown Street, Liverpool L69 3BX, UK. [6]Faculty of Biology, University of Latvia, Jelgavas iela 1, Riga, LV-1004, Latvia. [7]Center for Mediterranean Forest Research, Centre Tecnològic Forestal de Catalunya, InForest JRU, Solsona 25280, Spain. [8]REAF, Cerdanyola del Vallès 08193, Catalonia, Spain. [9]CSIC, Cerdanyola del Vallès 08193, Catalonia, Spain. [10]BirdLife International, The David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK. [11]MITO2000 National Committee; c/o Dream Italia, Via Garibaldi 3, 52015, Pratovecchio-Stia, Arezzo, Italy. [12]Ogólnopolskie Towarzystwo Ochrony Ptaków, Odrowąża 24,05-270 Marki, Poland. [13]Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warszawa, Poland. [14]BirdWatch Ireland, Unit 20 Block D Bullford Business Campus, Kilcoole, County Wicklow, Ireland. [15]Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise Street 46, 51014 Tartu, Estonia. [16]Estonian Ornithological Society, Veski 4, 51005 Tartu, Estonia. [17]Sociedad Española de Ornitología/BirdLife Melquiades Biencinto, 34, 28053 Madrid, Spain. [18]European Bird Census Council, Post Office Box 6521, 6503 GA Nijmegen, Netherlands. [19]Sovon Dutch Centre for Field Ornithology, Post Office Box 6521, 6503 GA Nijmegen, Netherlands. [20]Department of Animal Ecology and Ecophysiology, Institute for Water and Wetland Research, Radboud University, Post Office Box 9010, 6500 GL Nijmegen, Netherlands. [21]Dansk Ornitologisk Forening–BirdLife Denmark and University of Aarhus, Vesterbrogade 140, 1620 København V, Denmark. [22]European Bird Census Council–Catalan Ornithological Institute, Natural History Museum of Barcelona, Plaça Leonardo da Vinci 4-5, 08019 Barcelona, Catalonia, Spain. [23]Section for Science, Nord University, 7600 Levanger, Norway. [24]UMR7204 Sorbonne Universités-MNHN-CNRS-UPMC, CESCO, CRBPO, CP 135, 43 Rue Buffon, 75005 Paris, France. [25]The Helsinki Lab of Ornithology, Finnish Museum of Natural History, Post Office Box 17, 00014 University of Helsinki, Finland. [26]Biodiversity Unit, Department of Biology, Lund University, Ecology Building, S-223 62 Lund, Sweden. [27]The British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK. [28]Natagora, Département Études, Rue Nanon 98, B-5000 Namur, Belgium. [29]Institute for Environmental Studies, Faculty of Science, Charles University in Prague, Czech Republic. [30]Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacký University Olomouc, 17 Listopadu 50, 771 43 Olomouc, Czech Republic. [31]Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland. [32]Institute of Environmental Sciences, University of Nyíregyháza, Sóstói út 31/b, 4400 Nyíregyháza, Hungary. [33]BirdLife Austria, Museumsplatz 1/10/8, A-1070 Vienna, Austria. [34]Dachverband Deutscher Avifaunisten e.V. (Federation of German Avifaunists), An den Speichern 6, D-48157 Münster, Germany. [35]Statistics Netherlands, Post Office Box 24500, 2490 HA The Hague, Netherlands. [36]Pan-European Common Bird Monitoring Scheme, Czech Society for Ornithology, Na Bělidle 252/34, CZ-15000 Prague 5, Czech Republic.

***Corresponding author. E-mail: s.g.willis@durham.ac.uk**

**84** 1 APRIL 2016 • VOL 352 ISSUE 6281 sciencemag.org **SCIENCE**

Science AAAS

# Title: Consistent response of bird populations to climate change on two continents

**Authors:** Philip A. Stephens[1], Lucy R. Mason[2], Rhys E. Green[2,3], Richard D. Gregory[2], John R. Sauer[4], Jamie Alison[5], Ainars Aunins[6], Lluís Brotons[7,8,9], Stuart H.M. Butchart[3,10], Tommaso Campedelli[11], Tomasz Chodkiewicz[12], Przemysław Chylarecki[13], Olivia Crowe[14], Jaanus Elts[15,16], Virginia Escandell[17], Ruud P.B. Foppen[18,19,20], Henning Heldbjerg[21], Sergi Herrando[22], Magne Husby[23], Frédéric Jiguet[24], Aleksi Lehikoinen[25], Åke Lindström[26], David G. Noble[27], Jean-Yves Paquet[28], Jiri Reif[29,30], Thomas Sattler[31], Tibor Szép[32], Norbert Teufelbauer[33], Sven Trautmann[34], Arco J. van Strien[35], Chris A.M. van Turnhout[19,20], Petr Vorisek[30,36], Stephen G. Willis[1]*

**Affiliations:**

1 Conservation Ecology Group, School of Biological & Biomedical Sciences, Durham University, South Road, Durham, DH1 3LE, UK.

2 RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire SG19 2DL, UK.

3 Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK.

4 United States Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708, USA.

5 Institute of Integrative Biology, University of Liverpool, Crown Street, Liverpool, L69 3BX, UK.

6 Faculty of Biology, University of Latvia, Jelgavas iela 1, Riga, LV-1004, LATVIA.

7 CEMFOR-CTFC, InForest JRU, Solsona 25280, Spain.

8 CREAF, Cerdanyola del Vallès 08193, Catalonia, Spain

9 CSIC, Cerdanyola del Vallès 08193, Catalonia, Spain

10 BirdLife International, The David Attenborough Building, Pembroke Street, Cambridge, CB2 3QZ, UK.

11 MITO2000 National Committee; c/o Dream Italia, Via Garibaldi 3, 52015, Pratovecchio-Stia, Arezzo, Italy.

12 Ogólnopolskie Towarzystwo Ochrony Ptaków, Odrowąża 24,05-270 Marki, Poland.

13 Museum & Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warszawa, Poland.

14 BirdWatch Ireland, Unit 20 Block D Bullford Business Campus, Kilcoole, Co. Wicklow, Ireland.

15 Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise St. 46, 51014 Tartu, Estonia.

16 Estonian Ornithological Society, Veski 4, 51005 Tartu, Estonia.

17 SEO/BirdLife. Melquiades Biencinto, 34. 28053 Madrid. Spain.

18 European Bird Census Council PO Box 6521 6503 GA Nijmegen, The Netherlands.

19 Sovon Dutch Centre for Field Ornithology PO Box 6521 6503 GA Nijmegen, The Netherlands

20 Department of Animal Ecology & Ecophysiology, Institute for Water and Wetland Research, Radboud University, PO Box 9010, 6500 GL Nijmegen, The Netherlands.

21 DOF - BirdLife Denmark & University of Aarhus, Vesterbrogade 140, 1620 København V, Denmark.

22 European Bird Census Council-Catalan Ornithological Institute. Natural History Museum of Barcelona. Plaça Leonardo da Vinci 4-5, 08019 Barcelona, Catalonia, Spain.

23 Nord University, Section for Science, 7600 Levanger, Norway.

24 UMR7204 Sorbonne Universités-MNHN-CNRS-UPMC, CESCO, CRBPO, CP 135, 43 Rue Buffon, 75005 Paris, France.

25 The Helsinki Lab of Ornithology, Finnish Museum of Natural History, P.O. Box 17, 00014 University of Helsinki, Finland.

26 Department of Biology, Biodiversity unit, Lund University, Ecology Building, S-223 62 Lund, Sweden.

27 The British Trust for Ornithology, The Nunnery, Thetford, Norfolk, UIK, IP24 2PU.

28 Natagora, Département Études, Rue Nanon 98, B-5000 Namur, Belgium.

29 Institute for Environmental Studies, Faculty of Science, Charles University in Prague, Czech Republic.

30 Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacký University Olomouc, 17. listopadu 50, 771 43 Olomouc, Czech Republic.

31 Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland.

32 Institute of Environmental Sciences, University of Nyíregyháza, Sóstói út 31/b, 4400 Nyíregyháza, Hungary.

33 BirdLife Austria, Museumsplatz 1/10/8, A-1070 Vienna, Austria.

34 Dachverband Deutscher Avifaunisten e.V. (Federation of German Avifaunists), An den Speichern 6, D-48157 Münster/Germany.

35 Statistics Netherlands, P.O. Box 24500, 2490 HA The Hague, The Netherlands.

36 Pan-European Common Bird Monitoring Scheme, Czech Society for Ornithology, Na Bělidle 252/34, CZ-15000 Prague 5, Czech Republic.

*Correspondence to: s.g.willis@durham.ac.uk

**Abstract:** Global climate change is a major threat to biodiversity. Large-scale analyses have generally focused on the impacts of climate change on the geographic ranges of species, and on phenology, the timing of ecological phenomena. Here, we use long-term monitoring of the abundance of breeding birds across Europe and the USA to produce, for both regions, composite population indices for two groups of species: those for which climate suitability has been either improving or declining since 1980. The ratio of these composite indices, the Climate Impact Indicator (CII), reflects the divergent fates of species favored or disadvantaged by climate change. The trend in CII is positive and similar in the two regions. On both continents, interspecific and spatial variation in population abundance trends are well predicted by climate suitability trends.

**One Sentence Summary:** Common birds across Europe and the USA have been similarly affected by climate change over the last 30 years.

## Main Text:

Evidence that climate change is impacting biodiversity is accumulating (*1*). Most of this evidence reveals impacts on natural populations in the form of shifts in geographic ranges, changes in abundance, or changes in individual behavior or physiology (*2, 3*). Meta-analyses have identified widespread changes, consistent with expectations, in both the distribution of populations and the timing of events in the annual cycles of organisms (*4-6*). A growing body of evidence also suggests that morphological changes are a common response to altered climates (*7, 8*). However, despite some clear cases of climate-caused alterations of local population dynamics (*9, 10*), multi-species, large-scale analyses of population responses to global climate change are rare (*11, 12*).

One way to assess widespread population responses to anthropogenic drivers is to derive indicators from composite trends of species' abundance (*13*). Multi-species indicators are now widely used to aggregate biodiversity information in a way that is understood by policy makers and members of the public, enabling evaluations of progress towards biodiversity targets (*14, 15*). Less frequently, differences in composite trends for groups of species differentially affected by change are used to highlight the role of specific drivers of abundance. For example, large-scale aggregated trends in European species' abundance have been linked to expected future changes in climatic suitability within the region to produce composite trends for species expected either to gain or to lose climatically suitable range in the future (*16*). One shortcoming of that approach is that relating changes in a species' population at a sub-continental level to climate change ignores important information about variation in population trends in different areas within the sub-continent. A species showing climate-driven decline at the low-latitude range margin but climate-driven increase at its poleward range margin (*17*) might not show a clear overall trend in abundance across its range. Furthermore, accounting for spatial variation in species' population trends will reduce covariation between climate change and land use change (*18*).

Here, we develop an indicator to quantify the impacts of recent climate change on breeding range abundance in common birds, accounting for regional variation in both climate impacts and population trends. We apply this approach to two distinct sub-continents to evaluate, for the first time, how recent climate change has impacted large numbers of species over extensive biogeographical regions. Developing our indicator involves six steps, including: (1) selecting species abundance data for analysis; (2) fitting species' distribution models to species' occurrence data and concurrent long-term mean climate values for a single fixed time period, and applying those models to annual climate data to determine how climate suitability has changed for each species in each country or state within which it occurs; (3) checking that these climate suitability trends are informative predictors of abundance trends; (4) deriving composite multi-species abundance indices for each state or country, separately for species with positive climate suitability trends (hereafter, the CST+ group) and for those with negative climate suitability trends (the CST- group); (5) amalgamating country or state-level information to produce sub-continental CST+ and CST- indices; and (6) contrasting the CST+ and CST- indices to produce a climate impact indicator (CII), which reflects the divergent fates of species favored and disadvantaged by climate change.

For Europe, we assess indices of abundance for 145 species monitored by the Pan-European Common Birds Monitoring Scheme (*15*). For the USA, we use indices of abundance for 380 species monitored by the North American Breeding Bird Survey (BBS) (*19*). In both cases, we use data spanning the period from 1980 to 2010. To account for regional variation in climate impacts and species' trends, we used species' distribution models to identify the climate suitability trend for each species at the level of individual countries within Europe, or states within the USA. The species' distribution models allow the calculation of probability of occurrence of the species under a particular combination of climatic conditions, represented by bioclimate variables (*20*), using species' distribution maps and concurrent long-term mean climate data. The climate suitability trend for a species represents the trend in its expected annual probability of occurrence, as derived from species' distribution models applied to annual climate data (*20*). Importantly, these climate suitability trends are derived entirely independently of interannual changes in abundance within a focal species' range. We used linear mixed models to check that climate suitability trend was an informative explanatory variable for country- or state-level population trend, when potential confounding effects of life history and ecological covariates were allowed for (Fig. 1).

We allocated species at a country/state level to two groups: those expected from the species' distribution models to have been advantaged (climate suitability trend slope >0) or disadvantaged (climate suitability trend slope <0) by climate change during the study period (the CST+ and

CST- groups). We derived composite population indices for both groups at the individual country or state level (see Tables S1 and S2 for sample sizes in Europe and the USA, respectively). Individual species may occur in either group in different parts of their range. Within countries or states, composite population indices were derived by weighting abundance indices by the magnitude of species' climate suitability trends within CST+ and CST- groups (*20*). The result is that changes in populations of species that we expect (from species' distribution models) to be markedly affected by climate change would receive more weight in the composite index than would those of species for which climate suitability trend was negligible. To produce sub-continental scale composite indices for CST+ and CST- groups, composite indices for each group were combined without weighting (Fig. 2A,B) (*20*).

The ratio of these indices (CST+:CST-), the Climate Impact Indicator (CII, standardized to 100 in 1980), will be >100 in any year if populations expected to have been positively impacted by climate change have increased more or declined less than those expected to have been negatively affected. We derive sub-continental CII values separately for Europe and the USA (combining country/state CIIs respectively) (*20*). Calculating CIIs for these geographically distinct sub-continents with very different breeding bird species assemblages allows us to examine the transferability of our approach. Plotting these CII values over time can demonstrate long-term trends in the response of species to climate. As recent climate change is likely to have manifested itself in different ways across the two sub-continents, a common trend in the magnitude and direction of the CII would provide compelling evidence that recent climate change is impacting populations of many species across extensive areas of the world.

Overall trajectories of avian abundance in recent decades differ somewhat between the two sub-continents, suggesting rather different ecological backdrops. Specifically, the average trend of avian abundance in Europe has been largely negative since 1980 (*21*) whereas the average trend of avian abundance in the USA has been relatively stable over recent decades (*22*). This difference is reflected in the composite indices: whilst the CST+ group index has been largely static in Europe and the CST- group has declined, in the USA these groups have shown a pronounced increase (CST+) or remained stable (CST-). Nevertheless, in both regions, the CST+ and CST- indices show a striking divergence, in the expected direction, with the composite population indices of species in the former group being markedly more positive than those in the latter group.

The ratio of the CST+ to CST- composite indices amalgamated to the sub-continental scale gives the sub-continental CIIs (Fig. 2C,D). The CII for Europe is based on fewer species, fewer geographic sub-divisions and a less consistent duration of monitoring across the region. This results in it being more variable than that for the USA. Nevertheless, trends in the two CIIs show some striking similarities. In particular, both clearly deviate from a value of 100 (indicating the divergence of the CST+ and CST- groups) by the mid to late 1980s. Both then climb strongly to reach an index value of c. 140 by 2010, highlighting the markedly stronger performance of species in the CST+ group. An analysis of standardized climate variables over the period shows no evidence for differences in the rate or scale of climate change in the two regions (Fig. 3) (*20*).

The strength and consistency of the CII across two very different assemblages (only six species are common to both), which appear to be experiencing very different overall population trends, provides striking evidence that this phenomenon is not peculiar to a single sub-continent. Isolating the contribution of climate change on the two sub-continents from that of other potential drivers of avian population change should stimulate further research into the factors that underlie the strong differences between the USA and Europe in the trajectories of composite multispecies trends (both CST+ and CST-) (Fig. 2A,B). In both areas, the CII is more strongly positive than a previous index for Europe that linked multi-species trends in population size at a sub-continental level to the expected future effects of climate change (*16*). This emphasizes the value of using geographic variation of species' trends within the range and allowing a species to contribute to both the CST+ and CST- groups, according to differences in the suitability trend in different areas.

The widespread changes that we detect are based on the commonest bird species across a diversity of ecosystems in Europe and the USA. For example, the 145 European species we consider comprise circa 89% of the total number of individual terrestrial breeding birds in Europe (*23*). Common species dominate ecosystems, and even small changes in their abundance can lead to large changes in ecosystem structure, function and service provision (*24*). Therefore, the changes that we have detected in common birds are already likely to be impacting ecosystems and associated services. If similar abundance changes are occurring across common species in other taxa, ecosystems may be further impacted. Impacts arising from changes in bird abundances will become more pronounced if their populations continue to follow their current, climate-influenced trajectories. Although our index is based on the abundance of common bird species, population trends of rare species have also been shown to be related to climatic changes (*25*). Our indicator could be applied wherever sufficient monitoring data exist. However, because long-term population monitoring datasets are rare for large tropical and sub-tropical regions and for the southern hemisphere (*26*), we cannot evaluate whether the changes we have observed apply globally. Population monitoring at low latitudes and in the southern hemisphere should be a future priority to identify climate-driven changes that might be occurring in these areas.

Ecological indicators, including some indicators of climate change impacts, are already being used to monitor the global state of ecosystems (*13*). Our precursor CII (*16*), based on future climate projections, has been adopted as an indicator to assess progress towards achieving the UN Convention on Biological Diversity's Aichi biodiversity targets (*27*), as a metric of climate change impacts on terrestrial ecosystems. The new indicators we develop here provide a first means of assessing impacts of contemporary climate on the abundance of populations, and we have shown their utility across two large areas of the world. Future updates of the CII should provide a valuable means to track the extent of impact of future climate change on species.

**References and Notes:**

1. C. B. Field *et al.*, in *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. (Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2014), pp. 1-32.
2. M. M. Humphries, D. W. Thomas, J. R. Speakman, *Nature* **418**, 313 (Jul 18, 2002).
3. C. Bellard, C. Bertelsmeier, P. Leadley, W. Thuiller, F. Courchamp, *Ecology Letters* **15**, 365 (2012).
4. T. L. Root *et al.*, *Nature* **421**, 57 (Jan 2, 2003).
5. C. Parmesan, G. Yohe, *Nature* **421**, 37 (Jan 2, 2003).
6. I. C. Chen, J. K. Hill, R. Ohlemuller, D. B. Roy, C. D. Thomas, *Science* **333**, 1024 (Aug, 2011).
7. J. L. Gardner, A. Peters, M. R. Kearney, L. Joseph, R. Heinsohn, *Trends Ecol. Evol.* **26**, 285 (2011).
8. J. A. Sheridan, D. Bickford, *Nature Climate Change* **1**, 401 (2011).
9. A. Ozgul *et al.*, *Nature Climate Change* **466**, 482 (2010).
10. M. van de Pol *et al.*, *Ecology* **91**, 1192 (2010).
11. V. Devictor *et al.*, *Nature Climate Change* **2**, 121 (2012).
12. J. G. Illán *et al.*, *Glob. Change Biol.* **20**, 3351 (2014).
13. S. H. M. Butchart *et al.*, *Science* **328**, 1164 (May 28, 2010).
14. D. P. Tittensor *et al.*, *Science* **346**, 241 (Oct 10, 2014).
15. Biodiversity Indicators Partnership, *http://www.bipindicators.net/*, (2014).

16. R. D. Gregory *et al.*, *PLoS ONE* **4**, (Mar 4, 2009).
17. F. Jiguet *et al.*, *Proceedings Of the Royal Society B-Biological Sciences* **277**, 3601 (Dec 7, 2010).
18. M. Clavero, D. Villero, L. Brotons, *PLoS ONE* **6(4)**, e18581 (2011).
19. North American Breeding Bird Survey, *https://www.pwrc.usgs.gov/bbs/*, (2014).
20. See supplementary materials on Science Online.
21. EBCC, *http://www.ebcc.info/index.php?ID=510*, (2014).
22. J. R. Sauer, W. A. Link, *The Auk* **128**, 87 (2011).
23. BirdLife-International, *Birds in Europe: population estimates, trends and conservation status*. (BirdLife International, Cambridge, UK, 2004).
24. K. K. J. Gaston, R. A. R. Fuller, *Trends Ecol. Evol.* **23**, 14 (2008).
25. R. E. Green *et al.*, *Biology Letters* **4**, 599 (Oct 23, 2008).
26. WWF, "Living Planet report 2014: species and spaces, people and places" (2014).
27. Aichi Targets Passport, *http://www.bipindicators.net/resource/aichipassport*, (2014).
28. P. Voříšek, A. Klvaňová, S. Wotton, R.D. Gregory, *A best practice guide for wild bird monitoring schemes* (CSO/RSPB, 2008).
29. R.D. Gregory *et al. Phil Trans R Soc Lond B* **360**, 269 (2005).

30. R. J. Hijmans, S. E. Cameron, J. L. Parra, P. G. Jones, A. Jarvis, *Int. J. Climatol.* **25**, 1965 (Dec, 2005).
31. I. Harris, P. D. Jones, T. J. Osborn, D. H. Lister, *Int. J. Climatol.* **34**, 623 (2014).
32. I. C. Prentice *et al.*, *J. Biogeogr.* **19**, 117 (Mar, 1992).
33. J. M. Hagemeijer, M. J. Blair, *The EBCC atlas of European breeding birds: Their distribution and abundance*. (T & AD Poyser, London, 1997).
34. M. Barbet-Massin, W. Thuiller, F. Jiguet, *Ecography* **33**, 878 (Oct, 2010).
35. BirdLife-International, NatureServe, "Bird species distribution maps of the world. Version 3.0." (BirdLife International, Cambridge, UK and NatureServe, Arlington, USA, 2013).
36. R. Bagchi *et al.*, *Global Change Biology* **19**, 1236 (2013).
37. M. B. Araujo, R. G. Pearson, W. Thuiller, M. Erhard, *Glob. Change Biol.* **11**, 1504 (Sep, 2005).
38. A. M. Prasad, L. R. Iverson, A. Liaw, *Ecosystems* **9**, 181 (2006).
39. C. N. Meynard, J. F. Quinn, *J. Biogeogr.* **34**, 1455 (2007).
40. J. Elith, C. H. Graham, *Ecography* **32**, 66 (Feb, 2009).
41. J. Franklin, *Mapping species distributions*. (Cambridge University Press, Cambridge, 2009).
42. S. J. Wenger, J. D. Olden, *Methods in Ecology and Evolution* **3**, 260 (2012).
43. P. McCullagh, J. A. Nelder, *Generalized Linear models*. Monogrpahs on Statistics and Applied Probability (Chapman and Hall, London, UK, ed. Second Edition, 1989).
44. T. J. Hastie, R. Tibshirani, *Generalized Additive Models*. (Chapman and Hall, London, 1990).
45. S. N. Wood, *Generalized Additive Models: An Introduction with R*. (Chapman and Hall/CRC, Boca Raton, Florida, USA, 2006).
46. G. Ridgeway, *Generalized boosted regression models. Documentation on the R Package 'gbm', version 1.5-7*, (2006).
47. J. Elith, J. R. Leathwick, T. Hastie, *J. Anim. Ecol.* **77**, 802 (Jul, 2008).

48. D. R. Cutler, T. C. J. Edwards, K. H. Beard, A. Cutler, K. T. Hess, *Ecology* **88**, 2783 (2007).
49. L. Breiman, *Machine Learning* **45**, 5 (2001).
50. R. T. Moore, *blockTools: Blocking, Assignment, and Diagnosing Interference in Randomized Experiments. R package version 0.6-2*, (2015).
51. A. H. Fielding, J. F. Bell, *Environmental Conservation* **24**, 38 (1997).
52. R-Core-Team, Ed., *R: A language and environment for statistical computing*, (http://www.R-project.org/ Vienna, Austria, 2013).
53. S. Cramp, A. D. Simmons, C. M. Perrins, *Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palaearctic*. (Oxford University Press, 1977-1994), vol. 1-9.
54. BirdLife-International, in *World bird database http://www.birdlife.org/datazone/home*. (2014).
55. PECBMS, *http://www.ebcc.info/index.php?ID=491*, (2012).
56. BirdLife-International, *IUCN Red List for birds. http://www.birdlife.org*, (2013).
57. B. J. Speek, G. Speek, *Thieme's Vogeltrekatlas*. (Thieme & Cie, Zutphen, Netherlands, 1984).
58. G. Zink, F. Bairlein, *Der Zug Europäischer Singvögel: Atlas der Wiederfunde Beringter Vögel Band 1-3*. (Aula Verlag, Wiesbaden, Germany, 1987-1995).
59. C. V. Wernham *et al.*, *The Migration Atlas: movements of the birds of Britain and Ireland*. (Poyser, London, 2002).
60. F. Spina, S. Volponi, *Atlante della Migrazione degli Uccelli in Italia. Vol. 1-2*. (ISPRA – MATTM, Rome, Italy, 2008-2009).
61. A. Poole. (Cornell Laboratory of Ornithology, Ithaca, NY, 2005).
62. K. P. Burnham, D. R. Anderson, *Model selection and multimodel inference: a practical information-theoretic approach*. (Springer-Verlag, New York, USA., ed. 2nd Edition, 2002), pp. 488.
63. D. Bates, M. Maechler, *lme4: Linear mixed-effects models using S4 classes. http://CRAN.R-project.org/package=lme4*, (2009).
64. S.A.Richards. *J App. Ecol.* **45**, 218 (2008).

**Acknowledgments:** The climate suitability and population trend data for individual species at country/state level are provided as supplementarty material (Table S6) (*20*). Climate data are available from http://www.worldclim.org/. This work has been part-funded by the Royal Society for the Protection of Birds, the European Environment Agency, European Commission, and by Durham University's Grevillea Trust. We thank Anne Teller and Katarzyna Biała for support, Dr Martin Flade, Johannes Schwarz and Christoph Grüneberg for data provision, and Matthew Clement (USGS) and two anonymous referees for comments on an earlier draft.

**Fig. 1. Effect of climate suitability on bird population trends**. Standardised regression coefficient of population trend at a country/state level on CST (with 90% confidence intervals) for European (left two points) and USA breeding birds (right two points). Coefficients are from model averaging of multiple regression models (which consider body mass, habitat and migratory behaviour) of population trend on CST (filled circles), or from univariate models of population trend on CST (open circles) (*20*). All models contained the random effects of country/state and species.

**Fig. 2. Effect of climate on abundance trends of common birds.** Multi-species population indices for CST+ (▬) and CST- (▬) groups combined across all eligible countries of Europe (A) and states of the USA (B). Shaded polygons in each case indicate 90% confidence intervals (produced from 2,000 bootstrap replicates) (*20*). Annual values of the ratio of the CST+ index to the CST- index, the CII, are shown for Europe (C) and USA (D). In all four panels the index is arbitrarily set to 100 in 1980. Horizontal broken lines at index values of 100 show the expectation if there is no trend; in panels (C) and (D), these indicate the expectation if climatic suitability played no role and, thus, there was no difference in the composite trends for CST+ and CST- groups.

**Fig. 3. Recent changes in climate in Europe and the USA.** Changes in annual values of three measures of climate in the countries/states from which bird data were collected in Europe (A) and the USA (B): mean annual temperature (▬), mean temperature of the coldest month (▬) and growing degree days above 5°C (▬). Each variable is standardised to have zero mean and unit variance. Black lines show least squares regression fitted to the annual standardised values for all three variables combined. Analysis of covariance provided no support for different slopes for the three climate variables or differences between Europe and the USA.

Fig. 1

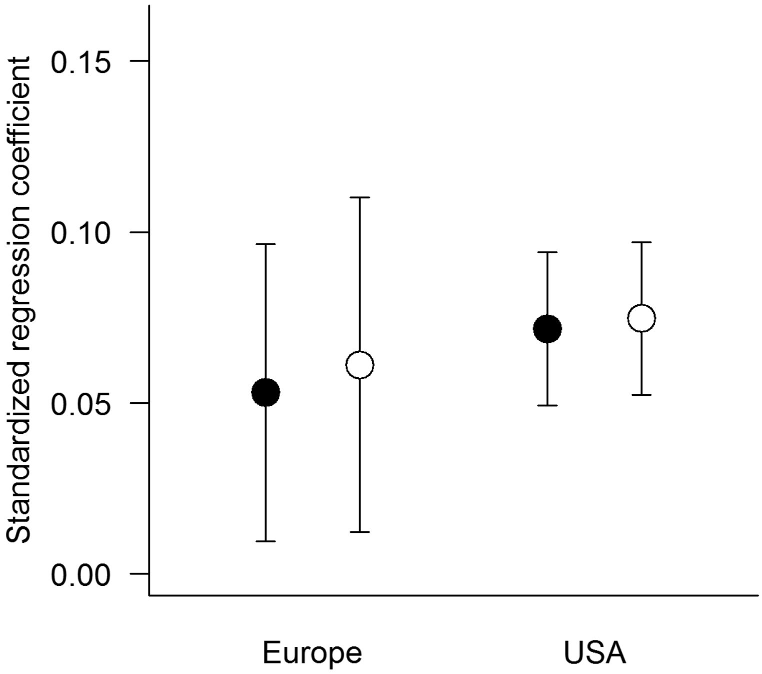

Standardized regression coefficient
0.15
0.10
0.05
0.00
Europe
USA

Fig. 2

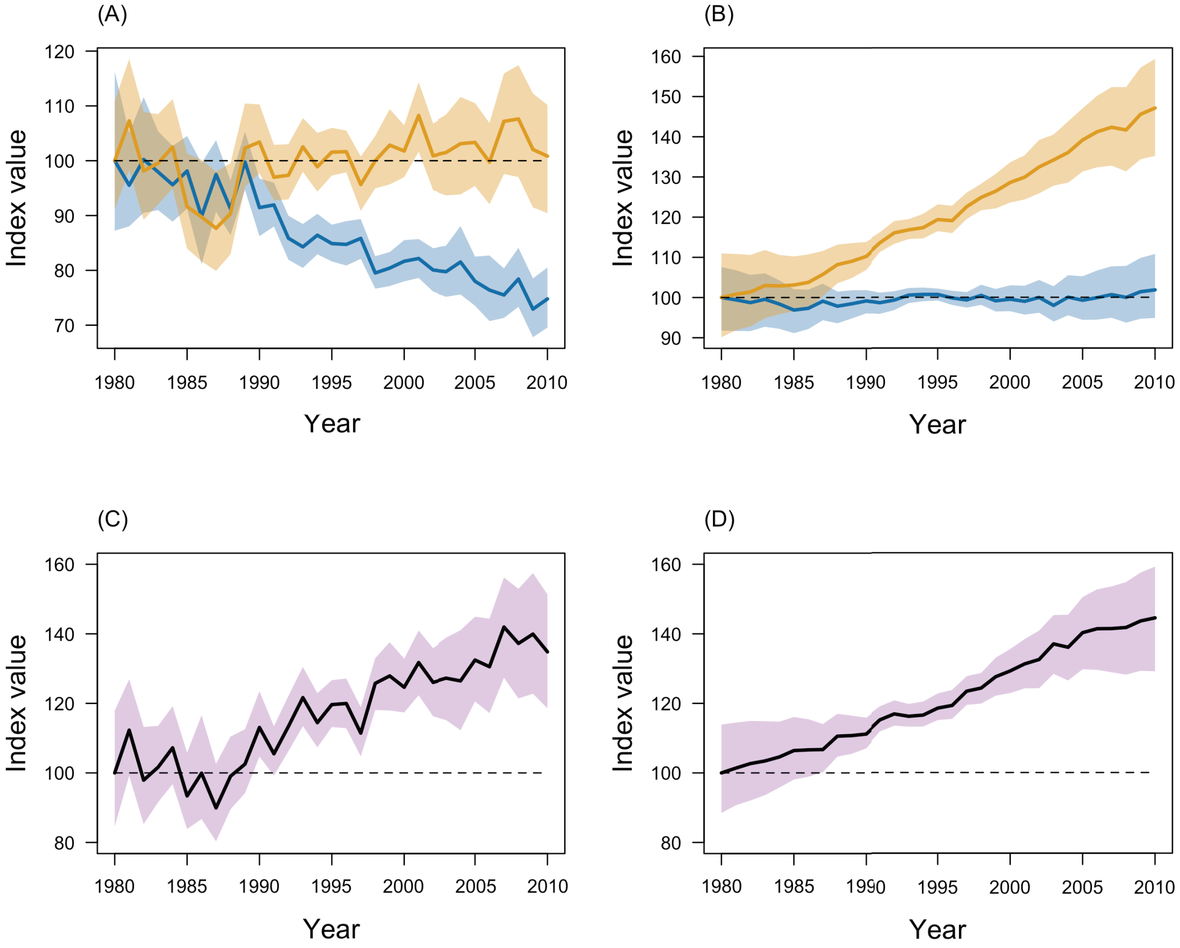
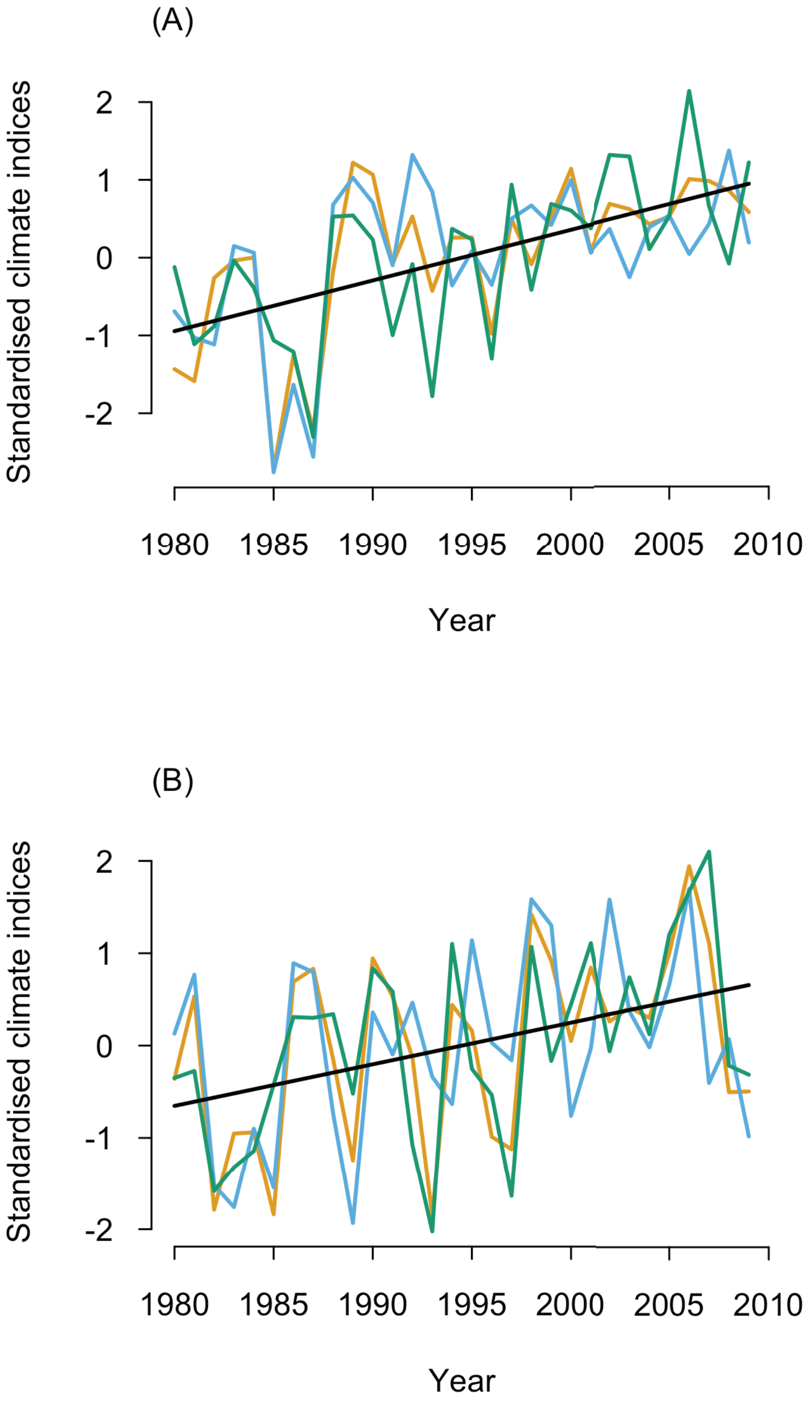

(A)
120
110
100
90
80
70
Index value
1980
1985
1990
1995
2000
2005
2010
Year
(B)
160
150
140
130
120
110
100
90
Index value
1980
1985
1990
1995
2000
2005
2010
Year
(C)
160
140
120
100
80
Index value
1980
1985
1990
1995
2000
2005
2010
Year
(D)
160
140
120
100
80
Index value
1980
1985
1990
1995
2000
2005
2010
Year

Fig. 3


(A)
Standardised climate indices
2
1
0
-1
-2
1980
1985
1990
1995
2000
2005
2010
Year
(B)
Standardised climate indices
2
1
0
-1
-2
1980
1985
1990
1995
2000
2005
2010
Year

# Supplementary Materials

Supplementary Materials for paper **I** are available online:

www.sciencemag.org/content/352/6281/84/suppl/DC1

Materials and Methods

Fig. S1

Tables S1 to S8

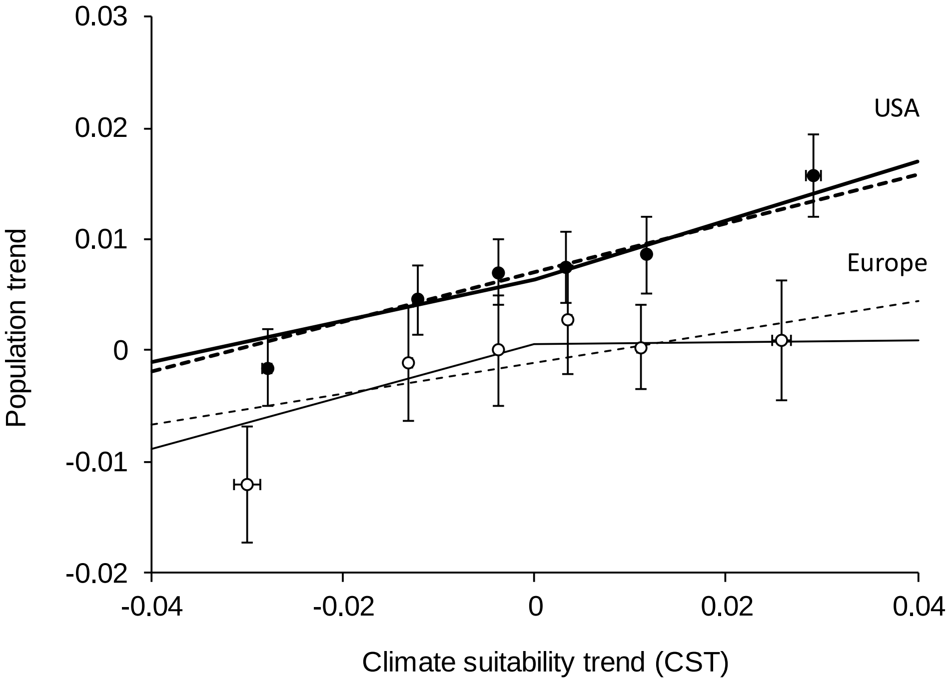
References (28–64)

# PAPER II

# Responses of bird populations to climate change on two continents vary with species' ecological traits but not with the direction of the change in climate suitability

**Mason, L.R.**, Green, R.E., Stephens, P.A., Willis, S.G., Aunins, A., Brotons, L., Chodkiewicz, T., Chylarecki, P., Escandell, V., Foppen, R.P.B., Herrando, S., Husby, M., Jiguet, F., Kålås, J.A., Lindström, Å., Massimino, D., Moshøj, C., Nellis, R., Paquet J.-Y., Reif, J., Sirkiä, P.M., Szép, T., Tellini Florenzano, G., Teufelbauer, N., Trautmann, S., van Strien, A., van Turnhout, C.A.M., Voříšek, P. & Gregory R.D.

Submitted to *Climatic Change*



# Responses of bird populations to climate change on two continents vary with species' ecological traits but not with the direction of the change in climate suitability

Short title: Bird population responses to climate change

Lucy R. Mason[1, †], Rhys E. Green[1, 2, †], Philip A. Stephens[3, †], Stephen G. Willis[3, †], Ainars Aunins[4, 5], Lluís Brotons[6, 7, 8, 9], Tomasz Chodkiewicz[10, 11], Przemysław Chylarecki[10], Virginia Escandell[12], Ruud P. B. Foppen[13, 14, 15], Sergi Herrando[6, 7], Magne Husby[16, 17], Frédéric Jiguet[18], John Atle Kålås[19], Åke Lindström[20], Dario Massimino[21], Charlotte Moshøj[22], Renno Nellis[23], Jean-Yves Paquet[24], Jiří Reif[25], Päivi M. Sirkiä[26], Tibor Szép[27], Guido Tellini Florenzano[28], Norbert Teufelbauer[29], Sven Trautmann[30], Arco van Strien[31], Chris A. M. van Turnhout[13, 14], Petr Voříšek[32, 33], Richard D. Gregory[1, 34, †]*

* Corresponding author: Richard D. Gregory, 01767 693049, richard.gregory@rspb.org.uk
† These authors contributed equally.

1 RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire SG19 2DL, UK.
2 Conservation Science Group, Department of Zoology, University of Cambridge, David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK.
3 Conservation Ecology Group, Department of Biosciences, Durham University, South Road, Durham, DH1 3LE, UK.
4 Faculty of Biology, University of Latvia, Jelgavas iela 1, Riga, LV-1004, Latvia.
5 Latvian Ornithological Society, Skolas iela 3, Riga, LV-1010, Latvia.
6 Catalan Ornithological Institute, Natural History Museum of Barcelona, Plaça Leonardo da Vinci 4–5, 08019, Barcelona, Catalonia, Spain.
7 CREAF, 08193 Cerdanyola del Vallès, Spain.
8 InForest Jru (CTFC-CREAF), Crta. Antiga St Llorenç de Morunys km 2, 25280, Solsona, Catalonia, Spain.
9 CSIC, Cerdanyola del Vallès, Spain.
10 Museum & Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warszawa, Poland.
11 Polish Society for the Protection of Birds, Odrowąża 24, 05-270 Marki, Poland.

12 Sociedad Española de Ornitología/BirdLife Melquiades Biencinto, 34, 28053 Madrid. Spain.
13 Sovon Dutch Centre for Field Ornithology, 6503, Nijmegen, The Netherlands.
14 Department of Animal Ecology and Ecophysiology, Institute for Water and Wetland Research, Radboud University, 6500, Nijmegen, The Netherlands.
15 European Bird Census Council, Post Office Box 6521, 6503, GA Nijmegen, Netherlands.
16 Nord University, Røstad, 7600 Levanger, Norway.
17 BirdLife Norway, Sandgata 30B, 7012 Trondheim, Norway.
18 MNHN, CRBPO, UMR7204 CESCO, Equipe Conservation et Restauration des Populations (CORPO), 43 rue Buffon, 75005, Paris, France.
19 Norwegian Institute for Nature Research, P.O.Box 5685 Torgarden, NO-7485 Trondheim, Norway.
20 Biodiversity Unit, Department of Biology, Lund University, S-223 62 Lund, Sweden.
21 British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK.
22 Dansk Ornitologisk Forening (BirdLife Denmark), Vesterbrogade 140, 1620 Copenhagen V, Denmark.
23 Estonian Ornithological Society, Birdlife Estonia, Veski 4, Tartu, Estonia.
24 Natagora, Département Études, Traverse des Muses 1, B-5000 Namur, Belgium.
25 Institute for Environmental Studies, Faculty of Science, Charles University, Prague, Benatska 2, 128 01 Praha 2, Czech Republic.
26 Zoology unit, Finnish Museum of Natural History, University of Helsinki, FI-00014 Finland.
27 Institute of Environmental Sciences, University of Nyíregyháza, Nyíregyháza, Sóstói út 31/b, 4401, Hungary.
28 Dream Italia, via R. Scoti 30, I-52011 Bibbiena (AR), Italy.
29 BirdLife Österreich, Museumsplatz 1/10/7-8, A-1070 Vienna, Austria.
30 Dachverband Deutscher Avifaunisten e.V. (Federation of German Avifaunists), An den Speichern 6, D-48157 Münster, Germany.
31 Statistics Netherlands, Post Office Box 24500, 2490 HA The Hague, Netherlands.
32 Pan-European Common Bird Monitoring Scheme, Czech Society for Ornithology, Na Bělidle 34, CZ-150 00 Prague 5, Czech Republic.
33 Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacký University in Olomouc, 17. listopadu 50, 771 43 Olomouc, Czech Republic.

34 Centre for Biodiversity & Environment Research, Department of Genetics, Evolution and Environment, University College London, Darwin Building, Gower Street, London, WC1E 6BT, UK

## ABSTRACT

Climate change is a major global threat to biodiversity with widespread impacts on ecological communities. Evidence for beneficial impacts on populations is perceived to be stronger and more plentiful than that for negative impacts, but few studies have investigated this apparent disparity, or how ecological factors affect population responses to climatic change. We examined the strength of the relationship between species-specific regional population changes and climate suitability trends (CST), using 30-year datasets of population change for 525 breeding bird species in Europe and the USA. Recent studies using the same data found a consistent positive relationship between population trend and CST across the two continents. Importantly, we found no evidence that this positive relationship differs between species expected to be negatively and positively impacted across the entire taxonomic group, suggesting that climate change is causing equally strong, quantifiable population increases and declines. Species' responses to changing climatic suitability varied with ecological traits however, particularly breeding habitat preference and body mass. Species associated with inland wetlands responded most strongly and consistently to recent climatic change. In Europe, smaller species also appeared to respond more strongly, while the relationship with body mass was less clear-cut for North American birds. These differences at even the continental scale suggest that generalising the impacts of ecological traits on species' responses to climate change from localised geographical studies with the aim of predicting global patterns of climate change adaption might not be robust, despite an increasing emphasis on such methods in climate change research.

Key words: body mass, breeding habitat, migratory behaviour, population trend, species distribution models, climate suitability trend

## INTRODUCTION

Correlational studies over large numbers of species, regions and taxonomic groups have revealed clear associations between recent climate change and observed changes in geographical range and abundance of many plant and animal taxa (Hickling et al. 2006; Parmesan and Yohe 2003; Spooner et al. 2018; Stephens et al. 2016). The evidence for positive changes in species abundance and distribution in response to beneficial recent climate change (i.e. in regions where this will lead to abundance increases and range extensions) is generally perceived to be stronger and more plentiful than for populations expected to be negatively impacted (e.g. Frishkoff et al. 2016; Parmesan et al. 1999; Parmesan and Yohe 2003; Root et al. 2003; Thomas et al. 2006; Thomas and Lennon 1999). However, this effect may be an artefact, particularly if there are time lags in the responses of populations to climate change, or if range retractions are more difficult to detect than expansions. For example, climate change may adversely affect an animal species through changes in vegetation affecting the suitability of its habitat, which take time to occur, leading to an extinction debt (Kuussaari et al. 2009). Such time lags may act in the opposite direction too, resulting in instances where beneficial effects, and therefore the responses of species predicted to benefit, may be delayed (Menéndez et al. 2006), but this would not explain the suggested excess of positive relative to negative effects on species distribution and population changes.

Range retractions may be more difficult to detect than expansions because local populations have to disappear from a large grid cell before a species is declared absent from it, whilst the colonisation of a single site within a similarly-sized cell may be easier to detect (Thomas et al. 2006). The enhanced detection of range expansions relative to retractions is particularly likely if survey effort in grid cells increases over time, as is common in repeated atlas studies (Keller 2017), or in large grid cells, as is evident from the enhanced detection of range retractions and declines linked to climate change by studies with fine-grained spatial resolution and systematic survey and mapping methods (e.g. Wilson et al. 2005). Overall, it is unclear whether the perceived difference in strength and quantity of evidence for positive relative to negative effects of climate change is an artefact or a true reflection of species' responses.

In some studies investigating the impacts of climate change, species distribution models (SDMs) relating geographical distribution to climatic variables are combined with annual meteorological data to estimate the direction and magnitude of changes in climate suitability over a given time period for different species or regions (Engler et al. 2017; Stephens et al. 2016). Variation among species in observed population changes over the same period in a given study area, or among regions for a given species, can then be compared to the modelled differences in climate suitability trend. A positive relationship between observed and expected change is taken as correlational evidence of a probable population-level response of distribution and/or abundance to climatic change (although see Clavero et al. 2011). Such studies have found positive relationships between climate suitability and populations, as expected, but have also identified substantial residual variation in the observed changes in distribution and abundance that is not accounted for statistically by measures of climatic change (Green et al. 2008; Stephens et al. 2016).

Species' populations and distributions are influenced by many factors other than climate (e.g. Clavero et al. 2011), and local climate adaptation may lead to different responses in different parts of a species' range (Visser et al. 2003), so such unexplained variation is unsurprising. Ecological factors might lead to interspecific variation in spatial patterns of sensitivity to climatic change, regardless of the expected direction of change in suitability (Pearce-Higgins et al. 2015). The phenological mismatch hypothesis is a good example of this, where the prevalence and magnitude of species' sensitivity to changes in life-cycle phenology relative to the phenology of prey or other resources (Franks et al. 2018) may vary because of differences in habitat, diet or migratory behaviour (Both et al. 2010). Changes, unrelated to climate change, in the suitability of habitats or impacts of environmental factors on demographic rates, such as changes in agricultural practices, land cover or pollution, may also counteract and mask the effects of climate change to a different extent for some groups of species (Clavero et al. 2011; Herrando et al. 2014; Kampichler et al. 2012). However, to our knowledge, the potential role of ecological traits in affecting species' responses to recent climatic change has not been explored comprehensively.

In this paper, we address these two issues – the apparent difference in response between species expected to benefit or be negatively impacted by climate change, and the role of ecological traits in influencing the relationship of population change to climate suitability trend – by examining the strength of the relationship between species- and region-specific population trends and trends in climate suitability using two of the best global datasets of recent long-term population changes for 525 bird species from Europe and the USA.

## MATERIALS AND METHODS

### Bird population trends

We obtained information on changes over time in breeding bird population size in Europe during the period 1980-2009 for 145 common species in 20 nation states (termed "states" henceforward) from the Pan-European Common Bird Monitoring Scheme (PECBMS 2012; Online Resources 1 & 2). For the USA, information on changes in breeding population size during the same period was obtained for 380 bird species in the 48 states of the contiguous USA (also termed "states") from the US Breeding Bird Survey (Sauer and Link 2011; Online Resources 3 & 4). For a given species, the information consisted of annual indices of population in the state derived from counts conducted annually using comparable methods at survey sites in all European or all USA states. The methods used to derive the annual population indices from the count data are given by PECBMS (2012) and Sauer and Link (2011) for Europe and the US respectively. The number of species for which annual indices were available for a given state ranged from 36 to 104 species (Europe) and from 66 to 215 species (USA). The duration of the time period of the data series used to calculate a population trend ranged from 10 to 30 years, depending on state and species (PECBMS 2012; Sauer and Link 2011).

Datasets were checked to eliminate state-level trends for species that: (i) were of limited temporal extent; or (ii) displayed anomalously-large inter-annual population fluctuations, possibly indicative of extensive population movements among states or of less robust population estimates. To do this we applied the following rules. First, state-wide indices of abundance for any species were included only if that species had been monitored since 2000 at the latest. Second, state-level abundance index series for any species that displayed population fluctuations too large to reflect local population processes, such as annual changes of a factor >10, were excluded (Gregory et al. 2009; Stephens et al. 2016). For Europe, this left 1686 species-state combinations with population data available for analysis, with 6760 species-state combinations available for the USA. For each species and state, a state-level mean annual population trend (*r*) was calculated as the slope of the ordinary least squares regression of the natural logarithm of the population index on calendar year, using the results for all years for which an eligible population index was available (Online Resource 5).

### Ecological traits

In examining the relationship between bird population trends and trends in climate suitability, we wished to account for ecological traits of species. We used information on three traits previously reported as important predictors of population trends and for which data could be summarised with a high level of confidence at the state-level for both European and North American species: mean body mass, breeding-season habitat association and migratory behaviour (Angert et al. 2011; Buckley and Kingsolver 2012). These traits are correlated with drivers of population trend (e.g. land-use change; Sanderson et al. 2006), and may act as proxies for other ecological traits (e.g. diet, clutch size, brain size, degree of habitat specialisation; Millien et al. 2006).

Body mass was obtained as the mean of the mean masses of male and female birds (g), or of unsexed birds where sex-specific information was not available. Mass data came from Cramp et al. (1977-1994) for European species, and from BirdLife International's World Bird Database for US species (BirdLife-International 2014). We used the natural logarithm of this mean body mass (Lmass) in analyses (Online Resources 1 & 3).

Species were assigned to one of four breeding-season habitat categories (HAB; Online Resources 1 & 3). For Europe species were assigned a primary breeding habitat, based on information from PECBMS (2012), Gregory et al. (2009), Tucker and Evans (1997) and expert opinion. For the USA, broad habitat use could not be differentiated at state level, so continent-wide habitat preferences were obtained from BirdLife-International (2014) and Poole (2005). Species were allocated to habitat categories if more than 50% of the population in each state used that particular habitat during the breeding season (Gregory et al. 2009). Habitat definitions in the sources consulted differed between Europe and the USA, so for comparability between the two continents we defined our own broad habitat categories as: *Forest*, comprising "forest" (Europe) and "forest and shrubland" (USA) habitats; *Farmland*, comprising "farmland" (Europe) and "grassland" (USA) habitats, both of which included arable and grassland; *Inland wetland*, comprising "wetland" (Europe) and "inland wetland" (USA) habitats, including rivers, lakes, marshes and other non-marine wetlands; *Other*, comprising all habitats not considered forest, farmland or inland wetland.

Each species in each state was assigned to one of four migratory behaviour categories (MIG; Onlines Resource 1 & 3) classifying the behaviour of all or most individuals: *Long-Distance Migrant*, *Short-Distance Migrant*, *Resident* and *Mixed Strategy* species (Gregory et al. 2009). For Europe, this was based on the text and maps in Cramp et al. (1977-1994) supplemented by available migration atlases (Speek and Speek 1984; Spina and Volponi 2008-2009; Wernham et al. 2002; Zink and Bairlein 1987-1995). For the USA, we based the classification on maps in Poole (2005). *Long-Distance Migrants* were defined as those usually making regular seasonal movements between their breeding range and either, for Europe, a non-breeding range outside the Palaearctic region (Snow and Perrins 1998), or, for the USA, a non-breeding range occurring south of latitude 25°N (the southern tip of Florida). We considered *Short-Distance Migrants* to be those usually making regular migratory or dispersive movements within the Palaearctic region (Europe) or north of latitude 25°N (USA). *Residents* were those where most individuals were non-migratory, making only irregular movements within the Palaearctic region (Europe) or where breeding and non-breeding ranges overlapped by >50% (USA). The *Mixed Strategy* category was only used in the USA in instances where information was insufficient to determine where birds from a state migrate to outside the breeding season, although the species was known to migrate to both short- and long-distance destinations in other states.

### Climate suitability trends

Climate suitability trends (CST) for each species and state were derived from SDMs, which linked annual grid-cell specific probability of occurrence estimates for a given species to grid-cell specific contemporaneous climatic data. Steps involved in fitting SDMs and using them to derive CSTs followed the methods of Stephens et al. (2016), and are described in the following sections.

#### *Species occurrence data for SDM fitting*

For European birds, species occurrence data (the presence or absence of each species as a breeding bird) was obtained for Europe, Turkey, Cyprus and North Africa (Mediterranean to latitude 20°N). The latter three regions, representing the southern margin of the Western Palaearctic realm, were added to include the southern range margins of as many species as possible, which was expected to improve the performance of the SDMs (Barbet-Massin et al. 2010). For Europe, occurrence data was available for 50x50 km UTM squares from

Hagemeijer and Blair (1997). Occurrence data for Turkey, Cyprus and North Africa was available for 0.5°x0.5° latitude-longitude grid cells (approximately equal to 50x50 km UTM squares) from BirdLife International Natureserve (2013). For the USA, we used bird species occurrence data for 0.5°x0.5° latitude-longitude grid cells spanning the whole of North America northwards from latitude 10°N from BirdLife International Natureserve (2013). Occurrence data on both continents was mostly derived from surveys conducted in the 1980s before the most rapid phase of recent climate change.

*Observed climate data for SDM fitting*

Monthly mean values for cloud cover, precipitation and temperature for the period 1961 to 1990 were obtained from www.worldclim.org (Hijmans et al. 2005) and CRUTS3.1 (Harris et al. 2014). Soil water capacity data were obtained from Prentice et al. (1992). Climate data were bilinearly interpolated onto the same grid structure as used for species occurrence data (50km UTM grid for Europe; 0.5° grid for Turkey, Cyprus, North Africa and North America). Bioclimate variables shown elsewhere to be highly influential were derived from climate data following Prentice et al. (1992) and Gregory et al. (2009), and included annual temperature sum above 5°C (GDD5), mean temperature of the coldest month (MTCO) and an estimate of the annual ratio of actual to potential evapotranspiration (APET). We restricted the number of bioclimate variables used to minimise the risk of overfitting and data-dredging, which can occur when large numbers of candidate explanatory variables are used in fitting SDMs (Pearce-Higgins and Green 2014). We chose these particular variables because they are known to influence the distribution of plant species and vegetation types and could therefore limit species' ranges directly through effects on species' physiology, or indirectly through effects on vegetation and habitats, or on prey, predators, competitors or diseases (Huntley et al. 2007; Pearce-Higgins and Green 2014).

*Fitting the SDMs*

For each species, we fitted four types of SDM following Bagchi et al. (2013) to 1980's occurrence data and the 1961-1990 values of the three bioclimate variables. The four SDM types used were: Generalized Linear Models (GLMS, McCullagh and Nelder 1989), semiparametric Generalized Additive Models (GAMS, Hastie and Tibshirani 1990), Generalized Boosted Models (GBMS, Elith et al. 2008) and Random Forests (Cutler et al. 2007), all of which perform well when compared with other SDM-fitting techniques (Araujo et al. 2005; Elith and Leathwick 2009; Franklin 2009; Meynard and Quinn 2007; Wenger and Olden 2012).

We used a cross-validation approach to fit each type of SDM. The occurrence data used to fit each model was divided into ten similarly-sized blocks each with similar mean values for the three bioclimate variables, but spanning the full range of bioclimates. Blocks comprised spatially disaggregated sampling units consisting of whole or partial global ecoregions (www.worldwildlife.org/science/data). SDMs were fitted to data from nine blocks, excluding each block in turn, with the fitted SDM from each of the ten iterations of this procedure being used, together with grid-cell-specific values of the 1961-1990 bioclimate data to calculate the probability of occupancy for each cell in the left-out block. These predicted probabilities of occupancy were then assembled for the entire area. Full details of model fitting methods, outcomes and measures of goodness-of-fit are presented in Stephens et al. (2016).

### *Calculating CST for 1980-2009*

For a given species and area (Europe or the USA), the ten models fitted using each SDM approach (i.e. the cross-validation models fitted with each block omitted) were applied to annual bioclimate data from all focal states for each of the years 1980-2009. The climatic data used for this were as described for the SDM fitting, but annual values of the bioclimate variables were used, in combination with the SDMs, to calculate annual values of expected probability of species occurrence for each grid cell. Predicted probabilities of occurrence were averaged across the ten models for each cell to give the probability of occurrence for that cell in that year from the given SDM method. Probability of occurrence for each cell was then averaged across the four SDM approaches to give an ensemble probability of occurrence for the given cell in the given year. For a given state and year, annual mean probability of occurrence was then averaged across all cells in the state.

For a given species in a given state, the CST was calculated as the slope of an ordinary least squares linear regression of logit annual mean ensemble probability of occurrence (as described above) regressed on calendar year. A positive CST slope indicates an increased probability of occurrence over time (species is predicted to benefit from climate change in that state); a negative slope indicates that the species is predicted to be disadvantaged by climate change. CST was calculated for the same time period over which species-state specific population trends were calculated, i.e. from 1980 or the first year of population data (whichever was later) to 2009 or the year after which there was no further data (whichever was earlier, Online Resource 5).

## Statistical analysis

The principal objective of our analysis was to examine the relationship between observed recent population trends (*r*) and trends in climate suitability (CST) at the species-state level for each continent. We had an *a priori* expectation that *r* was positively related to CST (Green et al. 2008), and wished to examine firstly whether the strength of this relationship differed between species-states for which climate suitability was expected to decrease (CST-) or increase (CST+), and secondly whether species- and state-specific ecological traits affected the strength of this relationship.

### *Population trend vs. CST relationships for species-states expected to be positively or negatively impacted by climate change*

To test whether responses to climate change differ between species-state combinations in which populations were expected to benefit from recent observed climate change (CST+) and those expected to be adversely affected (CST-), we compared the slope of the regression of *r* on CST for these two species-state groups separately through piecewise regression, assuming that the slope of the relationship would change at CST = 0. Linear mixed models (LMMs) were fitted using the lme4 package in R (Bates and Maechler 2009; R Core Team 2013) for Europe and the USA separately, incorporating the crossed random effects of species and state, thus accounting for the non-independence of trends among states within species, and among species within states. These random effects were found to provide the best fit in terms of AICc when compared to models with alternative random effect structures (Burnham and Anderson 2002). A piecewise test was incorporated into models by including both CST and also the dummy variable CST*, where CST* = 0 if CST < 0 (CST- species-states) and CST* = CST if CST ≥ 0 (CST+ species-states; Hardy 1993). The regression coefficient for CST* represents the estimated difference in slope between the CST- (CST < 0) and CST+ (CST ≥ 0) sections of the CST range. We took the *t* value for the effect of CST* as a test of whether regression slopes differed for CST- and CST+ species and used two-tailed significance tests because the difference in slope could plausibly have been in either direction.

*Population trend vs. CST relationships for species with different ecological traits*

To examine the effects of ecological traits on the relationship of *r* with CST we fitted LMMs, with the same random effects structure as above. We did this separately for Europe and the USA because two of the traits (HAB and MIG) had broadly similar, but not precisely equivalent, definitions on the two continents. We had no *a priori* expectations about the importance of the trait variables, so our model set of interest included all 27 possible models which included the main effect of CST and the main effects of Lmass, HAB and MIG, as well as their two-way interactions with CST (Online Resources 6 & 7). Including two-way interaction terms in this way allowed us to test the effects of trait variables on the slope of the *r vs.* CST relationship, which was the aim of this analysis. To avoid retention of overly complex models, selection followed the recommendations of Richards et al. (2011) whereby all models with ΔAICc < 6 were classed as a set of top models, excluding models that were more complex versions of those with a lower AICc.

We hypothesised that, should all three trait variables be upheld as important, we might expect to see a more positive *r* vs. CST regression slope for: i) species with smaller body mass, whose populations are likely to be favoured by the higher temperatures inherent in climatic change (Millien et al. 2006; Sheridan and Bickford 2011); ii) species associated with habitats more immediately-responsive to climate change, which might be expected to undergo more rapid population changes as a result of climate-driven habitat degradation or improvement (Erwin 2009; Foden et al. 2009); iii) long-distance migrants which may be more vulnerable to phenological changes on their breeding grounds (Both et al. 2010; Mayor et al. 2017; Vickery et al. 2014).

## RESULTS

### Comparing the *r* vs. CST relationship for species-states expected to be positively or negatively impacted by climate change

There was no significant difference in the slope of the relationship between population trend and CST between species-states with expected negative (CST-) and positive (CST+) effects of recent climate change (Table 1; Fig. 1). Slopes of the population trend on CST regression were positive for both species-state groups on both continents, though non-significantly so for the group of European species-states for which climate suitability was predicted to increase. Hence, there was no statistical support for a weaker relationship between observed and expected changes for species expected to be affected negatively by recent change.

**TABLE 1** Comparison of regression slopes (model coefficients b and their standard errors) between population trend and climate suitability trend (CST) for species-state populations expected to be adversely (CST-) or positively affected (CST+) by recent observed climate change on the two continents. For the CST- and CST+ species-state groups, P values indicate results of one-tailed tests of significance from a piecewise regression model including the random effects of species and state. Also shown are results of two-tailed tests of significance of the difference between the CST- and CST+ slopes from the piecewise models. Bold text indicates results significant at the 0.05 level.

| | CST- species-states | | | | | CST+ species-states | | | | | Difference in slope | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Continent | n | *b* | SE | *t* | *P* | n | *b* | SE | *t* | *P* | *t* | *P* |
| Europe | **852** | **0.236** | **0.104** | **2.27** | **0.012** | 834 | 0.008 | 0.125 | 0.06 | 0.475 | -1.23 | 0.218 |
| USA | **3788** | **0.183** | **0.069** | **2.64** | **0.004** | **2972** | **0.265** | **0.072** | **3.68** | **<0.001** | 0.71 | 0.447 |

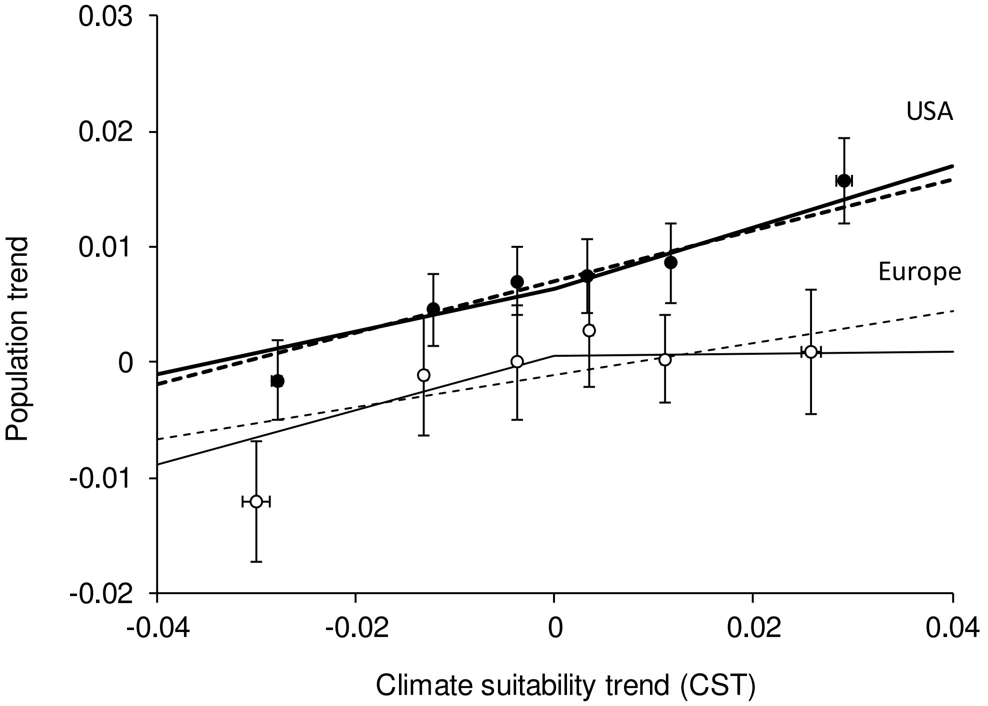


**Fig. 1** The effect of climate suitability (CST) on bird population trends (*r*) for Europe and the USA. Dotted lines represent continent-specific regression models of *r* on CST from analyses presented by Stephens et al. (2016). Solid lines are those predicted by continent-specific piecewise regression models with a breakpoint at CST = 0 (see Table 1 for model coefficients). All models also included the random effects of species and state. Plotted points are mean values of population trend and CST (± 95% confidence intervals, which are very small for CST) for species-state combinations binned according to their CST value for each continent (species states sorted by descending CST value and grouped into three bins containing approximately equal numbers of CST- species-states and three bins containing approximately equal numbers of CST+ species-states: CST- = 284 and 1263 per bin, CST+ = 278 and 991 per bin for Europe and USA respectively)

### Effects of ecological traits on the *r* vs. CST relationship

The same top model of the relationship of population trend to CST including ecological and life-history traits was selected for both continents (Table 2, Online Resources 6, 7 & 8). This model included the two-way interactions between body mass and CST, and habitat association and CST. Only one model was eligible for inclusion in the top set for Europe, but five other models were also selected in the top set for the USA. All of the USA top model set contained various combinations of the variables included in the top model. The effect of migratory behaviour was not included in any of the top models.

The direction and magnitude of the effect of species' body mass on the slope of the regression of population trend on CST differed between continents (Fig. 2, Online Resource 8). For European species, the relationship between the *r* vs CST regression slope and body mass was negative, so the relationship of *r* to CST was strongly positive for species of low body mass and became less positive as body mass increased (Fig. 2a), as we hypothesized *a priori*. However, for birds in the USA, the relationship between the *r* vs CST regression slope and body mass was positive, so the relationship of *r* to CST was least positive for species of low body mass and became more positive as body mass increased (Fig. 2b), counter to our expectation. This contrary effect appears to be driven by the strength of the response of the largest birds on this continent (Fig. 2). When only species of a comparable mass range (10-100g, spanning the interquartile range of body mass for European species and excluding the heaviest species in the USA, Fig. 2) were included in analysis on both continents, the interaction between *r* vs CST regression slope and body mass was no longer upheld as important in the top model for USA, although its effect in Europe remained unchanged (Online Resource 9).

On both continents, species associated with *Inland wetland* had the most positive relationship of *r* to CST. Species associated with *Other* habitats had the least positive relationship, and relationships for *Farmland* and *Forest* species were of intermediate strength (Fig. 2, Online Resource 8). The slope of the *r* vs CST regression was positive across the whole of the observed range of body mass for species associated with *Inland wetland* in Europe and for species associated with *Inland wetland*, *Farmland* and *Forest* in the USA. It was also positive across most of the observed range of body mass for species associated with *Farmland*, *Forest* and *Other* habitats in Europe but not for species associated with *Other* habitat in the USA.

**TABLE 2** Top sets of linear mixed models of population trend in relation to climate suitability trend (CST) and ecological traits of species for Europe and the USA. Both top sets include only those models simpler than the top model with ΔAICc <6. Models are shown in order of increasing AICc from the top model (shown in bold). Variables included in each model are denoted by codes: HAB = broad habitat association, Lmass = natural logarithm of body mass in grams. The log likelihood (logLik), number of fitted parameters (df) and Akaike weight (*w*) are shown for each model. Two-way interaction terms are coded by placing ":" between two variable codes. Results for the full set of models considered are presented in Tables S6 and S7.

| Continent | Variables retained | logLik | df | AICc | ΔAICc | *w* |
|---|---|---|---|---|---|---|
| Europe | **CST + Lmass + HAB + CST:Lmass + CST:HAB** | **3039.7** | **13** | **-6053.1** | **0.0** | **0.67** |
| USA | **CST + Lmass + HAB + CST:Lmass + CST:HAB** | **10855.6** | **13** | **-21685.2** | **0.0** | **0.23** |
| | CST + Lmass + HAB + CST:Lmass | 10852.3 | 10 | -21684.6 | 0.6 | 0.16 |
| | CST + Lmass + HAB + CST:HAB | 10854.1 | 12 | -21684.2 | 1.0 | 0.14 |
| | CST + Lmass + CST:Lmass | 10849.0 | 7 | -21684.0 | 1.3 | 0.12 |
| | CST + Lmass + HAB | 10850.3 | 9 | -21682.5 | 2.7 | 0.06 |
| | CST + Lmass | 10847.1 | 6 | -21682.2 | 3.0 | 0.05 |

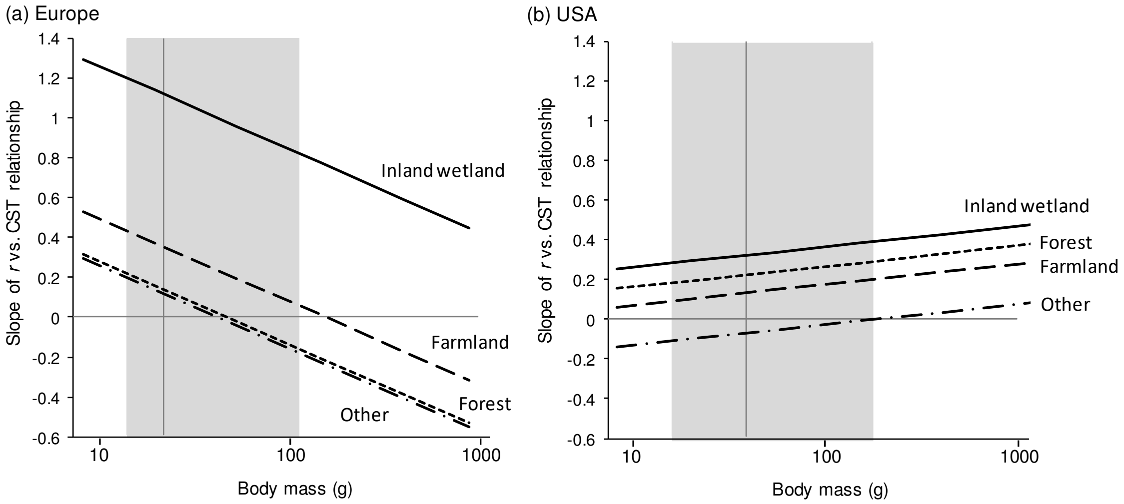


**Fig. 2** Regression slopes of the relationship between bird population trends (*r*) and climate suitability trend (CST) derived from the top model for (a) Europe and (b) USA. Top models for the two continents were the same and included the main effects of CST, log body mass (Lmass) and habitat and the two-way interactions of CST with each of Lmass and habitat (Table 2, Online Resource 8). Each line shows the modelled slope of the *r* vs. CST regression in relation to body mass for a single habitat type, with the horizontal extent of the line corresponding to the central 90% of body mass values for the species studied on each continent. The shaded area shows the interquartile range of body mass and the vertical line its median value. For Europe, the lines for *Forest* and *Other* almost coincide, so for clearer differentiation between these habitats the line for *Forest* has been jittered upwards by 0.02 (the direction indicated by the model). Line segments lying above the horizontal grey line represent positive modelled relationships between *r* and CST

## DISCUSSION

Our analyses of over 500 bird species confirm the overall positive relationship between population trend and climate suitability on our two focal continents in support of Stephens et al. (2016) and others. Importantly, we found no statistically supported difference in the strength of the relationship between population trend and climate suitability change between those species expected to benefit from climate change and those expected to be adversely impacted, failing to support previous suggestions that the positive effects of climate change have been more pronounced than its negative effects. Across our sample of 525 species over the two continents, we therefore found no strong evidence of a greater tendency for delay in effects of climate change on species' populations projected to be negatively impacted compared to those projected to be positively impacted by climate, in contrast to suggestions from previous, often finer-scale studies (e.g. see Thomas et al. 2006). The positive relationship between population trend and climate suitability largely persisted regardless of species ecology, although the strength of relationship varied with ecological traits, further increasing the causal evidence of a consistent effect of climate change on bird populations over recent decades.

It has been suggested that the evidence for range retractions and population declines linked to climate change may be less strong than for range expansions and population increases (e.g. Parmesan et al. 1999; Parmesan and Yohe 2003; Root et al. 2003; Thomas and Lennon 1999). However, our evidence of a positive relationship between population trend and CST was, if anything, more compelling for species-states expected to be negatively impacted rather than those expected to benefit (statistically significant for CST- species-states on both continents, but non-significant for CST+ species-states in Europe; Table 1). A similar study examining community composition found a similar effect of comparable contributions of both cold-dwelling (~CST-) and warm-dwelling (~CST+) species to regional climate-induced changes across a smaller geographic area (Tayleur et al. 2016). A possible explanation for why we found no evidence that species favoured by changing climate suitability have responded more strongly than species expected to be disadvantaged, may be that we compared range change predictions from models of distribution data with detailed abundance data in our analyses. Assessments of climate impact based on distribution data alone are more likely to be biased towards increases in range which are often more noticeable (Thomas and Abery 1995; Thomas et al. 2006), whilst abundance data from long-term population monitoring schemes, by being more sensitive to changes than range, are unlikely to share this bias. This therefore stresses the importance of long-term population monitoring schemes over simple spatial occupancy data for detecting large-scale species' responses to environmental changes.

The population trend vs. CST relationship was slightly less positive for CST+ species in Europe than the other groups tested, indicating that this group may be less able to take advantage of an increasingly suitable climate. This may reflect differences in the underlying trajectories of avian abundance between the two continents, with average trends in Europe predominantly negative since 1980 (EBCC 2014), while US bird populations have, on average, remained relatively stable (Sauer and Link 2011; Stephens et al. 2016). This is reflected in the lower mean values of population trend at a given value of CST in Europe compared to the USA evident in Fig. 1. These different patterns could be related to the proportion of rare species included in population monitoring data for the two continents. In Europe, rarer species have been faring better than more common species (Inger et al. 2015) but our European dataset is focussed on common birds (PECBMS 2012). Differences in land-use change on the two continents (Clavero et al. 2011; Kampichler et al. 2012) might also have a bearing on mean population trejectories.

Another explanation for why CST+ species may not be responding as positively in terms of population trend in Europe is if they are following the pattern of increasing climate suitability into an ecological trap due to changing land use and intensity patterns (Herrando et al. 2014). This could be the case if pressures other than climate change, such as agricultural intensification or land abandonment, were particularly prevalent in Europe compared to the USA (e.g. Lasanta et al. 2017). Alternatively, European species may have lower dispersal abilities due to the presence of latitudinal barriers in Europe that are absent from the USA. West-east running mountain chains (Alps and Carpathians), and continental marine areas (English Channel and Baltic Sea) in Europe intercept the dominantly south-north direction of climate change (Parmesan and Yohe 2003) and may reduce the ability of species resident to Central and Central-Eastern Europe to respond to increases in climate suitability by preventing colonisation and immigration into more suitable areas (Foden et al. 2013).

The strength of the relationship between population trend and climate suitability varied in relation to the same ecological traits on both continents, with similar patterns found for species associated with different habitat types; associations with body mass, however, were more complex. It has been proposed that a warming climate favours smaller species (Atkinson et al. 1994; Millien et al. 2006; Sheridan and Bickford 2011), and distribution shifts driven by climate change may be stronger in small-bodied species with more rapid reproduction and shorter generations (Devictor et al. 2012), so we expected that smaller species would respond more positively to warming climate and associated range changes. In accord with this hypothesis, we found that species with smaller body mass had a more positive population trend to CST relationship, but only in Europe.

In the USA, we found the opposite effect of body mass on the population trend to CST relationship, with larger species apparently having more positive population trend vs. CST relationships. This relationship was not supported when we considered equivalent mass ranges (10 – 100g) of species on both continents however, suggesting that it is driven by strong responses to climate change among the very largest species in the USA. The reasons for this finding are unclear but could be explained if there was an increasing reporting bias towards large, charismatic species in the USA (Titley et al. 2017) meaning their population estimates increase coincidentally with increasing climate suitability.

As hypothesised, species associated with different breeding habitats responded differently to changes in climate suitability, and these responses were largely consistent on both continents. Species associated with inland wetlands showed a consistently more positive relationship between *r* and CST than those associated with other habitat types. The biota of wetlands may be more resilient to environmental changes due to the already seasonal or stochastic nature and spatial or temporal patchiness of wetland habitats relative to less labile ecosystems (e.g. forests), which can withstand environmental changes for many decades without exhibiting large-scale community changes (Erwin 2009; Lindner et al. 2010). Wetland breeding birds may also make longer-distance non-migratory dispersal movements than those associated with dry habitats for the same reason (Paradis et al. 1998), so they may be better able to respond more rapidly to changing conditions. Strong and increasing protection of wetlands relative to other habitats, at least in Europe (Butchart et al. 2012), may also allow wetland bird populations to better track the direction of climate suitability without the trade-off of also adapting to habitat change and other threats (Gaüzère et al. 2016). These habitat changes and threats may also be more coherent with the impact of climatic changes (e.g. drainage and water abstraction similar to the drying effects of reduced rainfall and warmer temperatures; Erwin 2009), potentially explaining the enhanced the strength of the *r* and CST relationship for wetland species.

Surprisingly, migratory behaviour was not found to be important in affecting the strength of the relationship between population trend and CST on either continent. Long-distance migrants are less able to adapt their phenology and therefore more vulnerable to climate suitability changes on their breeding grounds, so might be expected to exhibit a stronger positive relationship between population trend and CST (Both et al. 2010; Franks et al. 2018; Mayor et al. 2017; Samplonius et al. 2018; Vickery et al. 2014). These migrant species are often affected by climate change and other threats in their non-breeding range however (e.g. McKellar et al. 2013; Peach et al. 1991; Rushing et al. 2016), which would weaken the *r* vs CST relationship on their breeding grounds, and may explain why the effect of migratory behaviour was not supported in our models. Additionally, because resident species have lower dispersal capability than migrants (Paradis et al. 1998), we might expect that they would be less able to respond to positive changes in climate suitability and would therefore exhibit a shallower *r*–CST relationship (Foden et al. 2013).

Taken together, our results indicate that ecological traits substantially affect the strength of bird population responses to changing climate suitability, but that their impact may not always be consistent even between continents. Much emphasis is currently placed on examining the likely impacts of ecological traits on species' responses to climate change, with the aim of predicting global patterns of climate change adaption (e.g. Angert et al. 2011; Jiguet et al. 2007; Jiguet et al. 2010; Pearson et al. 2014). Our results suggest that generalising the impacts of these traits from localised geographical studies, even those examining whole continents, to a universal scale may not be robust.

Thomas et al. (2006) highlighted the likely artefactual perception that range expansions and population increases as a result of climate change are more widespread than range retractions and population decreases. Here, we have shown that despite differences in species ecology, the relationship between population trend and climate suitability trend is persistently positive across an entire taxonomic group and two continents, with no evidence that species favoured by climate change have responded more strongly than those disadvantaged by it, thus providing unequivocal evidence that climate change is causing widespread strong, quantifiable population increases and declines in equal measures.

## ACKNOWLEDGEMENTS

The data used are held by individual institutes and collated by the United States Geological Survey and European Bird Census Council. This work was part-funded by the Royal Society for the Protection of Birds, the European Environment Agency, the European Commission, and Durham University Grevillea Trust. We acknowledge the tremendous fieldwork effort made by volunteers on both continents in gathering bird data, and thank all PECBMS national data providers. Stuart Butchart (Birdlife International) provided valuable comments on the manuscript.

## REFERENCES

Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ (2011) Do species' traits predict recent shifts at expanding range edges? Ecol. Lett. 14:677-689.

Araujo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. Global Change Biol. 11:1504-1513.

Atkinson D, Begon M, Fitter AH (1994) Temperature and Organism Size: A Biological Law for Ectotherms? Adv. Ecol. Res. Academic Press, pp. 1-58.

Bagchi R, Crosby M, Huntley B, Hole DG, Butchart SH, Collingham Y, Kalra M, Rajkumar J, Rahmani A, Pandey M (2013) Evaluating the effectiveness of conservation site networks under climate change: accounting for uncertainty. Global Change Biol. 19:1236-1248.

Barbet-Massin M, Thuiller W, Jiguet F (2010) How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models? Ecography 33:878-886.

Bates D, Maechler M (2009) lme4: Linear mixed-effects models using S4 classes. *http://CRAN.R-project.org/package=lme4*.

BirdLife-International (2014) World bird database. *http://www.birdlife.org/datazone/home*.

BirdLife International Natureserve (2013) Bird species distribution maps of the world. Version 3.0. BirdLife International, Cambridge, UK.

Both C, Van Turnhout CA, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RP (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proceedings of the Royal Society B: Biological Sciences 277:1259-1266.

Buckley LB, Kingsolver JG (2012) Functional and phylogenetic approaches to forecasting species' responses to climate change. Annual Review of Ecology, Evolution, and Systematics 43.

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: A practical information-theoretic approach. Springer-Verlag, Berlin.

Butchart SH, Scharlemann JP, Evans MI, Quader S, Arico S, Arinaitwe J, Balman M, Bennun LA, Bertzky B, Besancon C (2012) Protecting important sites for biodiversity contributes to meeting global conservation targets. PLoS ONE 7:e32529.

Clavero M, Villero D, Brotons L (2011) Climate change or land use dynamics: do we know what climate change indicators indicate? PLoS ONE 6:e18581.

Cramp S, Simmons AD, Perrins CM (1977-1994) Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palaearctic. Oxford University Press.

Cutler DR, Edwards TCJ, Beard KH, Cutler A, Hess KT (2007) Random forests for classification in ecology. Ecology 88:2783-2792.

Devictor V, van Swaay C, Brereton T, Brotons L, Chamberlain D, Heliola J, Herrando S, Julliard R, Kuussaari M, Lindstrom A, Reif J, Roy DB, Schweiger O, Settele J, Stefanescu C, Van Strien A, Van Turnhout C, Vermouzek Z, WallisDeVries M, Wynhoff I, Jiguet F (2012) Differences in the climatic debts of birds and butterflies at a continental scale. Nature Climate Change 2:121-124.

EBCC (2014) http://www.ebcc.info/index.php?ID=510.

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40:677-697.

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J. Anim. Ecol. 77:802-813.

Engler JO, Stiels D, Schidelko K, Strubbe D, Quillfeldt P, Brambilla M (2017) Avian SDMs: current state, challenges, and opportunities. J. Avian Biol. 48:1483-1504.

Erwin KL (2009) Wetlands and global climate change: the role of wetland restoration in a changing world. Wetlands Ecol. Manage. 17:71-84.

Foden W, Mace GM, Vié J-C, Angulo A, Butchart SHM, DeVantier L, Dublin H, Gutsche A, Stuart S, Turak E (2009) Species susceptibility to climate change impacts. in Vié J-C, Hilton-Taylor C, Stuart SN (eds.) Wildlife in a changing world - an analysis of the 2008 IUCN Red List of threatened species. IUCN, Gland, Switzerland, pp. 77-87.

Foden WB, Butchart SHM, Stuart SN, Vié J-C, Akçakaya HR, Angulo A, DeVantier LM, Gutsche A, Turak E, Cao L, Donner SD, Katariya V, Bernard R, Holland RA, Hughes AF, O'Hanlon SE, Garnett ST, Şekercioğlu Ç, H., Mace GM (2013) Identifying the world's most climate change vulnerable species: A systematic trait-based assessment of all birds, amphibians and corals. PLoS ONE 8:e65427.

Franklin J (2009) Mapping species distributions. Cambridge University Press, Cambridge.

Franks SE, Pearce-Higgins JW, Atkinson S, Bell JR, Botham MS, Brereton TM, Harrington R, Leech DI (2018) The sensitivity of breeding songbirds to changes in seasonal timing is linked to population change but cannot be directly attributed to the effects of trophic asynchrony on productivity. Global Change Biol. 24:957-971.

Frishkoff LO, Karp DS, Flanders JR, Zook J, Hadly EA, Daily GC, M'Gonigle LK (2016) Climate change and habitat conversion favour the same species. Ecol. Lett. 19:1081-1090.

Gaüzère P, Jiguet F, Devictor V (2016) Can protected areas mitigate the impacts of climate change on bird's species and communities? Divers. Distrib. 22:625-637.

Green RE, Collingham YC, Willis SG, Gregory RD, Smith KW, Huntley B (2008) Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. Biol. Lett. 4:599-602.

Gregory RD, Willis SG, Jiguet F, Voříšek P, Klaňová A, Strien Av, Huntley B, Collingham YC, Couvet D, Green RE (2009) An Indicator of the Impact of Climatic Change on European Bird Populations. PLoS ONE 4:e4678.

Hagemeijer WJ, Blair MJ (1997) The EBCC atlas of European breeding birds: their distribution and abundance. Poyser London.

Hardy MA (1993) Regression with dummy variables. Sage University Paper series on Quantitive Applications in the Social Sciences, 07-093. Sage, Newbury Park, Canada.

Harris I, Jones PD, Osborn TJ, Lister DH (2014) Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. International Journal of Climatology 34:623-642.

Hastie TJ, Tibshirani R (1990) Generalized Additive Models. Chapman and Hall, London.

Herrando S, Anton M, Sardà-Palomera F, Bota G, Gregory RD, Brotons L (2014) Indicators of the impact of land use changes using large-scale bird surveys: Land abandonment in a Mediterranean region. Ecol. Indicators 45:235-244.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biol. 12:450–455.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965-1978.

Huntley B, Green RE, Collingham YC, Willis SG (2007) A climatic atlas of European breeding birds. Durham University, The RSPB and Lynx Edicions, Barcelona.

Inger R, Gregory R, Duffy JP, Stott I, Voříšek P, Gaston KJ (2015) Common European birds are declining rapidly while less abundant species' numbers are rising. Ecol. Lett. 18:28-36.

Jiguet F, Gadot A-S, Julliard R, Newson SE, Couvet D (2007) Climate envelope, life history traits and the resilience of birds facing global change. Global Change Biol. 13:1672-1684.

Jiguet F, Gregory RD, Devictor V, Green RE, Voříšek P, Van Strien A, Couvet D (2010) Population trends of European common birds are predicted by characteristics of their climatic niche. Global Change Biol. 16:497-505.

Kampichler C, Van Turnhout CA, Devictor V, Van Der Jeugd HP (2012) Large-scale changes in community composition: determining land use and climate change signals. PLoS ONE 7:e35272.

Keller V (2017) Atlases as a tool to document changes in distribution and abundance of birds. Vogelwelt 137:43-52.

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Öckinger E, Pärtel M, Pino J, Roda F (2009) Extinction debt: a challenge for biodiversity conservation. Trends Ecol. Evol. 24:564-571.

Lasanta T, Arnáez J, Pascual N, Ruiz-Flaño P, Errea M, Lana-Renault N (2017) Space–time process and drivers of land abandonment in Europe. Catena 149:810-823.

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolström M (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259:698-709.

Mayor SJ, Guralnick RP, Tingley MW, Otegui J, Withey JC, Elmendorf SC, Andrew ME, Leyk S, Pearse IS, Schneider DC (2017) Increasing phenological asynchrony between spring green-up and arrival of migratory birds. Sci. Rep. 7:1902.

McCullagh P, Nelder JA (1989) Generalized Linear models. Chapman and Hall, London, UK.

McKellar AE, Marra PP, Hannon SJ, Studds CE, Ratcliffe LM (2013) Winter rainfall predicts phenology in widely separated populations of a migrant songbird. Oecologia 172:595-605.

Menéndez R, Megías AG, Hill JK, Braschler B, Willis SG, Collingham Y, Fox R, Roy DB, Thomas CD (2006) Species richness changes lag behind climate change. Proceedings of the Royal Society of London B: Biological Sciences 273:1465-1470.

Meynard CN, Quinn JF (2007) Predicting species distributions: a critical comparison of the most common statistical models using artificial species. J. Biogeogr. 34:1455-1469.

Millien V, Kathleen Lyons S, Olson L, Smith FA, Wilson AB, Yom-Tov Y (2006) Ecotypic variation in the context of global climate change: revisiting the rules. Ecol. Lett. 9:853-869.

Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. J. Anim. Ecol. 67:518-536.

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Peach W, Baillie S, Underhill L (1991) Survival of British Sedge Warblers Acrocephalus schoenobaenus in relation to west African rainfall. Ibis 133:300-305.

Pearce-Higgins JW, Green RE (2014) Birds and climate change: impacts and conservation responses. Cambridge University Press, Cambridge.

Pearce-Higgins JW, Ockendon N, Baker DJ, Carr J, White EC, Almond REA, Amano T, Bertram E, Bradbury RB, Bradley C, Butchart SHM, Doswald N, Foden W, Gill DJC, Green RE, Sutherland WJ, Tanner EVJ (2015) Geographical variation in species' population responses to changes in temperature and precipitation. Proceedings of the Royal Society of London B: Biological Sciences 282:20151561.

Pearson RG, Stanton JC, Shoemaker KT, Aiello-Lammens ME, Ersts PJ, Horning N, Fordham DA, Raxworthy CJ, Ryu HY, McNees J (2014) Life history and spatial traits predict extinction risk due to climate change. Nature Climate Change 4:217.

PECBMS (2012) http://www.ebcc.info/indebothx.php?ID=491.

Poole A (2005) The Birds of North America Online: http://bna.birds.cornell.edu/BNA/. Cornell Laboratory of Ornithology, Ithaca, NY.

Prentice I, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) A global biome model based on plant physiology and dominance, soil properties and climate. J. Biogeogr. 19:117-134.

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/ version 3.0.2.

Richards SA, Whittingham MJ, Stephens PA (2011) Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. Behav. Ecol. Sociobiol. 65:77-89.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57-60.

Rushing CS, Ryder TB, Marra PP (2016) Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. Proc. R. Soc. B 283:20152846.

Samplonius JM, Bartošová L, Burgess MD, Bushuev AV, Eeva T, Ivankina EV, Kerimov AB, Krams I, Laaksonen T, Mägi M (2018) Phenological sensitivity to climate change is higher in resident than in migrant bird populations among European cavity breeders. Global Change Biol. 24:3780-3790.

Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, Van Bommel FP (2006) Long-term population declines in Afro-Palearctic migrant birds. Biol. Conserv. 131:93-105.

Sauer JR, Link WA (2011) Analysis of the North American Breeding Bird Survey using hierarchical models. The Auk 128:87–98.

Sheridan JA, Bickford D (2011) Shrinking body size as an ecological response to climate change. Nature Climate Change 1:401-406.

Snow D, Perrins C (1998) The birds of the Western Palaearctic: concise edition. Oxford University Press, UK.

Speek BJ, Speek G (1984) Thieme's vogeltrekatlas: terugmeldingen van 181 vogelsoorten verzameld in 301 geografische kaarten. Thieme, Zutphen. [Dutch migration atlas].

Spina F, Volponi S (2008-2009) Atlante della Migrazione degli Uccelli in Italia. Vol. 1-2. ISPRA – MATTM, Rome, Italy.

Spooner FE, Pearson RG, Freeman R (2018) Rapid warming is associated with population decline among terrestrial birds and mammals globally. Global Change Biol. 00:1-11.

Stephens PA, Mason LR, Green RE, Gregory RD, Sauer JR, Alison J, Aunins A, Brotons L, Butchart SHM, Campedelli T, Chodkiewicz T, Chylarecki P, Crowe O, Elts J, Escandell V, Foppen RPB, Heldbjerg H, Herrando S, Husby M, Jiguet F, Lehikoinen A, Lindström Å, Noble DG, Paquet J-Y, Reif J, Sattler T, Szép T, Teufelbauer N, Trautmann S, van Strien AJ, van Turnhout CAM, Vorisek P, Willis SG (2016) Consistent response of bird populations to climate change on two continents. Science 352:84-87.

Tayleur CM, Devictor V, Gaüzère P, Jonzén N, Smith HG, Lindström Å (2016) Regional variation in climate change winners and losers highlights the rapid loss of cold-dwelling species. Divers. Distrib. 22:468-480.

Thomas C, Abery J (1995) Estimating rates of butterfly decline from distribution maps: the effect of scale. Biol. Conserv. 73:59-65.

Thomas CD, Franco AM, Hill JK (2006) Range retractions and extinction in the face of climate warming. Trends Ecol. Evol. 21:415-416.

Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. Nature 399:213.

Titley MA, Snaddon JL, Turner EC (2017) Scientific research on animal biodiversity is systematically biased towards vertebrates and temperate regions. PLoS ONE 12:e0189577.

Tucker GM, Evans MI (1997) Habitats for birds in Europe: A conservation strategy for the wider environment. BirdLife International, Cambridge, UK.

Vickery JA, Ewing SR, Smith KW, Pain DJ, Bairlein F, Škorpilová J, Gregory RD (2014) The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis 156:1-22.

Visser M, Adriaensen F, Van Balen J, Blondel J, Dhondt A, Van Dongen S, Du Feu C, Ivankina E, Kerimov A, De Laet J (2003) Variable responses to large-scale climate change in European Parus populations. Proceedings of the Royal Society B-Biological Sciences 270:367-372.

Wenger SJ, Olden JD (2012) Assessing transferability of ecological models: an underappreciated aspect of statistical validation. Methods Ecol. Evol. 3:260-267.

Wernham C, Toms M, Marchant J, Clark J, Siriwardena G, Baillie S (2002) The migration atlas: Movements of the birds of Britain and Ireland. T & AD Poyser, London.

Wilson RJ, Gutiérrez D, Gutiérrez J, Martínez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits and extent of species ranges associated with climate change. Ecol. Lett. 8:1138-1146.

Zink G, Bairlein F (1987-1995) Der Zug Europäischer Singvögel: Atlas der Wiederfunde Beringter Vögel Band 1-3. Aula Verlag, Wiesbaden, Germany.

## Supplementary Materials

Supplementary Materials for paper **II** are available in an appendix at the end of this thesis.

Online Resource 1. European bird species
Online Resource 2. European countries ("states")
Online Resource 3. North American bird species
Online Resource 4. USA states
Online Resource 5. State-level CST and population trends
Online Resource 6. Ecological trait analysis model selection table (Europe)
Online Resource 7. Ecological trait analysis model selection table (USA)
Online Resource 8. Ecological trait analysis regression coefficients
Online Resource 9. Ecological trait analysis for species with comparable mass ranges

# PAPER III

# Continued declines of Redshank *Tringa totanus* breeding on saltmarsh in Great Britain: is there a solution to this conservation problem?

**Malpas, L.R.**, Smart, J., Drewitt, A.L., Sharps, E. & Garbutt, A.

*Bird Study* (2013), **60**: 370–383. http://doi.org/10.1080/00063657.2013.781112

© Mike Langman rspb-images.com

*Bird Study* (2013) **60**, 370–383
http://dx.doi.org/10.1080/00063657.2013.781112

# Continued declines of Redshank *Tringa totanus* breeding on saltmarsh in Great Britain: is there a solution to this conservation problem?

LUCY R. MALPAS[1]*, JENNIFER SMART[1], ALLAN DREWITT[2], ELWYN SHARPS[1,3,4] and ANGUS GARBUTT[3]

*[1]Royal Society for the Protection of Birds, UK Headquarters, The Lodge, Sandy, Beds SG19 2DL, UK; [2]Natural England, Eastbrook, Shaftesbury Road, Cambridge, CB2 8DR, UK; [3]Centre for Ecology and Hydrology, Environment Centre Wales, Deiniol Road, Bangor, Gwynedd LL57 2UW, UK and [4]Bangor University, School of Ocean Sciences, Menai Bridge, Anglesey LL59 5AB, UK*

**Capsule:** Over 50% of saltmarsh breeding Common Redshank have been lost since 1985, with current conservation management having only limited success at halting these declines.
**Aims:** To update population size and trend estimates for saltmarsh-breeding Redshank in Britain, and to determine whether conservation management implemented since 1996 has been successful in influencing grazing intensity and Redshank population trends.
**Methods:** A repeat national survey of British saltmarsh was conducted in 2011 at sites previously visited in 1985 and 1996. Redshank breeding density and grazing pressure were recorded at all sites; the presence of conservation management was additionally recorded for English sites. Results from all three national surveys were used to update population size and trend estimates, and to investigate changes in grazing pressure and breeding density on sites with and without conservation management.
**Results:** Of the 21 431 pairs breeding on saltmarsh in 1985, 11 946 pairs remained in 2011, with the highest proportion of this population found in East Anglia. From 1985, British breeding densities declined at a rate of 1 pair $\text{km}^{-2}$ $\text{year}^{-1}$, representing a loss of 52.8% of breeding pairs over 26 years, although regional trends varied across different time periods. Grazing pressures did not change markedly with conservation management. Redshank declines were less severe on conservation-managed sites in East Anglia and the South of England where grazing pressures remained low, though were more severe on conservation-managed sites in the North West where heavy grazing persisted.
**Conclusion:** Saltmarsh-breeding Redshank declines continue and are likely to be driven by a lack of suitable nesting habitat. Conservation management schemes and site protection implemented since 1996 appear not to be delivering the grazing pressures and associated habitat conditions required by this species, particularly in the North West of England, though habitat changes may not be linked to unsuitable grazing management in all regions. An in-depth understanding of grazing practices, how conservation management guidelines could be improved, and the likely success of more long-term management solutions is needed urgently.

The Common Redshank *Tringa totanus* is a species of conservation concern in the UK and Europe, having lost more than a quarter of its population in 25 years, a decline attributed to the loss and degradation of important wetland breeding sites (Tucker & Heath 1994, BirdLife International 2004a, 2004b, Eaton *et al.* 2009). Great Britain is an internationally important breeding ground for this species, supporting over 18% of the estimated 100 000–172 000 pairs breeding in northwest Europe (Piersma 1986, Batten *et al.* 1990, BirdLife International 2004a, 2004b). Redshank breed on lowland wet grassland and upland rough pasture habitats in Britain (Hale 1988), although a nationally and internationally important proportion of the population nests on saltmarsh, with over 45% of breeding pairs found on the coast (Brindley *et al.*

*Correspondence author. Email: lucy.malpas@rspb.org.uk

1998). National surveys of British saltmarsh identified a 22.9% reduction in the density of nesting pairs over 11 years, with the estimated saltmarsh breeding population declining from 21 022 in 1985 to 16 433 pairs in 1996 (Allport *et al.* 1986, Brindley *et al.* 1998). Although Redshank populations in the Wadden Sea – one of the most internationally important saltmarsh sites in continental Europe – have remained relatively stable or experienced only moderate declines since 1991 (Koffijberg *et al.* 2006, Hötker *et al.* 2007a, 2007b, JMBB 2010), surveys of individual sites in Britain indicate that the decline here may have continued since 1996 (e.g. Smart *et al.* 2003, Tyas 2008). Whether this decline has continued at a national scale is unknown however.

Reductions in breeding success are known to drive population declines of other wader species (e.g. Eurasian Oystercatcher *Haematopus ostralegus*, Northern Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa*, Eurasian Curlew *Numenius arquata*) nesting in both inland and coastal habitats across northwest Europe (Roodbergen *et al.* 2012). Low breeding success due to a reduction in the availability of saltmarsh nesting habitat in suitable condition was implicated as a key driver of the decline in British Redshank breeding density between 1985 and 1996 (Brindley *et al.* 1998, Norris *et al.* 1998). Such reductions in saltmarsh habitat condition are often attributed to environmental changes such as sea level rise and erosion (Woodworth *et al.* 1999, Natural England 2006), though increases in detrimental management practices (Pye & French 1993) – particularly changes in grazing management (Bakker 1985, Kiehl *et al.* 1996, Norris *et al.* 1997, Bouchard *et al.* 2003, Hannaford *et al.* 2006) – are likely to have heavily influenced the loss of Redshank pairs between 1985 and 1996. Lower Redshank breeding densities are found on heavily grazed or ungrazed sites compared to those lightly or moderately grazed, and densities declined more severely on sites where grazing intensity increased (Norris *et al.* 1998). Possible solutions to this problem could therefore involve encouraging the recovery of degraded saltmarsh by mitigating the effects of environmental processes and implementing more suitable grazing management (Davidson *et al.* 1991, Environment Agency 2005).

Site designation is a key mechanism through which threatened habitats and species may be protected, with the majority of saltmarsh sites in Britain designated as Sites of Special Scientific Interest (SSSIs) and forming part of larger national or international site designations such as Special Areas of Conservation (SACs), Special Protection Areas (SPAs) and Ramsar sites (Gaston *et al.* 2006, Natural England 2011). Additionally, management on nature reserves and private land in the form of agri-environment schemes (AES) with saltmarsh-specific options have been implemented since 1996 with the aim of improving saltmarsh habitat condition. These schemes focus largely on the implementation of sympathetic grazing practices, as well as the prevention of surface-damaging activities, cessation of fertilizer inputs and management of accumulated tidal debris (DEFRA 2004, Natural England 2010a). Emerging evidence suggests that similarly targeted environmental stewardship or protected area management, implemented on lowland wet grassland habitats in Britain and elsewhere in Europe where Redshank also breed, have had a positive effect on site occupancy and wader productivity (Schekkerman *et al.* 2008, Dillon *et al.* in prep.). However, little is known about whether similar management has been successful in halting Redshank population declines on saltmarsh.

Traditional saltmarsh management practices vary greatly by region around the British coast (Environment Agency 2005), as do saltmarsh habitats and the vegetation communities characterising them (Burd 1989, Natural England 2006). As such, it is likely that the drivers impacting on Redshank populations will vary between regions, and that a regionally-specific management approach will be required to facilitate population recovery. In this study we aimed to generate up-to-date national and regional estimates of Redshank breeding population abundance and trends on British saltmarsh by conducting a repeat national survey in 2011 at sites visited in 1985 and 1996. Using grazing pressure and management information, we then aimed to determine whether management schemes implemented since 1996 have successfully improved grazing practices or effectively influenced Redshank population trends, and whether grazing and Redshank responses to this conservation management differ between regions.

## METHODS

Survey and analysis methods used in 2011 matched those used in 1985 and 1996 as far as possible to ensure compatibility between historical and contemporary results. These methods are described in detail by Brindley *et al.* (1998) and Norris *et al.* (1998), with key elements and minor changes reported below.

## Study sites

Seventy-seven saltmarsh sites were surveyed in 1985, encompassing 2548 ha (about 6%) of vegetated saltmarsh and representing the range and distribution of vegetation types in Great Britain (Allport *et al.* 1986, Brindley *et al.* 1998). Of these original sites, 64 were resurveyed in 1996 (83%) and 57 were resurveyed in 2011 (74%). Data from all three years for an additional site (Langstone Harbour, Hampshire, Ordnance Survey grid reference SU693046; Site 78, Fig. 1) became available in 2011, collected using the same survey methods and with Redshank densities similar to those found elsewhere in the same region. This site was also included in analyses (final site count: 1985 = 78, 1996 = 65, 2011 = 58).

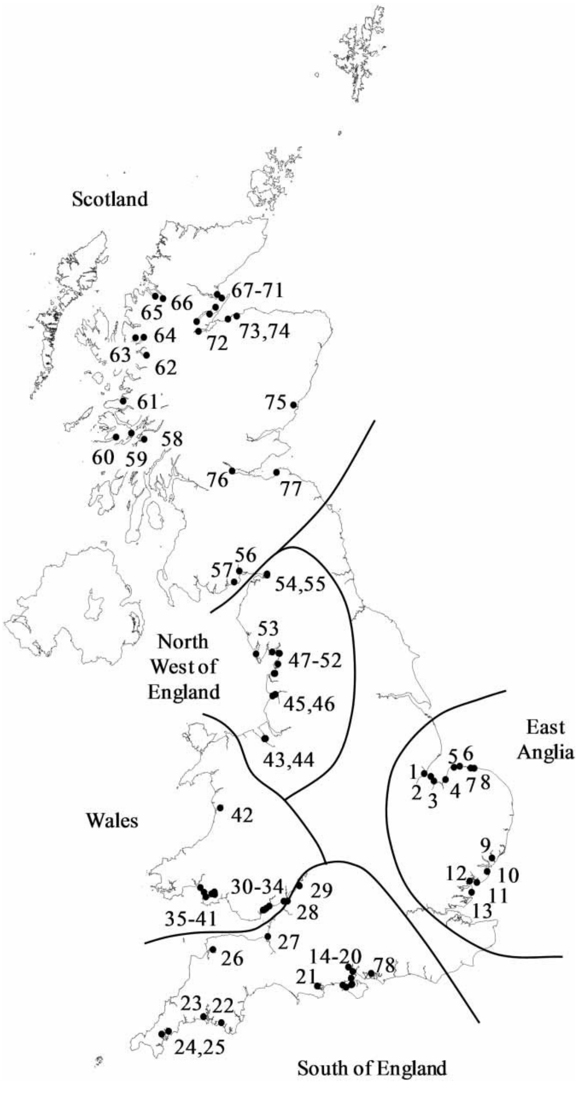


**Figure 1.** Locations of saltmarsh sites surveyed in Great Britain in 1985, 1996 and 2011, and the regional divisions used in analyses. All sites were surveyed in 1985 ($n = 78$); sites 1–8, 10–31, 36, 38–60, 67 and 69–78 were re-surveyed in 1996 ($n = 65$); sites 1–22, 24–33, 40, 42–57, 67–74 and 78 were re-surveyed in 2011 ($n = 58$).

Brindley *et al.* (1998) and Norris *et al.* (1998) grouped study sites into nine British regions based on Nature Conservancy Council (NCC) administration areas. We reduced this number to five broader geographic regions that incorporated the boundaries of the original nine (East Anglia [EA], South of England [SE], North West of England [NW], Wales and Scotland; Fig. 1) to better represent the separation between major saltmarsh biophysical types (Burd 1989) and the likely scale at which management solutions will be required. The majority of sites surveyed were SSSIs, with the exception of one site in Wales and seven sites in Scotland which had no statutory protection. Many sites also formed part of large-scale national and international protected areas, with 38, 39 and 34 sites in England (total sites = 43), 13, 14 and 4 sites in Scotland (total sites = 22) and 10, 10 and 13 sites in Wales (total sites = 13) forming part of Ramsar sites, SPAs and SACs respectively.

Where it was sensible to do so, to minimize the variation in habitat and management within study units, sites were split into sub-plots separated by changes in topography (e.g. the presence of major creeks) which represented barriers between different grazing regimes and homogeneous habitat zones (mean no. of plots per site = 1.7, range = 1–5; mean plot area = 31.8 ha, range = 4.7–257 ha; total no. of sites/plots surveyed in 1985 = 130, 1996 = 111, 2011 = 96). In 2011, three teams of two surveyors covered sites in East Anglia (sites 1–13), the South of England (sites 14–21, 27–29 and 78) and the North West of England (sites 43–55); the remaining sites in the South of England, Scotland and Wales were surveyed by experienced volunteers.

## Breeding Redshank surveys

Breeding Redshank were surveyed using standard methods developed by Green *et al.* (1984) and Green (1986) as described in Brindley *et al.* (1998). All sites were visited three times between mid-April and the end of May with at least 10 days between survey visits, with surveyors walking a standard route developed for each site which approached 100 m of all areas. The timing of surveys was governed by the tide, with access to most sites only possible when tides were low or receding. No surveys were undertaken in rain or winds greater than Gale Force 5. For each site or plot (for larger sites), the mean total number of Redshank counted on survey visits up to 31 May, excluding flocks of more than six individuals and pairs behaving as if they had young, was used as an estimate of the peak number of nesting pairs (Green *et al.* 1984, Smart *et al.* 2006). Numbers of pairs at the plot-level were divided by the area of the plot to give plot-level Redshank breeding density estimates (pairs km$^{-2}$). Site-level density estimates (pairs km$^{-2}$) were calculated by summing the number of pairs across all plots within a site and dividing this total by the area of the site.

Ordnance Survey (OS) maps with hand-drawn site/plot boundaries were used to record historical survey data, with site areas (ha) estimated by eye from these maps in 1985. To provide blank maps for surveyors in 2011, historical boundaries were digitally redrawn by hand and the site areas (Cartesian ha) estimated within a GIS programme (MapInfo Professional v.6 2000). Although historical site boundaries were digitized as accurately as possible in 2011, there were small differences in the site areas estimated from the 1985 and 2011 maps (paired $t$-test: mean difference in area = 2.7 ha ±1.17 se, $t = 2.31$, $P < 0.05$). Though these small differences are likely to result from the greater accuracy of GIS area estimation compared to visual estimation techniques, a true difference in the area surveyed would affect density estimates if the same area estimate was used in all years. To control for this, the site areas estimated by eye from historical survey maps were used to estimate breeding densities in 1985 and 1996, with 2011 GIS area estimates used to calculate 2011 breeding densities.

### Estimating Redshank abundance and conservation status

Regional density estimates were calculated by averaging observed site-level Redshank breeding density (pairs km$^{-2}$) across sites in England, Scotland, Wales and within the three English regions (EA, NW and SE). A bootstrapping procedure was then used to calculate 95% confidence limits around these observed means: breeding densities at sites in each region in each survey year were randomly re-sampled with replacement 999 times, a mean density value was calculated for each of the 999 re-samples in each region/year, and the 2.5% and 97.5% percentiles from the resulting distributions of mean densities used as the 95% confidence limits for the observed mean density for that region/year (Brindley *et al.* 1998). Estimates for Great Britain were calculated by summing observed means and bootstrapped confidence limits from England, Scotland and Wales.

Regional density estimates were then divided by the proportion of the area surveyed that was vegetated in 1985 (Redshank nest on vegetated saltmarsh only; proportion vegetated in Great Britain = 75.93%, England = 83.51%, Scotland= 88.91%, Wales = 50.17%, EA = 96.86%, NW = 84.25%, SE = 70.87%; Brindley *et al.* 1998). We found no evidence to suggest that the area of vegetated saltmarsh had changed significantly between survey years on our study plots (1985–1996: $t = -0.20$, df = 82, $P > 0.05$; 1985–2011: $t = -0.19$, df = 73, $P > 0.05$; 1996–2011: $t = 0.51$, df = 66, $P > 0.05$). Finally, these corrected density estimates were multiplied by the total area of vegetated saltmarsh as reported by the 1989 Saltmarsh Survey of Great Britain (Burd 1989) to provide an estimate of the total number of breeding pairs present in each region in each year. The extent of vegetated saltmarsh across England and Wales has not changed substantially since 1989, although individual estuaries have experienced differing levels of accretion/erosion (Phelan *et al.* 2011).

Sites re-surveyed in Scotland in 1996 had significantly higher densities in 1985 than the sites which were not resurveyed (see the Endnote and Brindley *et al.* 1998). To prevent this bias resulting in inflated population estimates for Scotland, density estimates expected on sites not resurveyed in 1996 in Scotland were estimated using the linear equation $y = 0.378x + 4.273$, relating breeding density at all sites surveyed in both 1985 ($x$) and 1996 ($y$); this equation differs slightly to that reported in Brindley *et al.* (1998) due to corrections made to the dataset in 2011 and the addition of Langstone Harbour. Although not all sites in Wales were resurveyed in 1996, and not all sites in Wales or Scotland were resurveyed in 2011, we found no evidence to suggest that these sites had significantly different densities in 1985 to those resurveyed (see Endnote). The majority of sites in England (42 of 43) were resurveyed in both 1996 and 2011.

Trends in regional Redshank populations were determined by calculating the absolute change in site-level breeding density at each site (e.g. 1996 density minus 1985 density) across three time periods (1985–1996, 1996–2011, 1985–2011), using data from sites surveyed in both years only. The observed mean changes, averaged across all sites within each region, were then calculated and 95% confidence intervals around these means estimated using bootstrapping procedures as above (Brindley *et al.* 1998). Mean density changes and confidence limits were again corrected for the area of vegetated saltmarsh by dividing by the proportion of the area surveyed that was vegetated in 1985. Density estimates for sites in Scotland not resurveyed in 1996 (based on 1985 densities and the regression equation as above) were not included.

Redshank abundance and conservation status estimates were recalculated for the 1985 and 1996 survey years and 1985–1996 survey period due to the inclusion of data from the additional site in the South of England (Langstone Harbour).

## Grazing and management

We collected basic information on grazing and protected area/AES management during breeding Redshank surveys. Grazing pressure on each site/plot was scored on a 4-point scale in all three survey years (0 = no grazing, 1 = light grazing, 2 = moderate grazing, 3 = heavy grazing) in relation to the vegetation communities present, the physical evidence of grazing (height of vegetation, hoof prints, faeces) and the number and type of livestock present, following the methods described by Allport *et al.* (1986). The grazing levels characterizing these categories could be described as: 0 = matted vegetation, no standing crop removed; 1 = majority of standing crop not removed; 2 = majority of standing crop removed; 3 = all standing crop removed, sward height < 10cm (Environment Agency 2005). Although it represents an indirect measure of grazing intensity, this scoring method has been shown to reflect actual livestock activity reasonably well (Norris *et al.* 1997). As grazing pressure information was recorded in less than 10 sites/plots in Scotland and Wales in 2011, these regions were excluded from region-specific investigations of grazing pressure change.

The inclusion of English sites in AES and the date when such schemes began (all after 1996) were provided by Natural England (an English Governmental organization), as were the designation of sites as National Nature Reserves (NNRs) managed by Natural England, or privately managed nature reserves (which may or may not be part of NNRs). Only sites with active Higher Level Stewardship AES agreements (options HP5/HP6: Maintenance/Restoration of coastal saltmarsh) or Countryside Stewardship AES agreements (option IT1: Managing inter-tidal habitats) were considered to be implementing AES management relevant to breeding Redshank ecology (such as sympathetic grazing management; DEFRA 2004, Natural England 2010a). Privately managed nature reserves either had active AES agreements with options HP5/HP6 or IT1, or were considered likely to be implementing beneficial saltmarsh management similar to that prescribed by these options. Management on Natural England-managed saltmarsh NNRs is also similar to that prescribed under the AES options HP5/HP6 and IT1 (Natural England 2010b). Due to these similarities, all sites with operational AES agreements or managed as part of NNRs or other nature reserves were categorized as implementing some sympathetic conservation management (conservation-managed: ConsMan) compared to sites without any formal conservation management scheme (no-ConsMan). No reliable AES or nature reserve management information was available for Scotland or Wales, so these regions were not included in management investigations.

To determine whether grazing management had changed since 1996 across England, regionally and on plots implementing conservation management, we ran a multivariate linear mixed model (LMM) using the lme function in R (package nlme; Pinheiro *et al.* 2009, R Development Core Team 2009) with plot-level grazing pressure as a continuous response variable. This allowed the inclusion of study plot (PLOT) as a random intercept term to control for the non-independence of repeated grazing pressure measures between survey years on the same site/plot. Models included the independent effects of survey Year (1996, 2011), conservation management (ConsMan, no-ConsMan), Region (EA, NW, SE) and all two- and three-way interactions between these factors. Pairwise contrasts between all category combinations were conducted by changing the reference level of the three-way interaction term (Trebilco *et al.* 2010, Mueller *et al.* 2011). To determine whether breeding Redshank had responded to changes in grazing or conservation management, we repeated this modelling process using the number of Redshank breeding pairs per plot (rounded to the nearest pair) as the response variable in a generalized linear mixed model (GLMM) with a Poisson error distribution, and with the natural log of plot area ($km^2$) as an offset term. Models specified in this way return estimates of breeding density (pairs $km^{-2}$). We used the function glmmPQL (in R, package MASS; Venables & Ripley 2002), which accounted for zero-inflation (overdispersion) in the response variable by estimating and incorporating an overdispersion parameter in the model.

## RESULTS

### Redshank abundance and conservation status

We estimate the saltmarsh breeding Redshank population to have been 21 431 pairs in 1985, declining to 17 007

**Table 1.** Regional and national population estimates for Redshank breeding on saltmarshes in Great Britain. Observed mean densities and estimated numbers of breeding pairs are reported with bootstrapped 95% confidence intervals (in parentheses). Data on the area of vegetation saltmarsh are from Burd (1989). Population estimates for Great Britain were obtained by summing the population sizes of England, Wales and Scotland for each survey. 1985 and 1996 estimates are comparable to those presented by Brindley *et al.* (1998) but differ slightly due to the random nature of the bootstrapping procedure and the inclusion of an additional site (78, Langstone Harbour).

| Population | Density (pairs km$^{-2}$) 1985 | Density (pairs km$^{-2}$) 1996 | Density (pairs km$^{-2}$) 2011 | Saltmarsh area (ha) | Breeding pairs 1985 | Breeding pairs 1996 | Breeding pairs 2011 |
|---|---|---|---|---|---|---|---|
| England | 54.99 | 46.15 | 32.47 | 31 066 | 17 083 | 14 338 | 10 086 |
| | (42.95–66.54) | (35.50–57.71) | (23.92–43.25) | | (13 344–20 670) | (11 028–17 928) | (7430–13 437) |
| *East Anglia* | 66.75 | 57.61 | 50.59 | 12 747 | 8508 | 7344 | 6449 |
| | (52.67–82.72) | (47.02–67.62) | (35.06–68.83) | | (6714–10 544) | (5993–8619) | (4468–8773) |
| *North West* | 55.81 | 40.30 | 26.99 | 10 557 | 5892 | 4255 | 2850 |
| | (38.89–73.63) | (27.65–55.02) | (15.22–40.65) | | (4105–7773) | (2919–5808) | (1607–4291) |
| *South* | 43.40 | 42.14 | 18.16 | 4712 | 2045 | 1986 | 856 |
| | (20.75–69.48) | (17.32–70.27) | (8.10–30.43) | | (978–3274) | (816–3312) | (382–1434) |
| Scotland | 26.51 | 14.83 | 5.73 | 5969 | 1582 | 885 | 342 |
| | (16.67–36.84 | (9.07–20.74) | (1.56–10.60) | | (995–2199) | (542–1238) | (93–633) |
| Wales | 40.98 | 26.43 | 22.51 | 6748 | 2765 | 1784 | 1519 |
| | (21.07–69.11) | (8.26–48.43) | (9.83–34.89) | | (1422–4664) | (558–3268) | (663–2354) |
| Great Britain | | | | 43 783 | 21 431 | 17 007 | 11 946 |
| | | | | | (15 761–27 532) | (12 127–22 434) | (8186–16 424) |

pairs in 1996 and further declining to 11 946 pairs in 2011 (Table 1). Breeding densities were significantly higher in England than in Scotland or Wales in all three survey years, with each country supporting 84%, 3% and 13% of the British population respectively in 2011. Within England, East Anglia supported the largest number of pairs, with 84% of pairs in 2011 found in this region, compared to 28% and 8% found in the North West and South of England respectively.

Redshank breeding density declined significantly across Great Britain in all three time periods (1985–1996, 1996–2011 and 1985–2011), with an overall loss of 28.82 pairs km$^{-2}$ since 1985 (Table 2). Redshank breeding density also declined in all regions and across

**Table 2.** Changes in Redshank density 1985–1996, 1996–2011, and 1985–2011. Observed mean changes in density (pairs km$^{-2}$) are shown along with bootstrapped 95% confidence limits (in parentheses). Means and confidence limits were corrected to give estimates of the change in Redshank density for vegetated saltmarsh. Negative values indicate declines in density; positive values indicate increases. 1985–1996 estimates are comparable to those presented by Brindley *et al.* (1998) but differ slightly due to the random nature of the bootstrapping procedure and the inclusion of an additional site (78, Langstone Harbour).

| Population | Density change 1985–1996 | Significance | Density change 1996–2011 | Significance | Density change 1985–2011 | Significance |
|---|---|---|---|---|---|---|
| England | –8.38 | | –14.46 | | –23.83 | |
| | (–18.76 to +1.31) | n.s. | (–25.48 to –4.09) | * | (–34.67 to –13.27) | *** |
| *East Anglia* | –9.37 | | –4.09 | | –16.16 | |
| | (–22.88 to +4.56) | n.s. | (–20.85 to +12.77) | n.s. | (–35.72 to +6.12) | n.s. |
| *North West* | –15.50 | | –13.31 | | –28.81 | |
| | (–39.15 to +6.29) | n.s. | (–30.07 to +4.46) | n.s. | (–47.16 to –8.54) | ** |
| *South* | –1.26 | | –26.61 | | –27.95 | |
| | (–14.72 to +11.25) | n.s. | (–50.19 to –7.29) | *** | (–49.71 to –10.34) | *** |
| Scotland | –16.02 | | –2.67 | | –23.01 | |
| | (–26.94 to –6.55) | *** | (–9.37 to +4.32) | n.s. | (–37.11 to –8.92) | ** |
| Wales | –5.89 | | –11.95 | | –32.12 | |
| | (–20.42 to +9.74) | n.s. | (–37.29 to +13.38) | n.s. | (–75.54 to +0.73) | n.s. |
| Great Britain | –10.76 | | –13.18 | | –25.82 | |
| | (–17.84 to –2.79) | ** | (–22.70 to –4.24) | ** | (–36.56 to –15.20) | *** |

Significance: $P < 0.05$ (*); $P < 0.01$ (**); $P < 0.001$ (***); not significant (n.s.).

all time periods, although confidence limits show that few of these declines were significant. The decline in density across Great Britain as a whole between 1985 and 1996 can be explained by a significant decline in Scotland during this time period (Table 2). Similarly, the British decline between 1996 and 2011 can be explained by a significant decline in the South of England. Across the whole 26 years covered by the three surveys, British declines are explained by the significant declines in these two regions, as well as a decline in the North West of England which became significant across this longer timescale.

We estimate that if mean changes in Redshank density across Great Britain are assumed to reflect density changes across the total area of vegetated saltmarsh (43 782 ha; Burd 1989), then 4713 breeding pairs were lost between 1985 and 1996 (95% confidence intervals: 1223–7811 pairs), 5770 pairs were lost between 1996 and 2011 (1858–9940 pairs), and 11 306 pairs were lost across the 26 years between 1985 and 2011 (6655–16 008 pairs). This represents a decline of 22.0% (5.7–36.4%) between 1996 and 1985, a decline of 26.9% (8.7–46.4%) between 1996 and 2011 and an overall decline of 52.8% of breeding pairs (31.1–74.7%) between 1985 and 2011, at a rate of 2.0% of breeding pairs (1.2–2.9%) or 1 pair km$^{-2}$ (0.6–1.4 pair km$^{-2}$) on average per year.

## Grazing and management

Redshank breeding densities were higher on lightly and moderately grazed plots compared to ungrazed or heavily grazed plots in 2011 (Fig. 2c). Although not significant, this pattern was similar to those found in 1985 and 1996 by Norris *et al.* (1998; Fig. 2a,b), where heavily grazed sites supported significantly

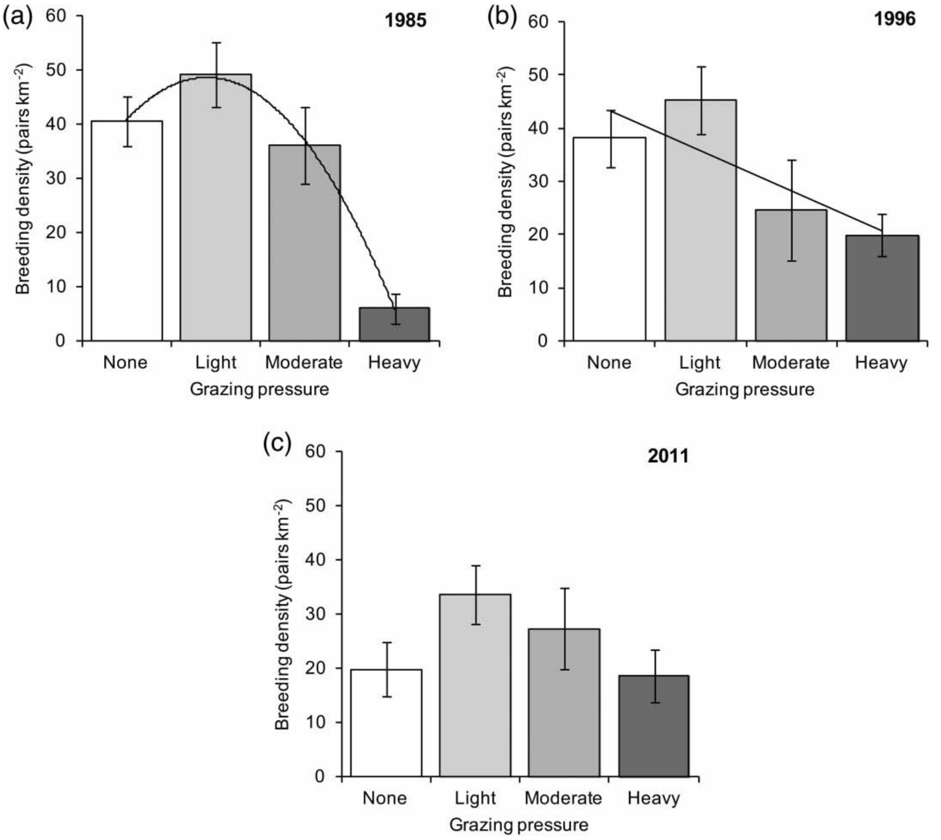


**Figure 2.** Mean (± se) Redshank breeding density (pairs km$^{-2}$) in relation to grazing pressure across all sites surveyed in (a) 1985, (b) 1996 and (c) 2011 where both Redshank and grazing pressure data were available. Figures (a) and (b) are redrawn from Norris *et al.* (1998) including data from an additional site (78, Langstone Harbour). The linear regression relationships between plot-level Redshank breeding density and grazing pressure indicated by solid lines in (a) and (b) are described by the functions $y = 40.79 + 17.64x - 9.81x^2$ ($F_{2,127} = 6.14$, $P < 0.01$) and $y = 43.47 - 7.14x$ ($F_{1,99} = 7.5$, $P < 0.01$), respectively (also see Norris *et al.* 1998). No significant linear relationship was found in 2011 ($y = 20.71 + 17.89x - 6.30x^2$, $F_{2,84} = 2.34$, $P = 0.10$).

**Table 3.** Effects of saltmarsh conservation management on (a) grazing pressure and (b) Redshank breeding density (pairs km$^{-2}$) on saltmarsh plots in England between 1996 and 2011. Shown are outputs (degrees of freedom, *F*-values and significance) from multivariate mixed models controlling for the influence of study plot (random term) and testing the effects of survey year, conservation management and region along with their two- and three-way interactions. For biological significance and parameter estimates see Fig. 3. In (a), grazing pressure was modelled as a normally distributed continuous variable in a LMM. In (b), Redshank breeding density was modelled by using the number of Redshank breeding pairs per plot as the response variable in a GLMM with ln plot area (km$^{-2}$) as an offset term, specifying an overdispersed-Poisson error distribution and log-link.

| | | Factor *(categories)* | df | *F*-value | *P*-value |
|---|---|---|---|---|---|
| (a) | Grazing pressure | Year *(1996, 2011)* | 1, 128 | 0.0 | 0.92 |
| | | Management *(ConsMan, no-ConsMan)* | 1, 128 | 2.7 | 0.10 |
| | | Region *(EA, NW, SE)* | 2, 128 | 64.1 | <0.001 |
| | | Year : Management | 1, 128 | 1.1 | 0.30 |
| | | Year : Region | 2, 128 | 2.0 | 0.14 |
| | | Management : Region | 2, 128 | 1.6 | 0.21 |
| | | Year : Management : Region | 2, 128 | 0.3 | 0.73 |
| | | Random term: PLOT, sd = 0.71; Residual, sd = 0.51 | | | |
| (b) | Redshank breeding density | Year *(1996, 2011)* | 1, 146 | 4.3 | <0.05 |
| | | Management *(ConsMan, no-ConsMan)* | 1, 146 | 12.1 | <0.001 |
| | | Region *(EA, NW, SE)* | 2, 146 | 7.2 | <0.01 |
| | | Year : Management | 1, 146 | 0.0 | 0.96 |
| | | Year : Region | 2, 146 | 1.0 | 0.39 |
| | | Management : Region | 2, 146 | 0.7 | 0.51 |
| | | Year : Management : Region | 2, 146 | 1.7 | 0.20 |
| | | Random term: PLOT, sd = 0.93; Residual, sd = 1.47 | | | |
| | | Overdispersion parameter = 2.15 | | | |

Management: ConsMan = conservation management implemented since 1996, no-ConsMan = no conservation management.
Region: EA = East Anglia, NW = North West of England, SE = South of England.

lower Redshank breeding densities than those lightly or moderately grazed.

Across England, there was no significant change in grazing pressure between 1996 and 2011 (Table 3a, Year effect; mean grazing pressure 1996 = 1.4 ±0.14 se, 2011 = 1.4 ±0.12 se, $n = 70$). Regionally, only East Anglia experienced significant changes, with grazing pressure increasing between 1996 and 2011 though from a low level (from no grazing to light grazing; Table 3a, Region effect; Fig. 3a). Grazing pressure remained consistently high in the North West of England (moderately to heavily grazed) and consistently low in the South of England (lightly to moderately grazed) between 1996 and 2011 (Fig. 3a).

Of the 81 plots in England surveyed originally in 1985, 59% were implementing conservation management by 2011. Grazing pressure was recorded on 86% of plots in both 1996 and 2011 (45 ConsMan plots, 25 no-ConsMan plots). There was no difference in grazing pressure between plots with and without conservation management before or after 1996 in any region, nor was there any overall change in grazing pressure on plots of either management category in England between 1996 and 2011 (Table 3a, Year : Management effect). Regionally, grazing pressure was similar between years on plots of both management categories in the North West and South of England where grazing remained at high and low–moderate levels respectively. The same was true on plots with no conservation management in East Anglia, although there was a significant increase from no grazing to light grazing on conservation-managed plots in this region (Table 3a; Fig. 3a).

Redshank breeding density declined on both conservation-managed plots and those with no conservation management across England between 1996 and 2011, though densities were higher overall on conservation-managed plots (Table 3b, Year and Management effects: mean pairs km$^{-2}$ in 1996 on no-ConsMan plots = 20.79 ± 6.05 se, ConsMan plots = 31.33 ± 6.81; 2011 no-ConsMan plots = 11.57 ± 3.52, ConsMan plots = 24.17 ± 5.34). Regionally, although differences in breeding density between management categories and between years on conservation-managed plots were not statistically significant, they may have been biologically important, with declines in breeding

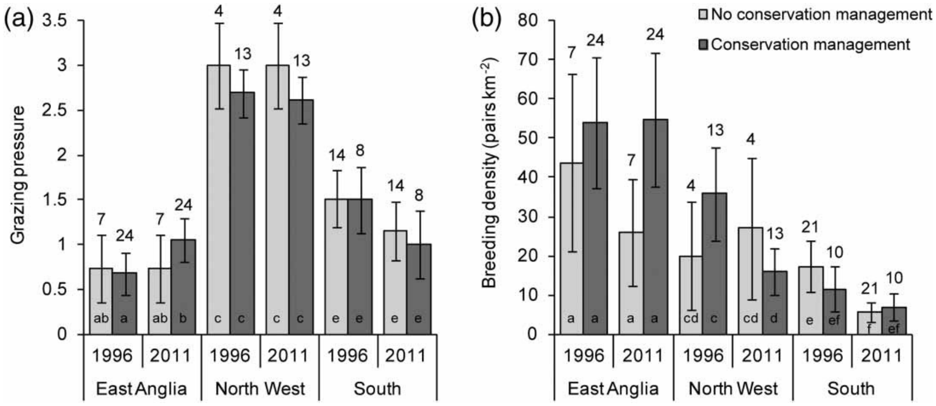


**Figure 3.** Mean ± se (a) grazing pressure and (b) Redshank breeding density (pairs km$^{-2}$) in 1996 and 2011 on plots with no conservation management (no-ConsMan) and on plots which implemented conservation management after 1996 (ConsMan) in East Anglia, the North West and the South of England. In (a), means and standard errors are those reported by a multivariate LMM that included the effects of year, management, region and all two-way and three-way interactions, with study plot as the random term (Table 3). In (b), means and standard errors were backtransformed from ln[*x*] estimates reported by a multivariate GLMM which included the same effects and random term as in (a) (standard errors were added/subtracted to the mean before backtransforming to calculate the upper/lower limits). Numbers above bars indicate sample sizes (number of plots) for each factor level combination. Letters a–b, c–d and e–f show the results of pairwise comparisons between factor level combinations for East Anglia, the North West and South of England respectively, different letters indicating significant differences.

density less severe on conservation-managed plots in East Anglia and the South of England (Table 3b, Fig. 3b). A reduction in mean density of over 17 pairs km$^{-2}$ (more than the decline identified across Great Britain over the same time period, Table 2) occurred on plots with no conservation management in East Anglia, while densities on conservation-managed plots remained stable (Fig. 3b). In the South of England, densities declined by 12 pairs km$^{-2}$ on plots with no conservation management, while only declining by 5 pairs km$^{-2}$ on conservation-managed plots (Fig. 3b). Redshank densities declined statistically significantly on conservation-managed plots in the North West of England, while remaining stable on plots with no conservation management (Fig. 3b). Densities were also higher on conservation-managed plots than on plots with no conservation management in 1996, but lower on conservation-managed plots in 2011 in this region, though this difference in effect direction was not statistically significant (Table 3b, Year : Region : Management effect; Fig. 3b).

## DISCUSSION

The 2011 survey results suggest that the decline in saltmarsh Redshank abundance and breeding density identified in 1996 has continued at a constant rate, with an average loss of 2% of breeding pairs or 1 pair km$^{-2}$ year$^{-1}$. The magnitude of this trend varies between British regions, with declines in Scotland 1985–1996, the South 1996–2011 and the North West of England 1985–2011 driving the national decline since 1985. This negative trend is in sharp contrast with that of other European breeding Redshank, where saltmarsh populations have remained relatively stable despite widespread declines in inland habitats (Koffijberg *et al.* 2006, Hötker *et al.* 2007a, 2007b, JMBB 2010). We estimate that there has been a 52.8% reduction in the number of breeding pairs on British saltmarsh, which equates to a loss of almost a quarter of the total UK breeding population and a 4–6% reduction in the European population since 1985 (assuming 45% of British Redshank breed on the coast, and 18% of European Redshank breed in Britain; Reed 1985, Piersma 1986, Batten *et al.* 1990, Brindley *et al.* 1998, BirdLife International 2004a, 2004b). The continued decline on British saltmarsh is therefore of both national and international concern.

Although it is possible that the differences in abundance between surveys on which our population trend estimates are based are simply the result of inter-annual variation in breeding density and site selection, this is unlikely. Annual survey data from sites in two regions where such evidence exists also indicate significant negative trends in Redshank density since 1985, with the rate of decline in both regions approximating to the 1 pair km$^{-2}$ year$^{-1}$ loss identified by the national survey (Fig. 4). It is also unlikely that

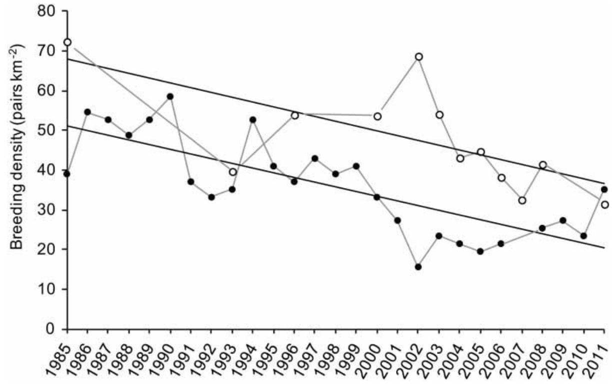


**Figure 4.** Redshank breeding density (pairs km$^{-2}$) recorded during annual surveys of saltmarsh at Langstone Harbour in the South of England (site 78; closed circles) and three saltmarsh sites in Essex, East Anglia (site 10 Hamford Water, 11 Colne Point and 12 Ray Island; open circles). Each circle represents an annual survey; dotted lines between circles represent gaps of more than one year between surveys. The linear regression of breeding pairs on year for each area (straight solid lines) indicate significant negative trends in Redshank breeding density (Langstone Harbour $y = -1.18x + 52.19$, $F_{1,24} = 34.4$, $P < 0.001$; Essex, East Anglia $y = -1.21x + 69.24$, $F_{1,10} = 8.4$, $P < 0.05$).

the declines seen on saltmarsh represent a migration of pairs away from the coast, as British census data suggest that inland populations have not increased at a comparable rate (O'Brien 2001, Wilson *et al.* 2005, Dillon *et al.* in prep.). The changes in breeding density observed on saltmarsh are therefore likely to represent a true population decline.

Saltmarshes in Great Britain have experienced several changes that may influence Redshank breeding success and therefore drive declines in breeding density. Although the majority of sites are now protected from agricultural drainage and land claim, many have been abandoned, become more heavily grazed or have undergone changes in livestock type (Norris *et al.* 1997, 1998), with pressures from wild grazers also increasing in some regions (Kirby 1995, Hannaford *et al.* 2006). Site abandonment or large increases in grazing intensity from an optimum low–moderate level (0.5–1 cow ha$^{-1}$ or 1.5–3 sheep ha$^{-1}$; Kiehl *et al.* 1996, Berg *et al.* 1997, Norris *et al.* 1997, 1998, Esselink *et al.* 2000, Ausden *et al.* 2005; Fig. 2) can result in a loss of vegetation communities and the sward heterogeneity required by Redshank for nesting and feeding (Hale 1988, Norris *et al.* 1997, Milsom *et al.* 2000, Smart 2005), creating either long, rank or short, uniform swards, respectively (Andresen *et al.* 1990, Kiehl *et al.* 1996, Bouchard *et al.* 2003). Grazing changes may also influence the abundance and diversity of invertebrate species (Meyer *et al.* 1995, Ford *et al.* 2012), potentially limiting Redshank prey resources. Even sites with suitable sward structures may act as ecological traps for Redshank if grazing pressures are unsuitable: high stocking rates or an early onset of grazing (April–May) are likely to increase nest losses from trampling (Green *et al.* 1984, Smart 2005, Pakanen *et al.* 2011), and nest susceptibility to predation may increase (Thyen & Exo 2004) if livestock create pathways through vegetation and expose nest sites. For these reasons, it is reasonable to assume that the sustained heavy grazing now characteristic of saltmarsh management in the North West of England (Fig. 3a; having risen from a mean grazing pressure of 1.5 ± 0.24 se in 1985) is the main driver of Redshank density declines in this region (Table 2, Fig. 3b).

Conservation management – currently the only mechanism through which grazing pressure and other habitat conditions on existing saltmarsh may be improved – was unsuccessful at lowering grazing pressures in the North West of England, and this lack of change is the likely reason for the significant drop in Redshank density on managed plots in this region. There was also no effect of conservation management on grazing across England as a whole, and Redshank density declined across Britain in spite of conservation management and the SSSI status of most sites, indicating that in their current form neither conservation management nor site designation represent an effective means to manage saltmarsh grazing and are therefore unlikely to provide a conservation solution for Redshank. The success of management did however differ between regions, with limited success in the South of England and East Anglia. Here, though grazing remained largely unchanged, Redshank breeding density remained stable or declined less severely on conservation-managed plots (grazing pressure changes in East Anglia are unlikely to be the result of management intervention, because on 70% of the plots where increases in grazing were recorded the only grazers present were wild geese).

Conservation management may fail to deliver nationally or in any region if (i) the guidelines supplied to landowners are insufficiently detailed, (ii) those guidelines are not suitably enforced, or (iii) there is a lack of understanding of the need to improve particular management aspects, such as the grazing regime. In contrast, it is possible that conservation management may benefit or appear to benefit Redshank despite having no apparent effect on grazing if (i) grazing improved, but in a way that we could not detect (e.g. starting later in the year or with reduced stocking rates), (ii) Redshank benefit from an aspect of management other than grazing manipulation (such as the retention of seaweed accumulations and reduction in fertilizer inputs (Natural England 2010a) potentially leading to a more diverse invertebrate prey community), or (iii) Redshank responses on managed plots are related to better a priori habitat quality rather than any true conservation effect. Without detailed knowledge of the saltmarsh grazing regimes in use, however, or the details of individual AES agreements and management plans, we have no way of determining what aspect of conservation management is failing in the North West, why it may be working in other regions, or how it could be improved. Further research is urgently needed to establish how improvements to existing and future schemes can be made.

Redshank breeding densities declined in the South of England and East Anglia between 1996 and 2011 (Table 2) despite the fact that grazing pressures remained within the low–moderate range preferred by nesting Redshank (Figs 2 & 3a). This suggests that factors other than grazing such as the effects of predation or environmental change may be driving trends in density in these regions. Although predation often limits the population recovery of wader species breeding on inland habitats (MacDonald & Bolton 2008), and can account for up to 50–80% of the daily mortality of Redshank nests on saltmarsh (Green *et al.* 1984, Smart 2005, Thyen & Exo 2004, Thyen *et al.* 2005), the extent to which predation impacts on saltmarsh Redshank population trends, and whether predation rates on saltmarshes in Britain have changed in recent decades, is unclear.

Conversely, sea-level rise driven by isostatic land movements (Woodworth 1987, Shennan 1989, Shennan & Horton 2002) and climate change (Woodworth *et al.* 1999, Church *et al.* 2001, Smart & Gill 2003) have caused and may increasingly lead to the direct loss of saltmarsh habitats suitable for Redshank nesting on the south and east coasts of Britain, either through erosion (Harmsworth & Long 1986, Natural England 2006) or changes in vegetation communities (Boorman 1992), particularly where saltmarsh is squeezed against hard sea defences preventing natural landward migration (Doody 2004). Increases in the frequency of tidal inundation through more frequent storm events may also directly affect Redshank breeding success by increasing rates of nest and chick mortality through flooding and drowning (van de Pol *et al.* 2010). Other climatic changes such as rising temperatures and decreased summer rainfall may also act to dry the saltmarsh surface between high tides, potentially reducing the availability of invertebrate prey and thereby limiting chick growth rates and survival (Smart 2005). As a result of these environmental changes it is highly likely that existing saltmarsh habitats in Britain, particularly in the south and east, may be lost or at least become increasingly unsuitable for Redshank breeding in the future. The conservation management of existing sites may therefore only act as a short-term solution to the problem of Redshank declines in these regions.

Longer-term solutions to combat saltmarsh loss could include the creation of new saltmarsh or the re-wetting of coastal grasslands to encourage breeding pairs away from existing saltmarsh that is eroding or in poor condition. New saltmarsh is being created with increasing frequency around the British coast through managed realignment (Pye & French 1993). However, as these newly created sites may require in excess of 80–100 years to match the community diversity and sward structure of established sites (Wolters *et al.* 2005, Garbutt & Wolters 2008, Mossman *et al.* 2012), it may be many decades before the habitat structure necessary for Redshank breeding is developed (Atkinson 2003, Smart 2005). Another conservation solution could be the rehabilitation or creation of coastal and inland wet grassland to provide compensatory habitat away from the coast (Smart 2005). Space and consent for habitat creation inland is less limited than in the coastal zone in Britain, and both rehabilitated grassland and arable reversion are successful at attracting and supporting successful populations of breeding Redshank (Smart 2005, Eglington *et al.* 2007, *et al.* 2009). Such grassland areas, in addition to surviving saltmarshes, could therefore act as source populations from which Redshank could colonize newly created saltmarsh sites once these develop suitable habitat structures.

By forming a highly visible part of the upper trophic levels of saltmarsh ecosystems, Redshank may act as an indicator of the condition of this habitat as a whole (Furness & Greenwood 1993, Boyd & Murray 2001), with rapid declines suggesting large-scale detrimental changes in saltmarsh ecology. As saltmarshes perform important ecosystem functions, with key roles in sea defence, fishery development, pollution sequestration, marine sediment and nutrient cycling (Boorman 1999), understanding these detrimental changes and developing solutions should be a high-priority conservation objective.

At the current rate of decline, breeding Redshank are likely to disappear from the majority of British saltmarshes within the next 25 years. Conservation solutions to halt this decline are therefore urgently needed. Current conservation management activities in England – where the majority of the saltmarsh population occurs – are however not delivering the necessary nesting habitat conditions, although Redshank responses to management differ between regions. Our understanding of why conservation management is not as successful as hoped, and the applicability of other more long-term solutions, is severely limited. We also have insufficient grazing pressure and conservation management data for saltmarsh sites in Scotland and Wales to draw meaningful conclusions about the likely drivers of the Redshank declines in these regions (Table 2). There is an urgent need to address these knowledge gaps, particularly our knowledge of grazing practices, regional management systems and the likely success of more long-term conservation solutions that counteract the effects of environmental change, so that the success of conservation measures can be improved.

## ACKNOWLEDGEMENTS

This survey was joint-funded by Natural England, the Centre for Ecology and Hydrology and The Royal Society for the Protection of Birds. We are grateful to private landowners and site managers for allowing access to saltmarsh sites, and to Natural England for organizing SSSI access and providing information on AES agreements. Special thanks go to the research assistants and volunteers who conducted survey work: H. Bernie, M. Carrier, N. Chambers, C. Cockburn, N. Cottle, G. Davies, S. Elliott, D. Fairlamb, A. Feather, C. Foot, C. Hodgson, A. Horn-Norris, K. Horsfall, K. Jones, H. Jones, R. Jones, K. Leslie, B. Mitchell, M. Passman, N. Redpath, E. Sharps, K. Sharps, S. Sheldon, E. Smith, D. Tomes, S. Tyler, A. Venables and W. Venables.

## ENDNOTE

a. Sites in Scotland re-surveyed in 1996: $n = 15$, mean ± se pairs km$^{-2}$ in 1985 = 29.8 ± 5.52; sites not re-surveyed: $n = 7$, mean ± se pairs km$^{-2}$ in 1985 = 10.3 ± 6.53; $t = 2.3$, df = 14.5, $P < 0.05$. Sites in Wales re-surveyed in 1996: $n = 8$, mean ± se pairs km$^{-2}$ in 1985 = 16.2 ± 5.24; sites not re-surveyed: $n = 5$, mean ± se pairs km$^{-2}$ in 1985 = 27.5 ± 14.35; $t = -0.7$, df = 5.1, $P = 0.49$. Sites in Scotland re-surveyed in 2011: $n = 10$, mean ± se pairs km$^{-2}$ in 1985 = 25.6 ± 5.72; sites not re-surveyed: $n = 12$, mean ± se pairs km$^{-2}$ in 1985 = 21.9 ± 7.27; $t = 0.4$, df = 19.6, $P = 0.70$. Sites in Wales re-surveyed in 2011: $n = 6$, mean ± se pairs km$^{-2}$ in 1985 = 27.4 ± 13.04; sites not re-surveyed: $n = 7$, mean ± se pairs km$^{-2}$ in 1985 = 14.7 ± 3.18; $t = 1.0$, df = 5.6, $P = 0.38$.

## REFERENCES

**Allport, G., O'Brien, M. & Cadbury, C.J.** 1986. *Survey of Redshank and other Breeding Birds on Saltmarshes in Britain 1985*. CSD Report no. 649. Nature Conservancy Council, Peterborough.

**Andresen, H., Bakker, J.P., Brongers, M., Heydemann, B. & Irmler, U.** 1990. Long-term changes of salt marsh communities by cattle grazing. *Vegetatio* **89:** 137–148.

**Atkinson, P.W.** 2003. Can we recreate or restore intertidal habitats for shorebirds? *Wader Study Group Bull* **100:** 67–72.

**Ausden, M., Badley, J. & James, L.** 2005. The effect of introducing cattle grazing to saltmarsh on densities of breeding redshank *Tringa totanus* at Frampton Marsh RSPB Reserve, Lincolnshire, England. *Conserv Evid* **2:** 57–59.

**Bakker, J.P.** 1985. The impact of grazing on plant communities, plant populations and soil conditions on salt marshes. *Plant Ecol* **62:** 391–398.

**Batten, L.A., Bibby, C.A., Clement, P., Elliott, G.D. & Porter, R.F.** 1990. *Red Data Birds in Britain*. Poyser, London.

**Berg, G., Esselink, P., Groeneweg, M. & Kiehl, K.** 1997. Micropatterns in *Festuca rubra*-dominated salt-marsh vegetation induced by sheep grazing. *Plant Ecol* **132:** 1–14.

**BirdLife International** 2004a. *Birds in Europe: Population Estimates, Trends and Conservation Status*. BirdLife International, Cambridge.

**BirdLife International** 2004b. *Birds in the European Union: A Status Assessment*. BirdLife International, Wageningen, The Netherlands.

**Boorman, L.A.** 1992. The environmental consequences of climatic change on British salt marsh vegetation. *Wetlands Ecol Manage* **2:** 11–21.

**Boorman, L.A.** 1999. Salt marshes – present functioning and future change. *Mangroves Salt Marshes* **3:** 227–241.

**Bouchard, V., Tessier, M., Digaire, F., Vivier, J.-P., Valery, L., Gloaguen, J.-C. & Lefeuvre, J.-C.** 2003. Sheep grazing as a management tool in Western European saltmarshes. *Comptes Rendus Biologies* **326:** S148–S157.

**Boyd, I.L. & Murray, A.W.A.** 2001. Monitoring a marine ecosystem using responses of upper trophic level predators. *J Anim Ecol* **70:** 747–760.

**Brindley, E., Norris, K., Cook, T., Babbs, S., Brown, C.F., Massey, P., Thompson, R. & Yaxley, R.** 1998. The abundance and conservation status of redshank *Tringa totanus* nesting on saltmarshes in Great Britain. *Biol Conserv* **86:** 289–297.

**Burd, F.** 1989. *The Saltmarsh Survey of Great Britain*. Research and Survey in Nature Conservation, No. 17, Peterborough: Nature Conservancy Council.

**Church, J.A., Gregory, J.M., Huybrechts, P., Kuhn, M., Lambeck, K., Nhuan, M.T., Qin, D. & Woodworth, P.L.** 2001. Changes in sea level. In Houghton, J.T. (ed.), *Climate Change 2001 – The Scientific Basis*: 639–694. Cambridge University Press, Cambridge.

**Davidson, N.C., Laffoley, D., Doody, J.P., Way, L.S., Gordon, J., Key, R., Pienkwoski, M.W., Mitchell, R. & Duff, K.L.** 1991. *Nature Conservation and Estuaries in Great Britain*. Nature Conservancy Council (JNCC), Peterborough.

**DEFRA** 2004. *The Countryside Stewardship Scheme (CSS) 2004: Information and How to Apply.* DEFRA (Department for Environment, Food and Rural Affairs), London.

**Dillon, I.A., Smart, J., Wotton, S.R., Cooke, A.I., Diack, I., Drewitt, A.L., Grice, P.V. & Gregory, R.D.** *in prep*. Conservation of lowland wet grassland breeding waders: positive benefits of site designation and agri-environment schemes in England.

**Doody, J.P.** 2004. Coastal squeeze – an historical perspective. *J Coast Conserv* **10:** 129–138.

**Eaton, M.A., Brown, A.F., Noble, D.G., Musgrove, A.J., Hearn, R.D., Aebischer, N.J., Gibbons, D.W., Evans, A. & Gregory, R.D.** 2009. Birds of Conservation Concern 3: the population status of birds in the United Kingdom, Channel Islands and Isle of Man. *Br Birds* **102:** 296–341.

**Eglington, S.M., Gill, J.A., Bolton, M. & Smart, M.A.** 2009. Reversion of arable land to wet grassland for breeding waders. *Conserv Land Manage* **7:** 5–9.

**Eglington, S.M., Gill, J.A., Bolton, M., Smart, M.A., Sutherland, W.J. & Watkinson, A.R.** 2007. Restoration of wet features for breeding waders on lowland wet grassland. *J Appl Ecol* **45:** 305–314.

**Environment Agency** 2005. *Saltmarsh Management Manual*. Environment Agency, DEFRA, Bristol. www.saltmarshmanagementmanual.co.uk.

**Esselink, P., Zijlstra, W., Dijkema, K.S. & Diggelen, R.v.** 2000. The effects of decreased management on plant-species distribution patterns in a salt marsh nature reserve in the Wadden Sea. *Biol Conserv* **93:** 61–76.

**Ford, H., Garbutt, A., Jones, L. & Jones, D.L.** 2012. Grazing management in saltmarsh ecosystems drives invertebrate diversity, abundance and functional group structure. *Insect Conserv Divers*. doi: 10.1111/j.1752-4598.2012.00202.x: 1–12.

**Furness, R.W. & Greenwood, J.J.D.** 1993. *Birds as Monitors of Environmental Change*. Chapman and Hall, London.

**Garbutt, A. & Wolters, M.** 2008. The natural regeneration of salt marsh on formerly reclaimed land. *Appl Veget Sci* **11:** 335–344.

**Gaston, K.J., Charman, K., Jackson, S.F., Armsworth, P.R., Bonn, A., Briers, R.A., Callagham, C.S.Q., Catchpole, R., Hopkins, J., Kunin, W.E., Latham, J., Opdam, P., Stoneman, R., Stroud, D.A. & Tratt, R.** 2006. The ecological effectiveness of protected areas: the United Kingdom. *Biol Conserv* **132:** 76–87.

**Green, R.E.** 1986. *The Management of Lowland Wet Grassland for Breeding Waders*, Chief Scientist's Directorate, No 626. Nature Conservancy Council, Peterborough.

**Green, R.E., Collins, D. & Johnson, T.** 1984. *An Intensive Survey of Breeding Redshank on the Wash, 1984*. RSPB, Sandy.

**Hale, W.G.** 1988. *The Redshank*. Shire Natural History Series, Shire, Aylesbury.

**Hannaford, J., Pinn, E.H. & Diaz, A.** 2006. The impact of sika deer grazing on the vegetation and infauna of Arne saltmarsh. *Mar Pollut Bull* **53:** 56–62.

**Harmsworth, G.C. & Long, S.P.** 1986. An assessment of saltmarsh erosion in Essex, England, with reference to the Dengie Peninsula. *Biol Conserv* **35:** 377–387.

**Hötker, H., Jeromin, H. & Melter, J.** 2007a. [Entwicklung der Brutbestände der Wiesen-Limikolen in Deutschland – Ergebnisse eines neuen Ansatzes im Monitoring mittelhäufiger Brutvogelarten]. *Vogelwelt* **128:** 49–65 (in German with an English summary).

**Hötker, H., Jeromin, H. & Melter, J.** 2007b. Monitoring grassland waders breeding in Germany. *Wader Study Group Bull* **113:** 57–65.

**JMBB** 2010. *Trends in Breeding Birds in the Wadden Sea 1991–2008*. JMBB (Joint Monitoring Group for Breeding Birds, Wilhelmshaven, Germany. Available at http://www.waddensea-secretariat.org/TMAP/Breeding_birds.html

**Kiehl, K., Eischeid, I., Gettner, S. & Walter, J.** 1996. Impacts of different sheep grazing intensities on salt marsh vegetation in northern Germany. *J Veget Sci* **7:** 99–106.

**Kirby, J.S.** 1995. Winter population estimates for selected waterfowl species in Britain. *Biol Conserv* **73:** 189–198.

**Koffijberg, K., Dijksen, L., Hälterlein, B., Laursen, K., Potel, P. & Südbeck, P.** 2006. *Breeding Birds in the Wadden Sea in 2001: Results of the Total Survey in 2001 and Trends in Numbers between 1991–2001*. Wadden Sea Ecosystem, No. 22. Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

**MacDonald, M.A. & Bolton, M.** 2008. Predation on wader nests in Europe. *Ibis* **150:** 54–73.

**Meyer, H., Fock, H., Haase, A., Reinke, H. & Tulowitzki, I.** 1995. Structure of the invertebrate fauna in salt marshes of the Wadden Sea coast of Schleswig-Holstein influenced by sheep-grazing. *Helgol Mar Res* **49:** 563–589.

**Milsom, T.P., Langton, S.D., Parkin, W.K., Peel, S., Bishop, J.D., Hart, J.D. & Moore, N.P.** 2000. Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. *J Appl Ecol* **37:** 706–727.

**Mossman, H.L., Davy, A.J. & Grant, A.** 2012. Does managed coastal realignment create saltmarshes with 'equivalent biological characteristics' to natural reference sites? *J Appl Ecol* **49:** 1446–1456.

**Mueller, T., Olson, K.A., Dressler, G., Leimgruber, P., Fuller, T.K., Nicolson, C., Novaro, A.J., Bolgeri, M.J., Wattles, D., DeStefano, S., Calabrese, J.M. & Fagan, W.F.** 2011. How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Glob Ecol Biogeogr* **20:** 683–694.

**Natural England** 2006. *Coastal Squeeze, Saltmarsh Loss and Special Protection Areas*. English Nature Research Report No. 710. Natural England (English Nature), Peterborough.

**Natural England** 2010a. *Higher Level Stewardship: Environmental Stewardship Handbook*. Natural England, Peterborough.

**Natural England** 2010b. *Ribble Estuary National Nature Reserve Management Plan*. Natural England, Lancashire.

**Natural England** 2011. *Protecting England's Natural Treasures: Sites of Special Scientific Interest*. Natural England, Peterborough.

**Norris, K., Brindley, E., Cook, T., Babbs, S., Forster Brown, C. & Yaxley, R.** 1998. Is the density of redshank *Tringa totanus* nesting on saltmarshes in Great Britain declining due to changes in grazing management? *J Appl Ecol* **35:** 621–634.

**Norris, K., Cook, T., O'Dowd, B. & Durdin, C.** 1997. The density of redshank *Tringa totanus* breeding on the salt-marshes of the Wash in relation to habitat and its grazing management. *J Appl Ecol* **34:** 999–1013.

**O'Brien, M.G.** 2001. Factors affecting breeding wader populations on upland enclosed farmland in northern Britain. Unpublished PhD thesis, University of Edinburgh.

**Pakanen, V.-M., Luukkonen, A. & Koivula, K.** 2011. Nest predation and trampling as management risks in grazed coastal meadows. *Biodivers Conserv* **20:** 2057–2073.

**Phelan, N., Shaw, A. & Baylis, A.** 2011. *The Extent of Saltmarsh in England and Wales: 2006–2009*. Environment Agency, Bristol.

**Piersma, T.** 1986. Breeding waders in Europe. *Wader Study Group Bull* **48:** 92–93.

**Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & team, R.C.** 2009, nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-93.

**Pye, K. & French, P.W.** 1993. *Targets for Coastal Habitat Re-creation*. Natural England (English Nature, Peterborough.

**R Development Core Team** 2009. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

**Reed, T.** 1985. Estimates of British breeding wader populations. *Wader Study Group Bull* **45:** 11–12.

**Roodbergen, M., van der Werf, B. & Hötker, H.** 2012. Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: review and meta-analysis. *J Ornithol* **153:** 53–74.

**Schekkerman, H., Teunissen, W. & Oosterveld, E.** 2008. The effect of 'mosaic management' on the demography of black-tailed godwit *Limosa limosa* on farmland. *J Appl Ecol* **45:** 1067–1075.

**Shennan, I.** 1989. Holocene crustal movements and sea-level changes in Great Britain. *J Quat Sci* **4:** 77–89.

**Shennan, I. & Horton, B.** 2002. Holocene land- and sea-level changes in Great Britain. *J Quat Sci* **17:** 511–526.

**Smart, J.** 2005, Strategies of sea-level rise mitigation for breeding redshank. PhD Thesis, University of East Anglia.

**Smart, J. & Gill, J.A.** 2003. Climate change and the potential impact on breeding waders in the UK. *Wader Study Group Bull* **100:** 80–85.

**Smart, J., Brooks, S., Pedder, J. & Deavin, H.** 2003. *Breeding Redshanks on Essex Saltmarshes 1985–2003*. RSPB, Sandy.

**Smart, J., Gill, J.A., Sutherland, W.J. & Watkinson, A.R.** 2006. Grassland-breeding waders: identifying key habitat requirements for management. *J Appl Ecol* **43:** 454–463.

**Thyen, S. & Exo, K.-M.** 2004. Wadden Sea saltmarshes: ecological trap or hideaway for breeding Redshanks *Tringa totanus*. *Wader Study Group Bull* **100:** 43–46.

**Thyen, S., Büttger, H. & Exo, K.M.** 2005. Nest-site selection of Redshanks *Tringa totanus* breeding in Wadden Sea salt marshes: consequences for reproduction, nest predation and management. *Vogelwelt* **126:** 365–369.

**Trebilco, R., Lawrence, E., Alderman, R., Robertson, G. & Baker, G.B.** 2010. Characterizing seabird bycatch in the eastern Australian tuna and billfish pelagic longline fishery in relation to temporal, spatial and biological influences. *Aquat Conserv* **20:** 531–542.

**Tucker, G. & Heath, M.** 1994. *Birds in Europe: Their Conservation Status*. Birdlife International, Cambridge.

**Tyas, C.** 2008. *Essex Saltmarsh Breeding Redshank Monitoring: 2006–2008*. RSPB, Essex.

**van de Pol, M., Ens, B.J., Heg, D., Brouwer, L., Krol, J., Maier, M., Exo, K.M., Oosterbeek, K., Lok, T., Eising, C.M. & Koffijberg, K.** 2010. Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *J Appl Ecol* **47:** 720–730.

**Venables, W.N. & Ripley, B.D.** 2002. *Modern Applied Statistics with S. Fourth Edition*. Springer, New York.

**Wilson, A.M., Vickery, J.A., Langston, R.H.W., Smallshire, D., Wotton, S. & Vanhinsbergh, D.** 2005. Changes in the numbers of breeding waders on lowland wet grasslands in England and Wales between 1982 and 2002. *Bird Study* **52:** 55–69.

**Wolters, M., Garbutt, A. & Bakker, J.P.** 2005. Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe. *Biol Conserv* **123:** 249–268.

**Woodworth, P.L.** 1987. Trends in UK mean sea level. *Mar Geol* **11:** 57–87.

**Woodworth, P.L., Tsimplis, M.N., Flather, R.A. & Shennan, I.** 1999. A review of the trends observed in British Isles mean sea level data measures by tide gauges. *Geophys J Int* **136:** 651–670.

(MS received 12 December 2012; revised MS accepted 24 February 2013)

# PAPER IV

# Nest trampling and ground nesting birds: quantifying temporal and spatial overlap between cattle activity and breeding Redshank.

Sharps, E., Smart, J., **Mason, L.R**., Jones, K., Skov, M.W., Garbutt, A. & Hiddink, J.G.

*Ecology and Evolution* (2017), **7**: 6622–6633. http://doi.org/10.1002/ece3.3271

© Kate Jones

Received: 8 May 2017 | Revised: 16 June 2017 | Accepted: 25 June 2017

DOI: 10.1002/ece3.3271

ORIGINAL RESEARCH

WILEY Ecology and Evolution Open Access

# Nest trampling and ground nesting birds: Quantifying temporal and spatial overlap between cattle activity and breeding redshank

Elwyn Sharps[1,2,3] | Jennifer Smart[3,4] | Lucy R. Mason[3] | Kate Jones[3,5] | Martin W. Skov[1] | Angus Garbutt[2] | Jan G. Hiddink[1]

[1]School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, UK

[2]NERC Centre for Ecology & Hydrology, Environment Centre Wales, Bangor, Gwynedd, UK

[3]RSPB Centre for Conservation Science, RSPB, Sandy, Bedfordshire, UK

[4]School of Biological Sciences, University of East Anglia, Norwich, UK

[5]Centre for Wildlife Assessment and Conservation, School of Biological Sciences, University of Reading, Reading, Berkshire, UK

**Correspondence**
Elwyn Sharps, RSPB North Wales Office, Unit 14 Llys Castan, Parc Menai, Bangor, Gwynedd, UK.
Email: elwyn.sharps@rspb.org.uk

## Abstract

Conservation grazing for breeding birds needs to balance the positive effects on vegetation structure and negative effects of nest trampling. In the UK, populations of Common redshank *Tringa totanus* breeding on saltmarshes declined by >50% between 1985 and 2011. These declines have been linked to changes in grazing management. The highest breeding densities of redshank on saltmarshes are found in lightly grazed areas. Conservation initiatives have encouraged low-intensity grazing at <1 cattle/ha, but even these levels of grazing can result in high levels of nest trampling. If livestock distribution is not spatially or temporally homogenous but concentrated where and when redshank breed, rates of nest trampling may be much higher than expected based on livestock density alone. By GPS tracking cattle on saltmarshes and monitoring trampling of dummy nests, this study quantified (i) the spatial and temporal distribution of cattle in relation to the distribution of redshank nesting habitats and (ii) trampling rates of dummy nests. The distribution of livestock was highly variable depending on both time in the season and the saltmarsh under study, with cattle using between 3% and 42% of the saltmarsh extent and spending most their time on higher elevation habitat within 500 m of the sea wall, but moving further onto the saltmarsh as the season progressed. Breeding redshank also nest on these higher elevation zones, and this breeding coincides with the early period of grazing. Probability of nest trampling was correlated to livestock density and was up to six times higher in the areas where redshank breed. This overlap in both space and time of the habitat use of cattle and redshank means that the trampling probability of a nest can be much higher than would be expected based on standard measures of cattle density. *Synthesis and applications:* Because saltmarsh grazing is required to maintain a favorable vegetation structure for redshank breeding, grazing management should aim to keep livestock away from redshank nesting habitat between mid-April and mid-July when nests are active, through delaying the onset of grazing or introducing a rotational grazing system.

KEYWORDS

agri-environment, animal movements, cow, shorebirds, waders

---

## 1 | INTRODUCTION

Grazing by wild or domestic animals is commonly used to conserve landscapes and ecosystems and to preserve their associated species and communities (WallisDeVries, 1998). Guidelines for conservation management tend to assume that grazing animals distribute themselves homogenously across a landscape (e.g., Adnitt et al., 2007; Green 1986). However, previous studies on the spatial distribution of livestock have found that their distribution can vary markedly in space and depends on numerous biotic and abiotic factors such as the availability of shelter, distance to drinking water, and forage quality and quantity (Bailey, 1995; Putfarken, Dengler, Lehmann, & Härdtle, 2008). These studies have focused mainly on intensively grazed highly managed pasture systems that tend to have a homogenous and species-poor vegetation with universal accessibility. Few studies have examined the distribution of domestic grazers on botanically and geomorphologically variable habitats with restricted access to some areas, such as saltmarshes.

Saltmarshes typically consist of a limited number of plant species adapted to regular immersion by the tides, with a characteristic zonation which ranges from a pioneer zone of extremely halophytic plants adapted to regular tidal immersion at a low elevation, through to a marsh largely composed of grassy less salt-tolerant species at higher elevations (Boorman, 2003; Gray, 1992). Many saltmarshes are grazed for conservation purposes to optimize sward structure for invertebrates, small mammals, and birds (Boorman, 2003; Davidson et al., 2017). European saltmarshes are an important breeding habitat for a range of ground nesting bird species, for example, common redshank (*Tringa totanus*: hereafter redshank; Figure 1), eurasian oystercatcher (*Haematopus ostralegus*), eurasian skylark (*Alauda arvensis*), and meadow pipit (*Anthus pratensis*). These species tend to nest in the higher elevation saltmarsh zones that are closer to the landward edge and therefore out of reach of most high tides (van Klink et al., 2016; Norris, Cook, Odowd, & Durdin, 1997). On British saltmarshes, numbers of breeding redshank are nationally and internationally important; in the 1980s and 1990s approximately 50% of the British breeding population occurred in this habitat (Brindley et al., 1998). However, redshank breeding on saltmarshes declined by 53% between 1985 and 2011, and this suggests that the current management of saltmarshes is not favorable for redshank (Malpas, Smart, Drewitt, Sharps, & Garbutt, 2013).

Light grazing at an intensity of ~1 cattle/ha can produce the patchy vegetation structure needed for redshank breeding (Norris et al., 1997; Sharps, Garbutt, Hiddink, Smart, & Skov, 2016). Redshank population declines on British saltmarshes have been linked to changes in grazing management as breeding densities are higher in light and moderate grazing than on heavily grazed or un-grazed saltmarshes (Malpas et al., 2013; Norris et al., 1998). However, Malpas et al. (2013) found that the number of breeding pairs declined by 51.6% in Northern England where grazing was more intensive, but also by 24.2% and 58.1%, respectively, in Eastern and Southern England where light grazing prevailed. The density of animals in a habitat can be a misleading indicator of habitat quality (Van Horne, 1983), as species can preferentially use habitat which acts as an "ecological trap" by lowering breeding success (Best, 1986; Schlaepfer, Runge, & Sherman, 2002). Sharps et al. (2016) demonstrated that grazing creates a trade-off for Redshank, by causing them to nest in poorer quality habitat but with more of their preferred vegetation types. Even light grazing can reduce redshank nest survival through nest trampling. Sharps, Smart, Skov, Garbutt, and Hiddink (2015) found that risk of redshank nest loss to livestock trampling increased from 16% at 0.15 cattle/ha to 98% at 0.82 cattle/ha on sites in north west England and that nests closer to the landward extent of saltmarshes may be more vulnerable to trampling. In practice livestock tend to be introduced in April or May and remain until September or October to cover the main period of vegetation growth (Doody, 2008). Saltmarsh management guidelines recommend starting grazing in April at an intensity of ~1 cattle/ha (Adnitt et al., 2007), which coincides with the April to July redshank nesting season (Green, 1984). Current conservation grazing management may therefore be causing high rates of nest trampling.

**FIGURE 1** Common redshank *Tringa totanus*. Copyright of Kevin Simmonds

On saltmarshes redshank build nests in the grasses *Festuca rubra*, *Elytrigia* spp., and occasionally *Puccinellia maritima* (Norris et al., 1997; Sharps et al., 2016; Thyen & Exo, 2005), which are found at higher elevations closer to the landward edge of the marsh (Adam, 1990; Allen & Pye, 1992). Grazing pressure can be higher in these areas and lower in the pioneer zone, which is closer to the seaward side of the marsh, possibly because these higher zones are composed of grasses which are more palatable to livestock (Esselink, Fresco, & Dijkema, 2002; Pehrsson, 1988). Livestock density also tends to be higher close to sources of fresh drinking water (Arias & Mader, 2011). On saltmarshes, there are typically no natural sources of freshwater and limited numbers of drinking troughs tend to be placed at the landward side of the marsh (typically 1–3 on a 200–400 ha saltmarsh). When water and food are spatially separated, cattle can spend up to 45% of their time grazing and 25% of their time walking, with the rest of the time spent sleeping or ruminating (Hughes & Reid, 1951).

Diet choice of grazing animals is based on maximizing energy intake and the quality and availability of forage intake (Vulink & Drost, 1991). It is plausible that livestock will first exploit the closest preferred vegetation types and will move onto the less preferred vegetation types further away from drinking troughs as vegetation becomes depleted (van Klink et al., 2016). However, livestock are more likely to forage on previously grazed vegetation as it regrows, rather than on previously ungrazed vegetation (McNaughton, 1984; Nolte, Esselink, Smit, & Bakker, 2014). Therefore, livestock distribution is likely to vary with time, but changes over time may not be linear due to depletion of preferential forage types or the need to return to drinking troughs more often in warm weather. Little is known about how the patchy distribution of livestock in space and time affects nest trampling rates of breeding birds.

The aim of this study was to investigate (i) the spatial and temporal distribution of cattle across the grazing season in relation to the distribution of preferred redshank habitats during the nesting period and (ii) the relationship between nest trampling rates and grazing pressure. Identification of the drivers of the distribution of livestock may allow improvements to grazing management that will maintain positive effects of grazing on the vegetation structure while reducing the negative effects of nest trampling. We hypothesize that: (i) livestock activity is not homogenous over the saltmarsh and is higher in zones where redshank nest; (ii) the furthest distance travelled by livestock increases over the grazing season; (iii) that the probability of nest loss to trampling is higher in parts of saltmarshes where livestock spend more time.

## 2 | MATERIALS AND METHODS

This study was carried out on four saltmarshes of the Wash estuary with grazing intensities well below the recommended ~1 cattle/ha (0.11–0.50 cattle/ha; Table 1; Figure 2). To investigate drivers of the spatial and temporal variation in livestock distribution, we used GPS loggers placed on cattle. To relate cattle density to avian nest loss due to trampling, we used dummy nests.

### 2.1 | Field sites

The Wash estuary contains over 4,000 ha of saltmarsh, which is approximately 10% of the total UK saltmarsh extent (Burd, 1989; Murby, 1997). The vegetation is typical of saltmarshes on the east coast of

**TABLE 1** Saltmarshes used in this study, showing seasonal cattle density per hectare (SCD) and GPS logger details

| Salt-marsh | Size (ha) | Herd size | SCD $ha^{-1}$ | LSU $ha^{-1}$ | No. cattle GPS tagged | Dates GPS logged | No. GPS positions | No. of cattle days |
|---|---|---|---|---|---|---|---|---|
| A | 322 | 116 | 0.36 | 0.29 | 4 | 19/05/13–10/08/13 | 11,819 | 205 |
| B | 126 | 39 | 0.31 | 0.25 | 4 | 19/05/13–26/10/13 | 31,958 | 432 |
| C | 201 | 100 | 0.50 | 0.40 | 5 | 28/04/14–20/07/14 | 23,967 | 326 |
| D | 477 | 60 | 0.13 | 0.10 | 3 | 05/05/14–17/08/14 | 11,328 | 105 |

LSU = livestock units. Cattle days are the number of days of cattle activity recorded from active collars.

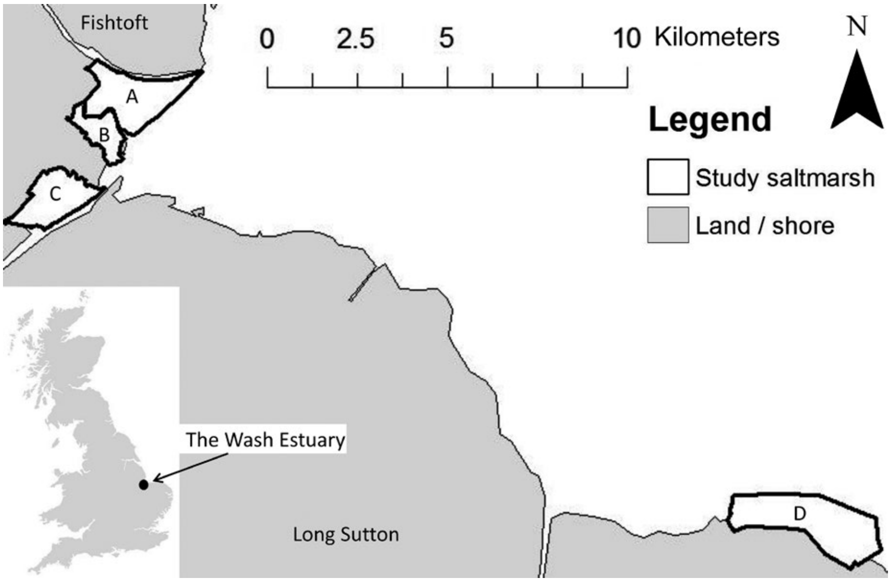


**FIGURE 2** Wash estuary, showing the study saltmarshes. A and B: Frampton Marsh, C: Kirton Marsh, D: Terrington Marsh. Although saltmarshes A and B are neighboring, they are separated by a large channel which is unpassable to livestock. Close to the landward edge of the marsh where the channel narrows, fencing has been installed. This means that livestock are unable to move between the two saltmarshes

the UK. *Salicornia* and other annual plant species form pioneer communities along with *Spartina anglica* at the lowest elevations. The mid-marsh areas are dominated by *Puccinellia maritima* communities, which form a short turf with occasional tussocks across most of their extent where grazed by livestock. In areas where livestock activity is limited or absent, the low growing shrub *Atriplex portulacoides* and the coarse grass *Elytrigia atherica* dominate, mainly through the central and upper parts of the marsh extending on to the vegetated flood defenses (Hill, 1988; Murby, 1997). All saltmarshes included in this study were bounded by a vegetated sea-wall flood defense at the landward edge. The study saltmarshes were grazed by free-roaming young cattle, which is commonplace on British saltmarshes (Adnitt et al., 2007). Young cattle may trample more nests than adults (Beintema & Muskens, 1987) possibly due to their more lively nature (Ausden, 2007).

Redshank populations have declined in the Wash estuary (Malpas et al., 2013). At Saltmarshes A, B, and C redshank populations decreased from approximately 140 pairs/km$^2$ to around 50 pairs/km$^2$ despite maintaining light grazing regimes between 0.3 and 0.6 cattle/ha (Feather, Mason, Smart, & York, 2016). Trends are not known for Saltmarsh D, but the site currently maintains a breeding redshank population of approximately 30 pairs/km$^2$ (Jones, 2014).

## 2.2 | GPS tracking

Eight cattle were fitted with GPS loggers on saltmarshes A and B from May to October 2013, and eight cattle were fitted with GPS loggers between April and August 2014 on saltmarshes C and D (Table 1). Although this number only represents 3%–10% of the animals in each herd, as cattle are herding animals (Howery, Provenza, Banner, & Scott, 1996, 1998), we assumed that the distribution of this subsample would be representative of the whole herd. GPS loggers were programmed to log a position every 20 min, when satellite signals were available. They were retrieved at the end of the grazing season. Although some collars stopped earlier than planned due to battery life, approximately 50% of the collars per saltmarsh logged the entire period. The logging dates, number of GPS positions, and number of cattle days for each of the saltmarshes are shown in Table 1.

Arc-GIS 10.1 was used to produce a 50 × 50 m grid over each saltmarsh, and to count the number of GPS records that fell into each grid cell per week. To obtain estimates of livestock density per cell, firstly the area of saltmarsh per grid cell was calculated by subtracting the area of any creeks and any area which fell outside of the saltmarsh boundary. Due to the accuracy of the GPS chipsets (recorded accuracy = 2.5 m), only grid cells which contained saltmarsh >6.25 m$^2$ were included in the analyses. Cattle activity was calculated as cattle hours ha$^{-1}$ hr$^{-1}$, which simplifies to cattle/ha, and therefore took account of both the number of cattle and the duration of their presence in a cell. This measure represents the average cattle abundance in a cell over the evaluated time period and was calculated using the formula:

$$\text{Cattle activity (ha}^{-1}) = \text{Herd size} \times (\text{No. GPS positions in cell} / \text{Total No. GPS positions}) / \text{Cell area (ha)}.$$

## 2.3 | Distribution of cattle activity and distance travelled

To quantify changes in cattle distribution over time, we calculated the percentage of grid cells that contained 100% of the cattle activity for each week ($CA_{100}$). If $CA_{100}$ is large, cattle use a larger fraction of the saltmarsh, and therefore, their activity is more spread out. We used a generalized least squares model (GLS) in the nlme package in the statistical program R (Pinheiro, Bates, DebRoy, & Sarkar, 2016), to test how $CA_{100}$ was affected by saltmarsh identity (A–D) and time (weeks, a continuous variable with week 1 starting on the 14th April as the start of the redshank nesting season). The response variable was $\log_{10}$ transformed to deal with uneven spread in the residuals. A quadratic term for time (week$^2$) and an interaction between saltmarsh and week (and saltmarsh and week$^2$) were also included in the global model. To account for temporal autocorrelation, an autoregressive model of order 1 was run, by adding the correlation structure term (corAR1, form = ~week|saltmarsh). The form argument specified the temporal order of the data (the variable "week"). By adding the grouping variable "saltmarsh," the correlation structure was only applied to observations within each saltmarsh. In this, and all subsequent analyses model selection was carried out by removing single terms from the global model until only predictors with $p < .05$ remained.

To investigate seasonal trends in livestock use of different saltmarsh habitats, we mapped the zonation of each saltmarsh in a field survey and then validated these maps using aerial photographs to create a GIS layer of zonation for each saltmarsh (Figs S1–S4), based on the suitability for redshank nesting. The saltmarsh zones that redshank use for nesting were easily recognizable as they select nests surrounded by grasses such as *F. rubra*, *P. maritima*, or *Elytrigia* species (Norris et al., 1997; Sharps et al., 2016; Thyen & Exo, 2005). The categories used (listed in order of proximity to the sea wall) were as follows: non-saltmarsh zone (the transition zone between saltmarsh and terrestrial vegetation, and any other non-saltmarsh areas which the cattle could access), mid-marsh redshank zone (dominated by *P. maritima* or *F. rubra* and found at high/mid elevation), *Elytrigia* redshank zone (dominated by *E. atherica* and found at high/mid elevation), non-redshank zone (dominated by *Atriplex* and/or pioneer vegetation, and found at low elevation). We then identified the areas of each grid cell that fell within each of the habitat categories. Where a grid cell fell within more than one habitat zone, we used the habitat zone that occupied the largest area of the grid cell.

A general linear model (GLM, with Gaussian error) of the effect of saltmarsh identity and time (weeks) on cattle activity in each zone was fitted separately. A quadratic term for time (week$^2$) and an interaction between saltmarsh and time (and saltmarsh and week$^2$) were also included because an initial examination of the data indicated a humped-shaped relationship between cattle density and time. Where necessary, the response variable was transformed (square root or $\log_{10} + 1$) to ensure normality of residuals and deal with heteroscedasticity. Following Zuur, Ieno, Walker, Saveliev, and Smith (2009) data were tested for temporal autocorrelation by running the global model for each habitat zone, using generalized least squares and inspecting autocorrelation function plots. There was no evidence of temporal autocorrelation.

To determine whether the maximum distance livestock travel from the sea wall varies with time, for all grid cells visited by livestock, the GLS model set was repeated, using the 95th percentile of the distance of all GPS records from the sea wall as the response variable. The 95th percentile was used to exclude any extreme outliers, for example, one off trips to a distant point. We did not use a 5th and 50th percentile as our focus was the maximum distance travelled.

## 2.4 | Nest loss to trampling

To allow greater replication than would be possible studying redshank nests, to determine whether the probability of nest loss to trampling is higher in parts of saltmarshes where livestock spend more time, we ran a dummy nest experiment using 110 mm black clay-pigeon shooting targets which have a similar diameter to redshank nests (e.g., 4 redshank eggs approximately 45–48 mm per egg), and like eggs they break if stepped on by livestock (Jensen, Rollins, & Gillen, 1990; Mandema, Tinbergen, Ens, & Bakker, 2013). This experiment could only be carried out on one of the four saltmarshes, but we expect the relationship between cattle density and trampling rate to be similar across study sites. Thirty positions were selected using a stratified random sampling method across Saltmarsh B, to cover the full range of distances from the sea wall, and all habitat zones (minimum distance between points = 50 m). At each of the 30 plots, nine discs were placed in grids of 9 m × 9 m, with 3 m between each disc. As preliminary observations suggested that cattle behavior was not affected by the presence of the black disks, we laid them directly onto the marsh without cover. The precise location of each disc was recorded using a Leica Viva GS08 Global Navigation Satellite System (accuracy 60 mm; Fig. S2). Discs were exposed to cattle on 22/5/13 when the cattle were first introduced to the saltmarsh during the mid-April to mid-July redshank nesting season (Green, 1984). They were checked after 14 days (5/6/13—period 1) and 28 days (19/6/13—period 2). Disks were recorded as intact (not trampled) or broken (trampled). All discs were recovered. When checking discs after period 1, broken discs were replaced with a new disc and all debris was removed. When checking discs after period 2, all intact discs and debris were removed. The daily trampling probability for both 14 day periods was calculated as:

$$\text{Daily trampling probability} = 1 - (1 - \text{trampling.prob.period})^{1/14}.$$

However, as the incubation period is 24 days for redshank and similar for many other shorebird species (Green, 1984), trampling probability (%) over 24 days was calculated based on the mean of the daily trampling probabilities of the two periods as:

$$\text{Trampling probability for 24 days} = 1 - (1 - \text{daily trampling probability})^{24}$$

It is expected that the relationship between the probability of nest trampling and cattle activity reaches an asymptote at high cattle densities. Trampling probability was therefore compared to cattle activity, for the 24-day period using a binomial Generalized Additive Model (GAM) to fit this relationship using R. The data were tested for spatial autocorrelation following Zuur et al. (2009) and Kubetzki and Garthe (2007), this indicated that independence could be assumed (Zuur et al., 2009); therefore, the final model used was a GAM with a smoothed term for cattle density and no additional terms to allow for spatial autocorrelation. Trampling probability maps were created for each saltmarsh by scaling cattle activity recorded over the first 24 days of grazing to model predictions from the GAM.

# 3 | RESULTS

## 3.1 | Distribution of cattle activity

The spatial extent of cattle activity was highly skewed, and varied by saltmarsh (Table 2) with between 58% and 78% of the saltmarsh never visited by cattle during the study (Figure 3). Cattle activity varied by habitat zone (Table 3) with most activity concentrated on the habitat zones close to the seawall, in non-saltmarsh habitat and in redshank nesting areas (Figure 4). Over time, cattle activity moved away from the non-saltmarsh habitat. In the mid-marsh redshank habitat, cattle activity gradually increased over the course of the redshank nesting season, but then decreased after the redshank nesting

**TABLE 2** Results of general linear models and generalized least squares models investigating spatial and temporal effects on livestock distribution and livestock activity ($CA_{100}$ = % of grid cells with 100% of the cattle activity)

| Response variable | Predictor | *df* | Res *df* | *F* | *p* value |
|---|---|---|---|---|---|
| $CA_{100}$ | Saltmarsh (A-D) | 3 | 49 | 22.99 | <.001 |
| | Week | 1 | 49 | 18.24 | <.01 |
| | $Week^2$ | 1 | 49 | 10.88 | <.01 |
| | Saltmarsh*week | 3 | 49 | 15.35 | <.001 |
| | $Saltmarsh*week^2$ | 3 | 49 | 0.20 | .89 |
| 95th percentile of distance to sea wall | Saltmarsh (A-D) | 3 | 49 | 5.90 | <.01 |
| | Week | 1 | 49 | 107.81 | <.001 |
| | $Week^2$ | 1 | 49 | 1.68 | .20 |
| | Saltmarsh*week | 3 | 49 | 11.73 | <.001 |
| | $Saltmarsh*week^2$ | 3 | 49 | 2.88 | .04 |

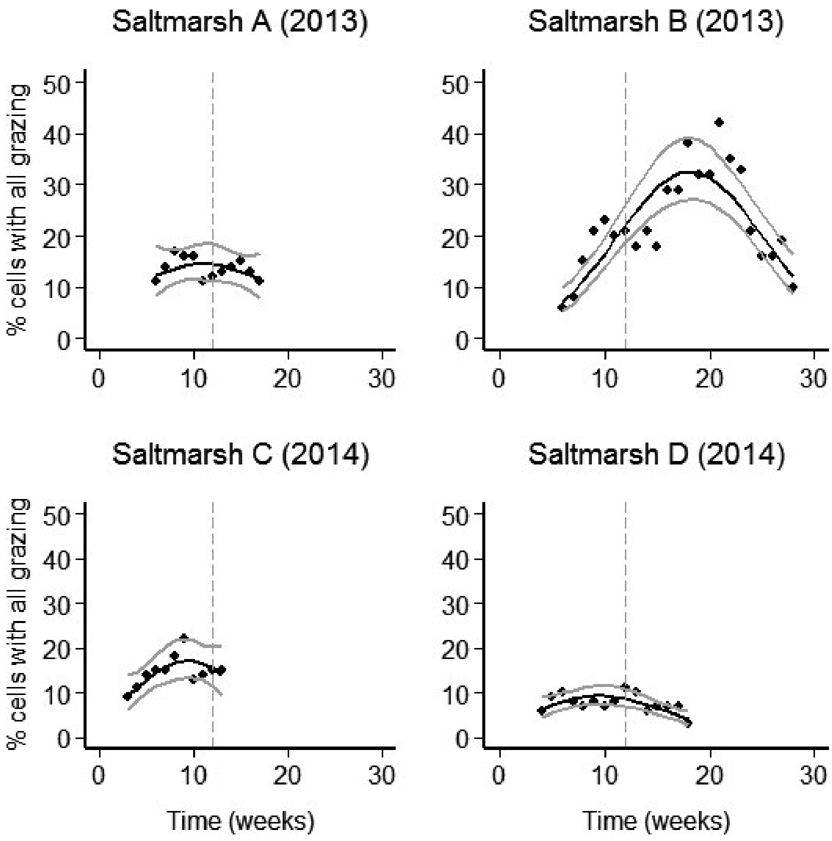


**FIGURE 3** Changes in the percentage of saltmarsh that was grazed over time. The percentage of cells containing all of the grazing is used as a measure of homogeneity of livestock distribution. Black lines are back-transformed model-fitted values. Confidence intervals (95%) are indicated by gray lines. The dashed gray vertical lines indicate the end of the redshank nesting season (1st July). Week 1 was the first week of the redshank season, beginning 14th April. Week 28 (the last week) ended on the 26th October

**TABLE 3** Results of general linear models investigating variation in livestock distribution in different saltmarsh zones over time

| Response variable | Predictor | *df* | *F* | *p* value |
|---|---|---|---|---|
| Cattle activity (ha$^{-1}$) in the non-saltmarsh zone | Saltmarsh (A-D) | 3, 49 | 7.1 | <.001 |
| | Week | 1, 49 | 5.7 | .02 |
| | Week$^2$ | 1, 49 | 0.5 | .48 |
| Cattle activity (ha$^{-1}$) in mid marsh redshank zone | Saltmarsh (A-D) | 3, 49 | 15.7 | <.001 |
| | Week | 1, 49 | 1.9 | .17 |
| | Week$^2$ | 1, 49 | 6.6 | .01 |
| Cattle activity (ha$^{-1}$) in *Elytrigia* redshank zone | Saltmarsh (A-D) | 2, 41 | 65.2 | <.001 |
| | Week | 1, 41 | 2.5 | .12 |
| | Week$^2$ | 1, 41 | 0.0 | .93 |
| Cattle activity (ha$^{-1}$) in non-redshank zone | Saltmarsh (A-D) | 2, 29 | 45.7 | <.001 |
| | Week | 1, 29 | 1.7 | .20 |
| | Week$^2$ | 1, 29 | 5.1 | .03 |

*df* = degrees of freedom. Res *df* = Residual degrees of freedom. *F* = F value. For each response variable, we included saltmarsh*week, and saltmarsh*week$^2$ in the model, but these were not significant.

season had finished (Figs S5–S8). The spatial extent of livestock activity increased over time and then decreased again, but the timing of the maximum spread of cattle activity was different between the four saltmarshes. In Saltmarsh B, this maximum spread occurred in August (week 19) with 42% of the available marsh, and in Saltmarsh C, this occurred in June (week 9) with 22% of the available marsh. In Saltmarshes A and D, cattle never used more than 17% of the available marsh (Figure 3).

### 3.2 | Furthest distance travelled

At the start of the redshank breeding season most livestock stayed within 500 m of the seawall, but were recorded further afield on some saltmarshes over time as suggested by the 95th percentile of the distance of all GPS records from the sea wall (hereafter referred to as furthest distance travelled; Table 2; Figure 5). At Saltmarsh B, where cattle activity was recorded for the longest period, the furthest

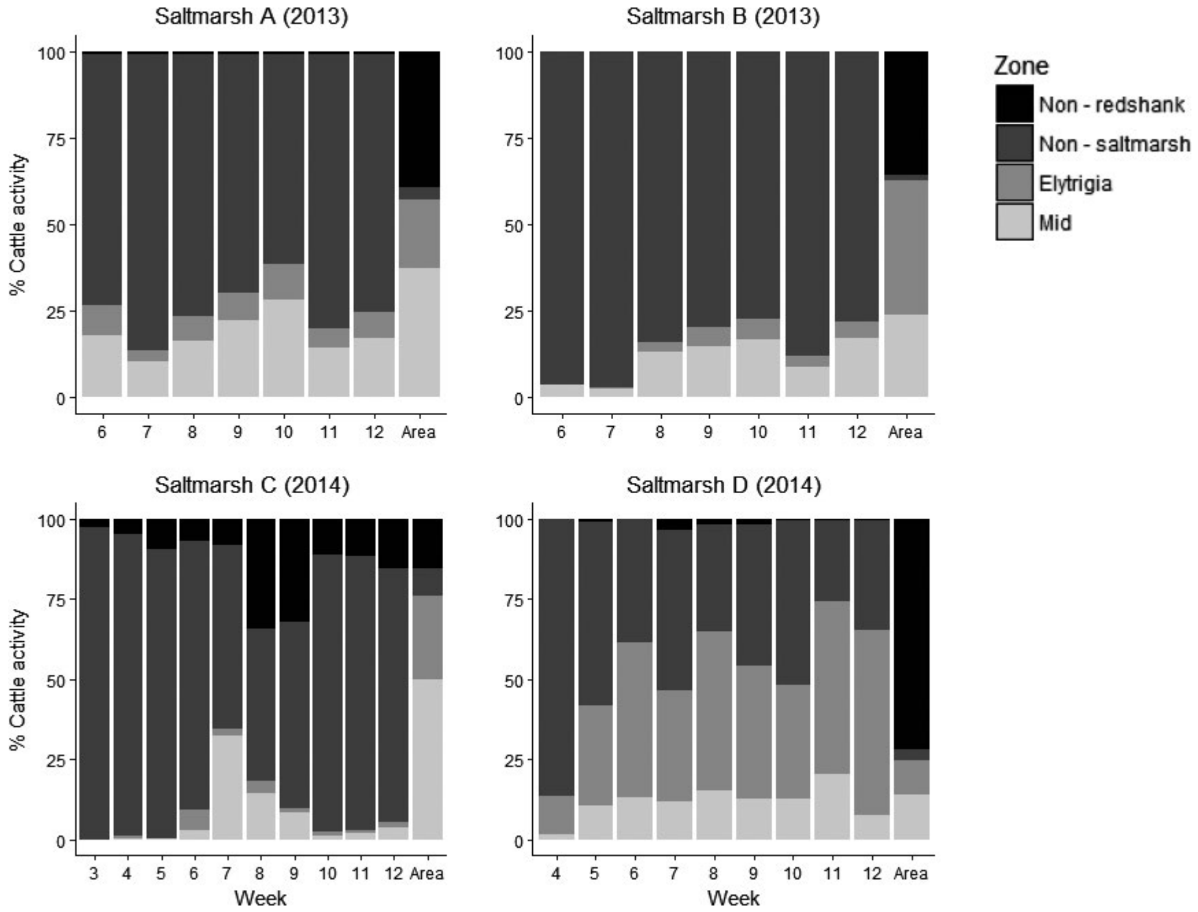


**FIGURE 4** The percentage of cattle activity in the different habitat zones during the redshank nesting season. Week 1 was the week beginning 14th April. Week 12 ended on the 7th July. In Saltmarsh A and B grazing started in Week 6 (19th April), In Saltmarsh C, grazing started in Week 3 (28th April). In Saltmarsh D, grazing started in Week 4 (5th April). The "Area" category on the *X*-Axis indicates the proportion of each habitat zone present on the saltmarsh in question. Redshank breed in the *Elytrigia* and Mid zones. The non-redshank and non-saltmarsh zones are unsuitable for Redshank breeding

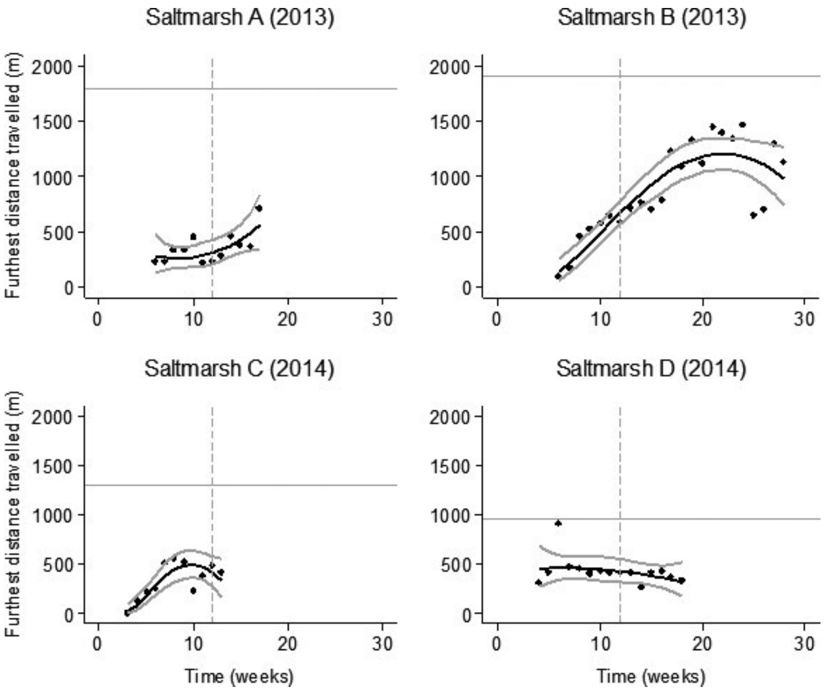


**FIGURE 5** 95th percentile of livestock distance to sea wall over time. Black lines are back-transformed model-fitted values. Confidence intervals (95%) are indicated by gray lines. The straight horizontal gray line indicates the maximum extent of the saltmarsh in meters. The dashed gray vertical lines indicate the end of the redshank nesting season (1st July). Week 1 was the week beginning 14th April. Week 28 (the last week) ended on the 26th October

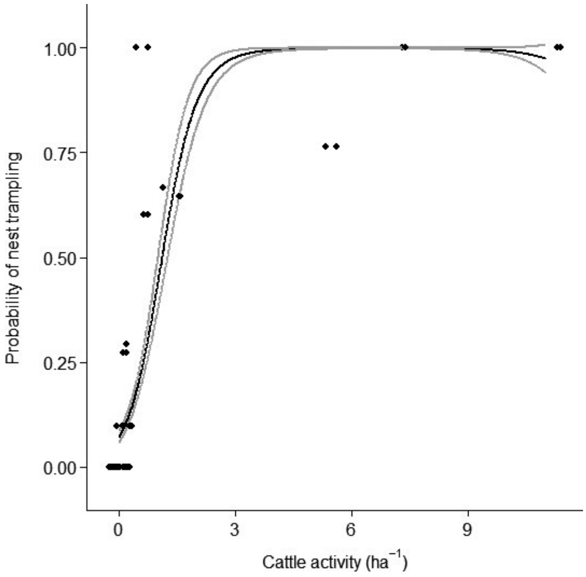


**FIGURE 6** The probability of nest loss to trampling in relation cattle activity (ha$^{-1}$). Black points indicate the study plots (false nests), and these have been jittered to display overlapping data points side by side. The black line is the model predicted values from the GAM. Gray lines indicate 95% confidence intervals

distance travelled increased from 129 m in May (week 6) to 1,500 m in September (week 22), but decreased to 1,189 m in October (week 26). This pattern of furthest distance travelled by livestock increasing over time was quadratic. As the effect of the interaction between saltmarsh and time on the maximum distance travelled by livestock was significant, the timing of the maximum travel varied between the saltmarshes. This can be expected as the stocking density, size, and vegetation were different between the different saltmarshes.

### 3.3 | Nest loss to trampling

The experimental plot that received the most grazing during the false nest experiment recorded cattle density of 11.29 cattle/ha, which is around 36 times higher than mean seasonal cattle density at this saltmarsh (B: 0.31 cattle/ha). The probability of nest trampling over a 24-day period increased from zero where no cattle were recorded to 100% with cattle >3 /ha (Figure 6, $R^2 = 0.75$, edf = 1.99, Ref. $df = 2$, $\chi^2 = 452.1$, $p < .001$ for smoothed cattle density term). Figure 7 presents the nest trampling probability recorded for each of the saltmarshes. This demonstrates that nest trampling rates are highly concentrated at some parts of the saltmarshes, particularly in areas close to the sea wall.

## 4 | DISCUSSION

These results show that cattle distribution on coastal saltmarshes is highly concentrated, with only 3%–42% of each saltmarsh being grazed, with much spatial and temporal variation. Early in the grazing season cattle concentrate on higher elevation habitats close to the sea wall, and move out further onto the saltmarsh as the season progresses. As redshank also nest in these higher elevation habitats, and breeding coincides with the early period of grazing (Adam, 1990; Hale, 1980), this pattern of grazing causes a much higher nest loss to trampling than would be expected merely based on the mean density of cattle on the saltmarsh, and means that some parts of the saltmarshes are grazed much more heavily than may be intended while large areas go completely ungrazed. This overlap in the habitat use of cattle and redshank means that the trampling probability of nests can be very high.

Livestock grazing is used as a management tool for conserving numerous target species and communities in a wide range of landscapes and ecosystems (WallisDeVries, 1998), including heathlands, grasslands, and woodlands (Bakker, De Bie, Dallinga, Tjaden, & De Vries, 1983; Eglington et al., 2009; Smart, Gill, Sutherland, & Watkinson, 2006). It may be expected that nest trampling pressure for ground nesting birds would be less in habitats with a uniform coverage of vegetation types preferred by livestock, and multiple sources of drinking water. On saltmarshes, livestock movements are also likely to be influenced by tidal conditions and the weather, which can be more extreme than terrestrial habitats due to their exposed locations (Yasué, Quinn, & Cresswell, 2003). By definition, saltmarshes are affected by varying degrees of tidal flooding (Adam, 1990). Total immersion of saltmarshes by sea water can occur on the highest tides of the spring neap tidal cycle (Armstrong, Wright, Lythe, & Gaynard, 1985), when livestock are forced to retreat to areas with high elevation such as the sea wall (Jensen, 1985). This may suggest that rates of nest trampling are higher on saltmarshes than in terrestrial habitats and highlights a need to change conservation management practices for redshank breeding on saltmarshes.

Because even light grazing of saltmarshes can lead to high rates of nest loss to trampling and predation (Sharps et al., 2015) and causes a trade-off for redshank by increasing the availability of suitable nesting habitat, but reducing its quality (Sharps et al., 2016) it is likely that this is trade-off is causing an ecological trap for redshank and contributing to the redshank population declines found by Malpas et al. (2013). Previously grazed saltmarsh vegetation is more palatable to cattle and therefore more likely to be re-visited (Bakker, 1985). Therefore, if light grazing occurs over a number of years, cattle are likely to select the same preferred areas. As our study shows that cattle only ever use a small proportion of the saltmarsh, we expect that over time an increasing proportion of a lightly grazed saltmarsh is never visited by cattle and therefore becomes less suitable for redshank. This would likely force more redshank into the cattle preferred areas bringing them more and more into conflict. This suggests that there is a need for habitat managers to focus on balancing the trade-off between improving the quality of the habitat by reducing nest trampling and predation rates (Sharps et al., 2015, 2016), while keeping the positive effects that grazing has of increasing the availability of preferred grass species (Sharps et al., 2016).

As we found that the probability of nest loss to trampling was higher in areas of saltmarshes subject to more livestock activity, our results show that GPS tagging from 3% to 10% of cattle in a herd can be

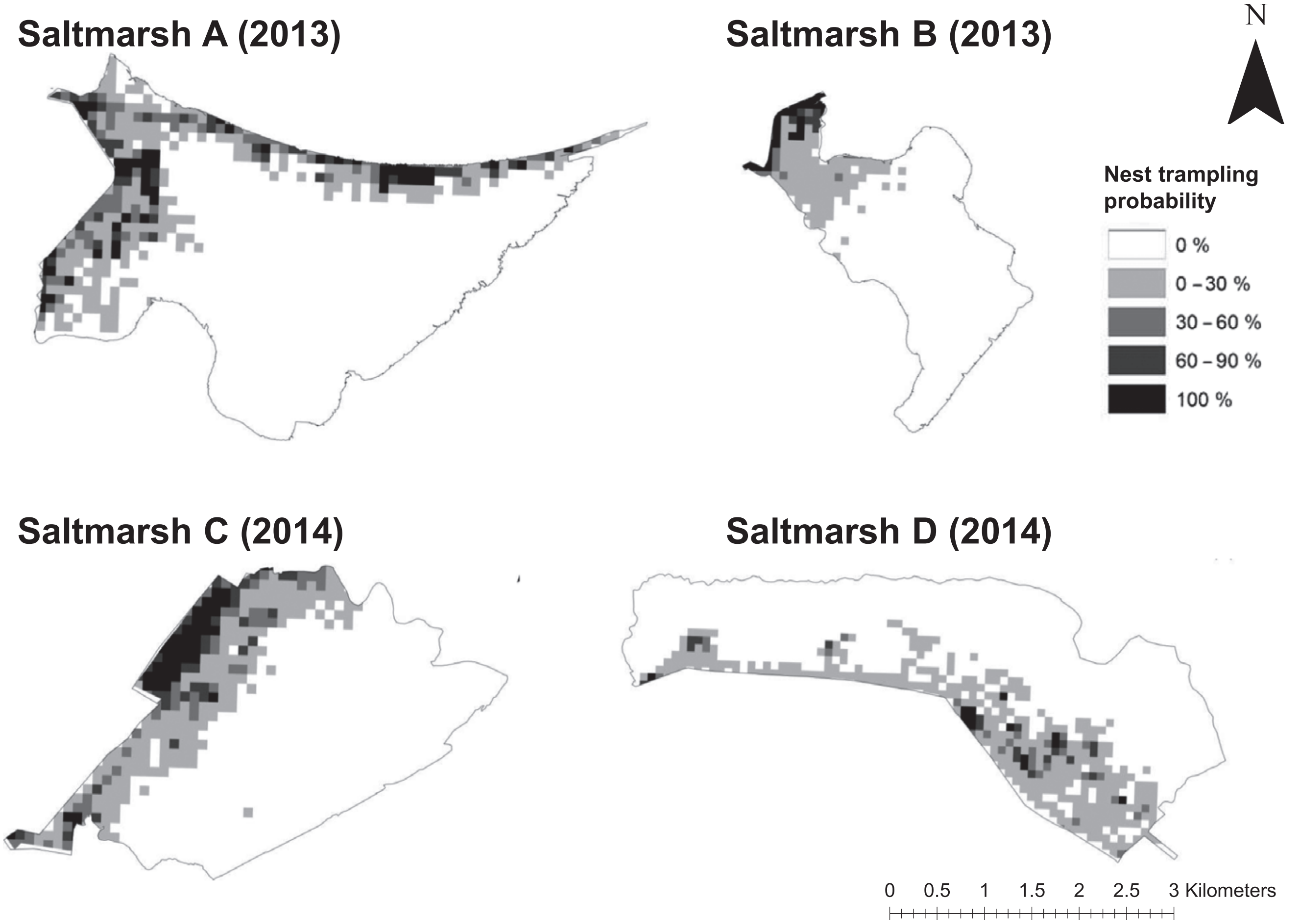


**FIGURE 7** The probability of nest loss to trampling on saltmarshes A–D. Calculated using model fitted values from Figure 6. See Figs S1–S4 for habitat maps of each saltmarsh

a good indicator of nest trampling probability. As we used false nests to calculate nest trampling probability, and they were placed following a stratified random sampling method, we were concerned that this may bias our findings as redshank do not select nest locations at random (Sharps et al., 2016). It is also unclear if cattle footfall is random, although previous studies suggest that they trample birds' nests in either long or short vegetation, and do not avoid grassy tufts where redshank nest (Beintema & Muskens, 1987; Pakanen, Luukkonen, & Koivula, 2011; Sharps et al., 2015). Although it would have been useful to also study real redshank nests, this would have been time-consuming and therefore not possible alongside the current study. However, Sharps et al. (2015) studied real redshank nests and found higher rates of nest trampling near the sea wall, on lightly grazed saltmarshes with high livestock densities. As our results demonstrate that livestock activity is largely concentrated in these areas, it is unlikely that using false nests affected our conclusions. Our preliminary observations suggested that cattle behavior was unaffected by the presence of the false nests. If cattle had avoided the false nests, this would underestimate trampling meaning our already high estimates are conservative.

These results demonstrate that understanding the mechanisms driving the spatial habitat use of cattle is important when formulating management strategies for ground nesting birds. In our study, livestock distribution and the maximum distance travelled by livestock increased with time and then decreased again. This could be related to simple food depletion on the higher elevation saltmarsh zones, if cattle are forced to venture further afield once vegetation closer to the sea wall has been heavily grazed, or during periods of slow vegetation growth. This trend appeared to reverse later in the summer months after the redshank breeding season perhaps as temperatures became too high for cattle to move far away from drinking water or as vegetation closer to the sea wall recovered from early season grazing. This has previously been demonstrated in North American pasture systems, where cattle stay close to their drinking water during the hottest periods (Bailey, 1995). The fact that livestock remained close to the sea wall for the majority of the grazing period could either be because this is where fresh drinking water sources are provided, or because vegetation in higher elevation zones in more palatable to livestock (Pehrsson, 1988). The sea wall is often where livestock are first introduced to the saltmarsh and represents a safe dry area during high tides (Doody, 2008). Livestock may therefore associate it with safety which might explain lack of movement from this area in the early part of the grazing period. Higher elevation habitats closer to the sea wall are also drier and less muddy as high tides seldom overtop these areas and dense vegetation growth consolidates sediments (Adam, 1990), so may be preferred through allowing easier livestock movement. This could explain the higher rates of nest trampling found in some dummy nests during our study.

While these results show a high concentration of livestock activity on parts of the saltmarsh that are most important for breeding redshank and several other bird species, the highest levels of livestock activity were found in the non-saltmarsh habitats closer to the landward extent of the saltmarsh, and this effectively draws cattle away from the breeding habitats. Such access to non-saltmarsh habitat is absent at many grazed saltmarshes (Skelcher, 2010). At these locations, it is likely that nest loss to trampling would be even greater as livestock activity may be further concentrated in the mid marsh.

## 4.1 | Synthesis and applications

The results of this work do not suggest that stopping livestock grazing on saltmarshes altogether will result in increased nesting success or breeding populations of redshank, because grazing also causes changes in vegetation structure that are beneficial to redshank, by opening the vegetation sward increasing the availability of patchy vegetation that is used for redshank nesting (van Klink et al., 2016; Sharps et al., 2016). Grazing is therefore an important part of saltmarsh management (Brindley et al., 1998; Norris et al., 1997, 1998). Cessation of grazing in previously grazed saltmarshes can result in reductions in numbers of breeding redshank as the vegetation becomes dominated by tall uniform vegetation which is unsuitable for redshank nesting (Norris et al., 1997). Furthermore, livestock grazing of saltmarshes can drive abundance and diversity of invertebrate prey (Ford et al. 2013). If UK Environment Agency guidelines are followed, grazed saltmarshes would have livestock present from April until October (Adnitt et al., 2007).

Several management measures could be considered to reduce the strength of the trade-off between grazing to maintain a suitable vegetation structure with the need to minimize nest trampling:

1. As our results show that cattle did not move more than 500 m away from the seawall in three of four marshes, grazing densities could be calculated only over the area of saltmarsh within 500 m of the sea wall then scaled to fulfill the 1 cattle/ha grazing recommendation (Norris et al., 1997). This approach would mean that the grazing intensity is adjusted to account for the higher livestock distributions close to sea wall in the most sensitive part of the saltmarsh for redshank. However, the exact distance from the seawall will have to vary for individual saltmarshes depending on the size of the redshank nesting zone, which may render this method impractical due to time constraints of land managers.
2. An alternative approach would be to delay the start date of grazing. Livestock are generally introduced in April or May because this is when vegetation starts to grow (Adnitt et al., 2007); therefore, bringing the start of grazing forward is not feasible. However, as the redshank nesting season lasts from mid-April to mid-July, grazers could be introduced when the redshank breeding season has finished. In other habitats, such as lowland wet grasslands, commencing grazing after the end of July has been shown to increase productivity in redshank and other shorebirds (Green 1986). The cattle stocking density would probably need to be higher overall to graze down the vegetation that has built up and to prepare the vegetation for the next spring. This would completely eliminate trampling of nests and might maintain the desired vegetation structure through grazing, although graziers would need to find alternative pasture early in the season. As breeding redshank are highly site faithful, but respond to changing vegetation conditions (Sharps et al., 2016; Thompson & Hale, 1989), this option may be preferable.
3. Alternatively, a rotational grazing regime where saltmarshes are grazed heavily in 1 year and left ungrazed in alternate years may improve breeding success by eliminating nest trampling in the ungrazed year. The saturating nature of the response of trampling probability to livestock grazing suggests that although this approach is likely to lead to total nest loss in the grazed year, it will reduce average nest loss over 2 or more years. Rotational grazing could be carried out using whole marshes or within smaller sections within marshes. This could require some fencing, which can be expensive and impractical in tidal areas where fences may accumulate debris, but creeks could be used as barriers to ensure lengths of fences are shorter. Compartments would need to enable access to water troughs and high tide refuges, which most likely would mean incorporating a section of seawall. However, care would need to be taken with this approach to ensure breeding redshank are not actively selecting the compartments with active grazing. This approach will only work if grazing in alternate years would keep the sward in a suitable condition for nesting.
4. Fencing off redshank habitat completely in the breeding season may be possible but is unlikely to be feasible as a routine solution as the grazers will need access to refuges from flooding during spring tides.
5. The strategic placement of water troughs further away from breeding areas could naturally restrict livestock movements. This approach is unlikely to be effective on a saltmarsh, as water troughs need to be located close to the landward extent of the marsh allow water to be piped to the trough, and so that cattle can access fresh water even during high tides.
6. Finally grazers other than cattle could be considered, but are unlikely to solve the problem. Sheep are more likely to produce shorter vegetation swards, which is unsuitable for redshank (Green 1986; Beintema & Muskens, 1987) and horses cause even higher trampling of nests (Mandema et al., 2013).

In conclusion, this work shows that the areas of the saltmarsh where redshank breed are much more intensively grazed during the breeding season than is desirable, because livestock concentrate in these areas. This results in high nest trampling probability; therefore, changes in grazing management on saltmarshes are necessary to increase the nesting success of redshank. Grazing management should aim to keep livestock away from redshank nesting habitat between mid-April and mid-July through delaying the onset of grazing or introducing a rotational grazing system. Trial management is required to test which of these options would maintain a favorable vegetation structure for redshank breeding, while reducing redshank nest loss.

## ACKNOWLEDGMENTS

We are grateful to the managers and graziers of Frampton, Kirton, and Terrington marshes for assisting with this study by allowing site access and facilitating the attachment/removal of collars. Many thanks to John Badley and the Frampton RSPB staff who played a key role in setting up this experiment. This work would not have been possible without assistance from Nigel Butcher, Andrew Asque, and Colin Gooch who designed and built the GPS collars.

## CONFLICT OF INTEREST

None declared.

## AUTHORS' CONTRIBUTIONS

E.A.S., J.S., L.R.M., M.S., A.G., and J.G.H. conceived the ideas and designed methodology; E.A.S. analyzed the data and led the writing of the manuscript; K.J. collected data in year 2 of this study. All authors contributed critically to the drafts and gave final approval for publication.

## REFERENCES

Adam, P. (1990). *Saltmarsh ecology*. Cambridge, UK: Cambridge University Press.

Adnitt, C., Brew, D., Cottle, R., Hardwick, M., John, S., Leggett, D., … Staniland, R. (2007). *Saltmarsh management manual*. Bristol, UK: Environment Agency.

Allen, J., & Pye, K. (1992). *Coastal saltmarshes: Their nature and importance*. Cambridge, UK: Cambridge University Press.

Arias, R., & Mader, T. (2011). Environmental factors affecting daily water intake on cattle finished in feedlots. *Journal of Animal Science*, *89*, 245–251.

Armstrong, W., Wright, E., Lythe, S., & Gaynard, T. (1985). Plant zonation and the effects of the spring-neap tidal cycle on soil aeration in a Humber salt marsh. *The Journal of Ecology*, *73*, 323–339.

Ausden, M. (2007). *Habitat management for conservation: A handbook of techniques*. Oxford: Oxford University Press.

Bailey, D. (1995). Daily selection of feeding areas by cattle in homogeneous and heterogeneous environments. *Applied Animal Behaviour Science*, *45*, 183–200.

Bakker, J. (1985). The impact of grazing on plant communities, plant populations and soil conditions on salt marshes. *Vegetatio*, *62*, 391–398.

Bakker, J. P., De Bie, S., Dallinga, J. H., Tjaden, P., & De Vries, Y. (1983). Sheep-grazing as a management tool for heathland conservation and regeneration in the Netherlands. *Journal of Applied Ecology*, *2*, 541–560.

Beintema, A. J., & Muskens, G. J. D. M. (1987). Nesting success of birds breeding in Dutch agricultural grasslands. *Journal of Applied Ecology*, *24*, 743–758.

Best, L. B. (1986). Conservation tillage: Ecological traps for nesting birds? *Wildlife Society Bulletin*, *14*, 308–317.

Boorman, L. (2003). *Saltmarsh Review: An overview of coastal saltmarshes, their dynamic and sensitivity characteristics for conservation and management*. Peterborough, UK: Joint Nature Conservation Committee.

Brindley, E., Norris, K., Cook, T., Babbs, S., Forster Brown, C., Massey, P., … Yaxley, R. (1998). The abundance and conservation status of redshank *Tringa totanus* nesting on saltmarshes in Great Britain. *Biological Conservation*, *86*, 289–297.

Burd, F. (1989). *Saltmarsh survey of Great Britain: An inventory of British Saltmarshes*. Peterborough, UK: Joint Nature Conservation Committee.

Davidson, K. E., Fowler, M. S., Skov, M. W., Doerr, S. H., Beaumont, N., & Griffin, J. N. (2017). Livestock grazing alters multiple ecosystem properties and services in salt marshes: A meta-analysis. *Journal of Applied Ecology*, https://doi.org/10.1111/1365-2664.12892.

Doody, J. P. (2008). *Saltmarsh conservation, management and restoration*. Houten, The Netherlands: Springer.

Eglington, S. M., Gill, J. A., Smart, M. A., Sutherland, W. J., Watkinson, A. R., & Bolton, M. (2009). Habitat management and patterns of predation of Northern Lapwings on wet grasslands: The influence of linear habitat structures at different spatial scales. *Biological Conservation*, *142*, 314–324.

Esselink, P., Fresco, L. F. M., & Dijkema, K. S. (2002). Vegetation change in a man-made salt marsh affected by a reduction in both grazing and drainage. *Applied Vegetation Science*, *5*, 17–32.

Feather, A., Mason, L. R., Smart, J., & York, M. (2016). Redshank conservation and saltmarsh grazing on the Wash Estuary. Research Report 58. RSPB Centre for Conservation Science, The Lodge, Sandy.

Ford, H., Garbutt, A., Jones, L., & Jones, D. L. (2013). Grazing management in saltmarsh ecosystems drives invertebrate diversity, abundance and functional group structure. *Insect Conservation and Diversity*, *6*, 189–200.

Gray, A. (1992). Saltmarsh plant ecology: Zonation and succession revisited. In *Saltmarshes: Morphodynamics, conservation and engineering significance* (pp. 63–79). Cambridge: Cambridge University Press.

Green, R. E. (1984). Nomograms for estimating the stage of incubation of wader eggs in the field. *Wader Study Group Bulletin*, *42*, 36–39.

Green, R. E. (1986). *The Management of Lowland Wet Grassland for Breeding Waders*. Sandy, Bedfordshire: The Royal Society for the Protection of Birds.

Hale, W. G. (1980). *Waders: New Naturalist Series number 54*. London, UK: Collins.

Hill, M. (1988). *Saltmarsh vegetation of the wash: An assessment of change from 1971–1985*. Peterborough: Nature Conservancy Council.

Howery, L. D., Provenza, F. D., Banner, R. E., & Scott, C. B. (1996). Differences in home range and habitat use among individuals in a cattle herd. *Applied Animal Behaviour Science*, *49*, 305–320.

Howery, L. D., Provenza, F. D., Banner, R. E., & Scott, C. B. (1998). Social and environmental factors influence cattle distribution on rangeland. *Applied Animal Behaviour Science*, *55*, 231–244.

Hughes, G. P., & Reid, D. (1951). Studies on the behaviour of cattle and sheep in relation to the utilization of grass. *The Journal of Agricultural Science*, *41*, 350–366.

Jensen, A. (1985). The Effect of cattle and sheep grazing on salt-marsh vegetation at Skallingen, Denmark. *Vegetatio*, *60*, 37–48.

Jensen, H. P., Rollins, D., & Gillen, R. L. (1990). Effects of cattle stock density on trampling loss of simulated ground nests. *Wildlife Society Bulletin*, *18*, 71–74.

Jones, K. (2014). *Do optimal cattle grazing densities on saltmarsh habitat present breeding Redshank with an ecological trap? A study of nest trampling rates by cattle on The Wash, East Anglia*. MSc, University of Reading.

van Klink, R., Nolte, S., Mandema, F. S., Lagendijk, D. G., WallisDeVries, M. F., Bakker, J. P., … Smit, C. (2016). Effects of grazing management on biodiversity across trophic levels–The importance of livestock species and stocking density in salt marshes. *Agriculture, Ecosystems & Environment*, *235*, 329–339.

Kubetzki, U., & Garthe, S. (2007). Nests with a view: Distribution, nest habitats and diets of roof-breeding Common Gulls (Larus canus) in northern Germany. *Waterbirds*, *30*, 602–608.

Malpas, L. R., Smart, J., Drewitt, A., Sharps, E., & Garbutt, A. (2013). Continued declines of Redshank Tringa totanus breeding on saltmarsh in Great Britain: is there a solution to this conservation problem? *Bird Study*, *60*, 1–14.

Mandema, F. S., Tinbergen, J. M., Ens, B. J., & Bakker, J. P. (2013). Livestock grazing and trampling of birds' nests: An experiment using artificial nests. *Journal of Coastal Conservation*, *17*, 1–8.

McNaughton, S. J. (1984). Grazing lawns: Animals in herds, plant form, and coevolution. *The American Naturalist*, *124*, 863–886.

Murby, P. (1997). *The wash natural area profile*. Grantham: Natural England.

Nolte, S., Esselink, P., Smit, C., & Bakker, J. P. (2014). Herbivore species and density affect vegetation-structure patchiness in salt marshes. *Agriculture, Ecosystems & Environment*, *185*, 41–47.

Norris, K., Brindley, E., Cook, T., Babbs, S., Brown, C. F., & Yaxley, R. (1998). Is the density of redshank *Tringa totanus* nesting on saltmarshes in Great Britain declining due to changes in grazing management? *Journal of Applied Ecology*, *35*, 621–634.

Norris, K., Cook, T., Odowd, B., & Durdin, C. (1997). The density of redshank *Tringa totanus* breeding on the salt-marshes of the Wash in relation to habitat and its grazing management. *Journal of Applied Ecology*, *34*, 999–1013.

Pakanen, V.-M., Luukkonen, A., & Koivula, K. (2011). Nest predation and trampling as management risks in grazed coastal meadows. *Biodiversity and Conservation*, *20*, 2057–2073.

Pehrsson, O. (1988). Effects of grazing and inundation on pasture quality and seed production in a salt marsh. *Vegetatio*, *74*, 113–124.

Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2016). *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-128. http://CRAN.R-project.org/package=nlme.

Putfarken, D., Dengler, J., Lehmann, S., & Härdtle, W. (2008). Site use of grazing cattle and sheep in a large-scale pasture landscape: A GPS/GIS assessment. *Applied Animal Behaviour Science*, *111*, 54–67.

Schlaepfer, M. A., Runge, M. C., & Sherman, P. W. (2002). Ecological and evolutionary traps. *Trends in Ecology & Evolution*, *17*, 474–480.

Sharps, E., Garbutt, A., Hiddink, J. G., Smart, J., & Skov, M. W. (2016). Light grazing of saltmarshes increases the availability of nest sites for Common Redshank Tringa totanus, but reduces their quality. *Agriculture, Ecosystems & Environment*, *221*, 71–78.

Sharps, E., Smart, J., Skov, M. W., Garbutt, A., & Hiddink, J. G. (2015). Light grazing of saltmarshes is a direct and indirect cause of nest failure in Common Redshank Tringa totanus. *Ibis*, *157*, 239–249.

Skelcher, G. (2010). *Ribble Estuary National Nature Reserve management plan*. Peterborough, UK: Natural England.

Smart, J., Gill, J. A., Sutherland, W. J., & Watkinson, A. R. (2006). Grassland-breeding waders: Identifying key habitat requirements for management. *Journal of Applied Ecology*, *43*, 454–463.

Thompson, P. S., & Hale, W. G. (1989). Breeding site fidelity and natal philopatry in the Redshank *Tringa totanus*. *Ibis*, *131*, 214–224.

Thyen, S., & Exo, K. M. (2005). Interactive effects of time and vegetation on reproduction of redshanks (*Tringa totanus*) breeding in Wadden Sea salt marshes. *Journal of Ornithology*, *146*, 215–225.

Van Horne, B. V. (1983). Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management*, *47*, 893–901.

Vulink, J., & Drost, H. (1991). A causal analysis of diet composition in free ranging cattle in reed-dominated vegetation. *Oecologia*, *88*, 167–172.

WallisDeVries, M. F. (1998). Large herbivores as key factors for nature conservation. In M. F. WallisDe Vries, J. P. Bakker & S. E. Van Wieren (Eds.), *Grazing and conservation management* (pp. 1–20). Berlin: Springer.

Yasué, M., Quinn, J. L., & Cresswell, W. (2003). Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in Redshanks. *Functional Ecology*, *17*, 727–736.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. London: Springer Science & Business Media.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Sharps E, Smart J, Mason LR, et al. Nest trampling and ground nesting birds: Quantifying temporal and spatial overlap between cattle activity and breeding redshank. *Ecol Evol*. 2017;7:6622–6633. https://doi.org/10.1002/ece3.3271

# Supplementary Materials

Supplementary Materials for paper **IV** are available online:

http://doi.org/10.1002/ece3.3271

Figures S1–S8

# PAPER V

## Are agri-environment schemes successful in delivering conservation grazing management on saltmarsh?

**Mason, L.R.**, Feather, A., Godden, N., Vreugdenhil, C.C. & Smart, J.

*Journal of Applied Ecology* (2019), 00: 1–13. http://doi.org/10.1111/1365-2664.13405

Received: 13 August 2018 | Accepted: 15 February 2019

DOI: 10.1111/1365-2664.13405

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

# Are agri-environment schemes successful in delivering conservation grazing management on saltmarsh?

**Lucy R. Mason**[1] | **Alastair Feather**[1] | **Nick Godden**[1] | **Chris C. Vreugdenhil**[1] | **Jennifer Smart**[1,2]

[1]RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire, UK

[2]School of Biological Science, University of East Anglia, Norwich, UK

**Correspondence**
Jennifer Smart
Email: jennifer.smart@rspb.org.uk

Handling Editor: Richard Fuller

## Abstract

1. Grasslands occur around the globe and, in temperate regions, their natural management by fire, drought and wild herbivores has largely been replaced by grazing with domestic livestock. Successful management for agriculture is not always suitable for conservation and can have a detrimental effect on biodiversity. Conservation grazing of saltmarshes, delivered through agri-environment schemes, may provide a solution to counteract biodiversity loss by providing farmers with financial incentives to graze these internationally important coastal wetlands more sensitively.
2. To assess whether conservation grazing is being achieved and whether agri-environment schemes are effective in delivering this management, we conducted a national survey on English saltmarshes, scoring the management on each site as optimal, suboptimal or detrimental in terms of suitability for achieving conservation aims for five aspects of grazing: presence, stock type, intensity, timing and habitat impact.
3. Although most saltmarshes suitable for grazing in England were grazed, conservation grazing was not being achieved. Sites under agri-environment management for longer did score higher and approached optimal levels in terms of grazing intensity in one region, but sites with agri-environment agreements were no more likely to be grazed at optimal conservation levels than sites without them overall, indicating that agri-environment schemes, in their current form, are an ineffective delivery mechanism for conservation grazing on saltmarsh.
4. The low specificity of agri-environment prescription wording may contribute to this failure, with prescriptions either being vague or specifying suboptimal or detrimental management objectives, particularly for grazing intensity, timing and stock type. These objectives are often set too high or too low, during unsuitable periods or using stock types inappropriate for achieving conservation aims.
5. *Synthesis and applications*. Our national survey indicates that agri-environment schemes are not currently delivering conservation grazing on English saltmarshes. Agri-environment schemes are the only mechanism through which such grazing

can be implemented on a national scale, so improving their effectiveness is a priority. Policymakers, researchers and managers need to work together to ensure better translation of conservation guidelines into schemes, increasing the specificity of management prescriptions and improving understanding of the need for management measures. A more detailed and reliable system of auditing to ensure that management activities are taking place would be beneficial or alternatively moving to a results-based scheme where payments are made on desirable outcomes rather than on evidence of management.

**KEYWORDS**

agri-environment schemes, countryside stewardship, grazing, higher level stewardship, livestock, saltmarsh, site condition, wetlands

## 1 | INTRODUCTION

Maintaining and enhancing biodiversity through conservation action requires appropriate habitat management to ensure suitable conditions for the species or community of interest. Such management can encourage a return to a near-natural habitat state, encouraging restoration of ecosystem functioning and stability (Ausden, 2007). Livestock grazing is an important tool used widely for conservation management across a wide range of grassland habitats, with livestock replacing the role of natural grazers where these have been lost (Ausden, 2007). Grazing, both for conservation management and for food production, is a major driver of vegetation structure and therefore resource availability in natural systems globally (Watkinson & Ormerod, 2001) and can help to counteract the negative impacts of climate change (Clausen, Stjernholm, & Clausen, 2013).

The restricted nature of livestock grazing for conservation management (such as lower stocking rates or timing restrictions) reduces its profitability relative to high-intensity farming, so uptake incentives are often provided to land managers in the form of payments for management through agri-environment schemes (AES; Batáry, Dicks, Kleijn, & Sutherland, 2015). These are a key mechanism by which conservation grazing can be delivered at national levels. Targeted AES have been successful in delivering conservation management to benefit many wetland systems (e.g. Schekkerman, Teunissen, & Oosterveld, 2008; Smart et al., 2014), but inadequate monitoring has made the overall assessment of AES effectiveness difficult (Kleijn & Sutherland, 2003).

Saltmarshes, that cover ~5.5 million hectares of land surface globally (McOwen et al., 2017), are an example of a system traditionally managed by livestock grazing (cattle, sheep, horses; Dijkema, 1990; Jones et al., 2011) for food production and where AES are commonly used to encourage conservation management. Saltmarshes are highly productive ecosystems supporting rich communities of halophytic plants, invertebrates and birds through their provision of important resources and habitat conditions for bird breeding, wintering and migratory staging, as well as important fish nursery grounds, human recreational opportunities and ecosystem services in the form of tidal defence, water quality regulation and carbon storage (e.g. Barbier et al., 2011; Boorman, 2003).

Over 50% of saltmarshes have been lost or degraded globally (Gedan, Silliman, & Bertness, 2009; UNEP, 2006), with the rate of degradation now exacerbated by climate change and associated sea level rise (Doody, 2004; FitzGerald, Fenster, Argow, & Buynevich, 2008; Hughes, 2004). In western Europe the biodiversity value of saltmarshes is declining despite protection under the EU Habitats and Water Framework Directives (Doody, 2008; Garbutt, de Groot, Smit, & Pétillon, 2017; McOwen et al., 2017), with over 50% of the European coastal protected sites network now in "unfavourable inadequate" or bad condition (European Environment Agency, 2009). Agricultural intensification is a key factor in these biodiversity declines, with increases in grazing intensity or abandonment in recent decades resulting in declines in saltmarsh-breeding birds and plant and invertebrate community changes (Chatters, 2004; Davidson et al., 2017; Norris et al., 1998).

Five aspects of grazing (termed "conservation grazing") are particularly important for the conservation management of saltmarshes in western Europe: (a) whether sites should be grazed or not, (b) stock type, (c) grazing intensity, (d) timing of grazing and (e) the resulting habitat structure. Although recommendations for these five aspects vary between species or communities of interest (e.g. Davidson et al., 2017), the consensus from published and accessible grey literature (see Table S1) is that "historically grazed" sites should continue to be grazed using cattle (Adnitt et al., 2007), in a mosaic or rotation of "low" to "moderate" grazing intensity (Doody, 2007; Lagendijk, Howison, Esselink, Ubels, & Smit, 2017; Mandema et al., 2015; van Klink et al., 2016) from April to October if targeting plant communities or from June to October if targeting breeding birds (winter grazing November–March prevents optimal sward regrowth and causes soil compaction, poaching and erosion, while grazing in spring causes considerable bird nest losses to trampling; e.g. Adnitt et al., 2007; Doody, 2008; Sharps et al., 2017). The resulting habitat should then present a mosaic of sward heights where the majority of standing crop is still present to support breeding birds and habitat diversity (JNCC, 2004; Malpas, Smart, Drewitt, Sharps, & Garbutt, 2013).

Despite these freely available conservation grazing recommendations (Adnitt et al., 2007; Doody, 2008), many saltmarshes in western Europe are still grazed at suboptimal levels (Malpas et al., 2013). In

England, "input-based" AES systems (where payments are made based on the agreed management being undertaken; Hanley, Banerjee, Lennox, & Armsworth, 2012), have existed since 1991 and include saltmarsh management or grazing options where implementation relies on a list of management prescriptions. These schemes and similar management on nature reserves, had little effect on grazing pressure on English saltmarsh and did not influence the associated decline in saltmarsh-breeding birds between 1996 and 2011, indicating they may not be delivering necessary habitat management or conservation outcomes (Malpas et al., 2013). There was therefore an urgent need to assess whether or not conservation grazing was being achieved on saltmarshes on a national scale, whether AES were effective in influencing this management and how they could be improved.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites

We surveyed 213 saltmarsh sites in three English regions in 2013 representing 50% (16,824 ha) of the vegetated saltmarsh in England (33,572 ha; Phelan, Shaw, & Baylis, 2011; Figure 1). The regions (East, Northwest and South) represent major divisions between saltmarsh types and grazing practices (Burd, 1989) and were managed by different statutory agency (Natural England) regional teams. Of our 213 study sites, 114 (54%) received payments for saltmarsh management and/or conservation grazing options through AES under Higher Level Stewardship (HLS, in the Environmental Stewardship Scheme; Natural England, 2013) or the Countryside Stewardship Scheme (CSS; DEFRA, 2004; Figure 1, Table 1, Table S2). These AES sites encompassed 94% (10,573 ha) of the vegetated saltmarsh under AES management in the three regions.

**FIGURE 1** Locations of the 213 saltmarsh survey sites in relation to the distribution of saltmarsh within three English regions. For site types and spatial-pairings see Figure S1

Outlines of UK Rural Land Registry land-holding parcels with saltmarsh management options for each AES agreement were used as site boundaries for AES sites. Most agreements (*n* = 99, 87%) included one or more contiguous parcel(s) of saltmarsh habitat, all of which we defined as one site. For the few agreements (*n* = 7) that incorporated multiple non-contiguous parcels of saltmarsh, each parcel was considered a separate site because grazing management and management prescriptions may differ between geographically separate parcels, even within the same agreement (max no. of separate parcels per agreement = 3; total no. AES agreements = 106). Non-AES site boundaries were hand-digitised with reference to Ordnance Survey 1:25,000 maps, online aerial imagery and seaward boundaries of predicted saltmarsh extent (Environment Agency, 2015) in GIS (MapInfo Professional v.6 2000). The area (ha) of each site was calculated using ArcGIS (version 10.3.1 2014).

Some sites comprised multiple grazing management blocks (hereafter "grazing areas") separated by fencing or natural barriers to livestock movement or formed part of larger grazing areas extending beyond site boundaries with livestock free to graze across the whole area (sometimes encompassing both saltmarsh and adjacent non-saltmarsh habitat). We therefore collected survey data at the grazing area scale to allow more-accurate assessment of conservation grazing per hectare of available grazing land associated with each site.

### 2.2 | Is conservation grazing being achieved on English saltmarshes?

### 2.2.1 | Grazing surveys

We visited each site up to four times during the core grazing period (April–October; mean no. survey visits to each site = 3.9, grazed sites = 122, 4 visits = 113, 3 visits = 6, 2 visits = 2, 1 visit = 1), with at least 4 weeks between visits and recorded the number, type, age-class and distribution of livestock in each grazing area on each visit. We assumed that the absence of grazing animals in any survey visit meant the area was not being grazed at that time. There is a small chance that livestock could be temporarily removed during spring high tides but in most sites, livestock had access to alternative areas not affected by tides (e.g. sea walls or inland fields) so would still be present and observable within the grazing area. Grazing intensities were expressed as Livestock Units (LUs) per hectare to allow direct comparison between stock types and sites. LUs were calculated from the number of adult livestock for each grazing area visit based on standard conversion coefficients (DEFRA, 2010), where 1 LU is equivalent to one dairy cow, nine lowland ewes and 0.8 horses respectively (Table S3). LUs/ha were calculated by summing the LUs recorded across all grazing areas per site-visit and dividing this total by the site area (ha).

We also assessed the longer-term impact of grazing on saltmarsh habitat in relation to the vegetation communities present (grazing alters the presence and diversity of saltmarsh plant

**TABLE 1** Agri-environment scheme (AES) management options and supplements relating to saltmarsh management and/or conservation grazing present on AES sites, the number of sites with each option and annual payments per ha

| | Management option | | | |
|---|---|---|---|---|
| AES | Code | Option | Payment | No. sites |
| CSS | IT1 | Managing intertidal habitats | £20 | 8 |
| HLS | HP5 | Maintenance of coastal saltmarsh | £30 | 82 |
| | HP6 | Restoration of coastal saltmarsh | £30 | 14 |
| | HP8 | Creation of intertidal and saline habitat on grassland | Up to £500 | 2 |
| | HP10 | Supplement for extensive grazing on saltmarsh | £70 | 36 |
| | HP11 | Saltmarsh livestock exclusion supplement | £40 | 4 |
| | HR1 | Grazing supplement for cattle | Up to £35 | 16 |

Abbreviation: CSS: Countryside Stewardship Scheme; HLS: Higher Level Stewardship.

communities, Hill, 1988) and the sward height and heterogeneity by assigning each site or grazing area within sites a "grazing index" value (Malpas et al., 2013; Norris et al., 1998). Here 0 = matted vegetation, no standing crop removed, low sward heterogeneity; 1 = majority of standing crop not removed, high sward heterogeneity; 2 = majority of standing crop removed, moderate sward heterogeneity; 3 = all standing crop removed, sward height <10 cm, low sward heterogeneity (JNCC, 2004). Although crude, this index gives a reasonable reflection of the habitat structure and grazing pressure (Norris, Cook, O'Dowd, & Durdin, 1997).

### 2.2.2 | Scoring "conservation grazing"

For each visit to each grazing area, we used survey data to derive scores for five aspects of saltmarsh conservation grazing according to whether they represented optimal, suboptimal or detrimental saltmarsh management practices in relation to their suitability for achieving conservation aims (Table 2). These conservation grazing scores, derived at the grazing area scale for each visit, were summarised at the site-level using methods in Table 2 to allow analysis at the site-visit level (each row in the resulting score dataset corresponding to an individual site-visit).

### 2.2.3 | Are sites achieving conservation grazing?

To assess the extent to which the five aspects of conservation grazing are being achieved nationally and whether this differs between regions with different traditional grazing practices, we ran a modelling analysis where the categorical effect of region was the only predictor. We ran generalised linear mixed models (GLMMs) in R (R Core Team, 2017) with site-visit scores for each aspect of conservation grazing as separate response variables. We included the random effect of site in all models to control for repeated site-visits. Model structures and error distributions were as specified in Table 3. For aspect 1 we included all sites in analysis; the score for this aspect was on a binomial scale (Table 2); results indicating the probability that sites that were suitable for grazing had grazing present (i.e. optimal for grazing presence). The achievement of conservation grazing for aspects 2–5 was only relevant for grazed sites however (Table 2), so for these models we included grazed sites only (Table 3) and used a Conway–Maxwell Poisson error distribution to account for underdispersion (response variable mean > variance; Lynch, Thorson, & Shelton, 2014). To assess how well grazed sites are achieving overall, we also analysed the number of grazing aspects scored as optimal as an additional response variable (max score = 4). The level of support for regional differences was assessed by comparing regional models ($M_{region}$) with national models ($M_{national}$; Table 3) with Information-Theoretic methods based on AIC (Burnham & Anderson, 2002).

### 2.3 | Are AES a successful mechanism for delivering conservation grazing and to what extent is AES agreement wording fit for purpose?

To compare conservation grazing management on sites experiencing similar environmental characteristics in the presence or absence of AES, we spatially-paired AES and non-AES sites. Paired sites were directly adjacent (where possible) or contiguous, in the same estuary or on the same immediate stretch of coastline if no adjacent sites existed (Figure S1). In some cases, multiple AES or non-AES sites were contiguous or on the same coastline stretch so these were included in one paired-group for analysis (Table S2). All paired-groups ($n$ = 76) contained at least one AES site and at least one non-AES site for direct comparison (total sites in paired-groups = 200; mean number of AES sites per group = 1.5, mean number of Non-AES sites = 1.1). One AES site and 12 non-AES sites could not be paired or grouped with others (no other sites in vicinity or no AES sites on the whole coastline stretch respectively) so these were excluded from analysis.

### 2.3.1 | Assessing AES as a delivery mechanism

To test whether scores for the five aspects of grazing (Table 2) differed between AES and Non-AES sites and whether the type of AES, the inclusion of specific grazing supplements or the agreement age (Table 4) influenced this difference, we ran GLMMs with site-visit scores for each grazing aspect as separate response variables (model structures in Table 5). We also included the number of grazing aspects scored as optimal on grazed sites as an additional response variable to assess how well sites achieved optimal management overall. Models for each response variable contained each of four partially-nested AES effect variables (Table 4) with or without a regional interaction (plus constituent main effects) as well as the null model. The effect of region was included to determine if the level of conservation grazing achieved by their

**TABLE 2** Optimal, suboptimal and detrimental levels of five aspects of conservation grazing and the methods used to summarise across grazing areas to generate site-visit conservation grazing scores for each aspect, along with rationalisation and evidence sources

| | | Conservation grazing level and scoring criteria | | |
|---|---|---|---|---|
| **Aspect** | **Scoring method** | **Optimal (score = 1)** | | **Detrimental (score = 0)** |
| (1) Presence/Absence | Sites suitable for grazing = directly accessible from land, with infrastructure to contain livestock and drinking water. Grazed = grazing recorded in at least one grazing area per site-visit. Binomial visit-level score (0, 1) | Site SUITABLE and GRAZED or Site UNSUITABLE and UNGRAZED | | Site SUITABLE and UNGRAZED or Site UNSUITABLE and GRAZED |
| Rationalisation/Source: Historically grazed sites should continue to be grazed at conservation levels (abandonment being detrimental to saltmarsh biodiversity) while historically ungrazed sites should remain ungrazed (Adnitt et al., 2007). The true grazing history of a site in the UK is difficult to determine however, particularly if sites were abandoned outside of living or documented memory. For the purposes of this study we considered that sites classed as suitable for grazing during surveys (i.e. accessible to livestock and agricultural workers from the sea wall and surrounded by agricultural land) will most likely have been utilised for grazing historically (Chatters, 2004). | | | | |
| | | **Optimal (score = 2)** | **Suboptimal (score = 1)** | **Detrimental (score = 0)** |
| (2) Stock type | Stock type categorised per grazing area per visit as: Cattle, Sheep, Horses, Mixed with Cattle, Mixed without Cattle or None (Table S3). Score based on the combination of stock type categories present across all grazing areas per site-visit. Numeric visit-level score (0–2) | CATTLE GRAZING ONLY<br>Stock type = Cattle in at least one grazing area; no other stock types recorded | SOME CATTLE GRAZING WITH OTHER STOCK TYPES PRESENT<br>Stock type = Cattle or Mixed with Cattle in at least one grazing area, in the presence or absence of other stock types. | NO CATTLE GRAZING or NO STOCK PRESENT<br>Stock type = Sheep, Horse, Mixed without Cattle or None in all grazing areas |
| Rationalisation/Source: Cattle produce more structurally diverse vegetation than sheep or horses (e.g. Adnitt et al., 2007). | | | | |
| (3) Grazing intensity | LUs calculated for each grazing area then summed across grazing areas for each site-visit. Score based on value of site-visit LUs/ha (summed site-visit LUs divided by site area). Numeric visit-level score (0–2) | LOW<br>$0 < \text{LUs/ha} \le 0.3$ | LOW-MODERATE<br>$0.3 < \text{LUs/ha} \le 0.7$ | HIGH or NONE<br>$\text{LUs/ha} > 0.7$ or $\text{LUs/ha} = 0$ |
| Rationalisation/Source: Criteria based on mean maximum LUs/ha values classed as low, low-moderate or high by 26 sources where this information was quantified and accompanied by an assessment of suitability for conservation grazing (Table S1). | | | | |
| (4) Timing of grazing | Grazing areas scored for optimal grazing timing for breeding birds and/or vegetation based on the first and last visit grazing was recorded. The minimum score from any grazing area per site then extended across all visits to provide a site-visit level score (accounting for the most detrimental grazing period from any part of a site). Numeric visit-level score (0–2) | BIRDS = Optimal<br>VEG = Optimal | BIRDS = Optimal, VEG = Suboptimal<br>or<br>BIRDS = Suboptimal, VEG = Optimal | BIRDS = Suboptimal<br>VEG = Suboptimal |
| Rationalisation/Source: BREEDING BIRDS: Optimal = grazing starts after the peak nesting period (end of May, i.e. after visit 1), Suboptimal = grazing starts visit 1 (April–May). Grazing in the peak nesting period causes considerable bird nest losses to trampling (Sharps et al., 2017). VEGETATION: Optimal = grazing April–October (grazing starts visit 1 or later, ends before visit 4), Suboptimal = grazing continues after October (grazing still recorded visit 4). Winter grazing after October prevents optimal sward regrowth and is likely to cause soil compaction, poaching and erosion (e.g. Adnitt et al., 2007; Doody, 2008). | | | | |
| (5) Habitat impact | Gazing index value assessed for each grazing area per visit. Score based on maximum grazing pressure index from any grazing area per site-visit (accounting for the most detrimental grazing impact from any part of a site). Numeric visit-level score (0–2) | Grazing index = 1 | Grazing index = 0<br>or<br>Grazing index = 2 | Grazing index = 3 |
| Rationalisation/Source: Grazing index indicates grazing impact on habitat where essentially 0 = no grazing, matted vegetation, no standing crop removed; 1 = light grazing, majority of standing crop not removed; 2 = moderate grazing, majority of standing crop removed; 3 = heavy grazing, all standing crop removed, sward height <10 cm (JNCC 2004). Breeding bird densities and habitat diversity highest where index = 1, intermediate where index = 0 or 2, lowest where index = 3 (Malpas et al., 2013). | | | | |

**TABLE 3** Results from generalised linear mixed models (GLMMs) assessing the spatial variation in scores for the five aspects of conservation grazing and the number of aspects scored as optimal on grazed sites, at national ($M_{national}$) and regional ($M_{regional}$) scales. Bold values indicate support for regional differences

| | $M_{national}$ ~ 1 + (1\|Site) | | | | $M_{regional}$ ~ Region + (1\|Site) | | | | Regional differences | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Response** | **AIC** | **logLik (df)** | ***w*** | **$\sigma^2$** | **AIC** | **logLik (df)** | ***w*** | **$\sigma^2$** | **ΔAIC** | **Ratio** |
| (1) Grazing presence score (0,1)[a] | 839.9 | −418.0 (3) | 0.38 | 7.92 | 838.9 | −415.5 (5) | 0.62 | 7.54 | 0.95 | 1.6 |
| (2) Stock type score (0–2)[b] | 1,133.3 | −563.7 (3) | 0.06 | 0.70 | **1,127.8** | **−559.9 (5)** | **0.94** | **0.65** | **5.47** | **15.4** |
| (3) Grazing intensity score (0–2)[b] | 1076.2 | −535.1 (3) | 0.10 | 0.46 | **1,071.8** | **−530.9 (5)** | **0.90** | **0.41** | **4.38** | **8.9** |
| (4) Grazing timing score (0–2)[b] | 594.2 | −294.0 (3) | 0.06 | 1.35 | **588.7** | **−289.4 (5)** | **0.94** | **1.21** | **5.46** | **15.3** |
| (5) Habitat impact score (0–2)[b] | 608.3 | −301.1 (3) | 0.00 | 2.18 | **594.4** | **−292.2 (5)** | **1.00** | **2.01** | **13.88** | **1,034.3** |
| No. of aspects with optimal score[b] | 965.6 | −479.8 (3) | 0.41 | 0.16 | 964.9 | −477.5 (5) | 0.59 | 0.15 | 0.70 | 1.4 |

*Notes*: Support for regional differences assumed where AIC($M_{regional}$) < AIC($M_{national}$) and ΔAIC > 2 (Burnham & Anderson, 2002).
Abbreviation: AIC: AIC value; logLik: log-likelihood; df: degrees of freedom; *w*: Akaike weight (the relative likelihood of each model (exp[−0.5 * ΔAIC] divided by the sum of these values across both models); $\sigma^2$: variance of the random effect term (1|Site); ΔAIC: the difference in AIC between the model with the lowest (emboldened) and highest AIC for the two models; ratio: ratio of relative support for $M_{regional}$ over $M_{national}$ [evidence ratio = $w(M_{regional})/w(M_{national})$].

[a] All sites, *n* = 213, site-visits = 822; binomial error distribution, logit link, Laplace likelihood, lme4 (Bates, Maechler, Bolker, & Walker, 2015).

[b] Grazed sites only, *n* = 122, site-visits = 475; Conway–Maxwell Poisson error distribution, log link, ML, glmmTMB (Magnusson et al., 2017).

AES sites relative to Non-AES sites varied among different statutory agency teams. For aspect 1, all sites within AES paired-groups were included (Table S2); for aspects 2–5 which are only relevant for grazed sites, we only included sites from paired-groups where at least one AES and one Non-AES site were grazed (i.e. comparing spatially-paired grazed AES and Non-AES sites; Table 5). To directly compare spatially-paired AES and non-AES sites within models and to control for repeated site-visits, models incorporated the random effect of site nested within paired-group. Support for AES and regional effects was assessed using Information-Theoretic methods based on AIC.

### 2.3.2 | Is AES agreement wording fit for purpose?

We examined AES agreement documents for 104 of our 106 AES agreements (two not available) and extracted the wording for management prescriptions associated with saltmarsh management and grazing options (Table 1). Management prescriptions were scored in relation to whether they were specific or not combined with how optimal they were for conservation grazing (Table 6), following criteria in Table 2 and Table S4. Prescription scores were on the same scales and therefore directly comparable with conservation grazing scores defined above.

**TABLE 4** Agri-environment scheme (AES) effect variables used in the assessment of AES as a delivery mechanism for conservation grazing

| AES variable | Type: Levels (* reference category) or range | Hypothesis |
|---|---|---|
| Site type | Categorical: Non-AES*, AES | AES sites expected to attain higher conservation grazing scores if AES are a successful delivery mechanism |
| AES type | Categorical: Non-AES*, CSS, HLS | Different AES may differ in the specificity of conservation grazing prescribed and therefore the conservation grazing score attained. CSS = Countryside Stewardship; HLS = Higher Level Stewardship |
| Grazing options | Categorical: Non-AES*, AES-, AES+ | AES with supplements paid specifically for conservation grazing management (HP10/HP11/HR1, Table 1) expected to attain a higher conservation grazing score. AES- = AES without HP10/HP11/HR1, AES+ = AES with HP10/HP11/HR1 |
| Years in AES | Continuous: 0–10 | Agreement age in 2013: older agreements have had more time to implement conservation grazing or younger agreements may be based on more recent conservation grazing research recommendations, thereby affecting conservation grazing score. Years in AES = 0 (*intercept*, average score for Non-AES sites), Years in AES = 1–10 (*gradient*, score relative to agreement age for AES sites) |

**TABLE 5** Results from generalised linear mixed models (GLMMs) assessing the regional variation in scores for five aspects of conservation grazing and the number of aspects scored as optimal on grazed sites (aspects 2–5 only), in relation to AES effects (~X = AES variables singly, ~X*R = their interaction with Region plus constituent main effects and ~1 = the null model). For each response variable the AIC of the best model (lowest AIC, dark-grey shaded) is reported, with the difference in AIC between the focal model and the best model (ΔAIC) reported for all other models (models with similar support to the best model [ΔAIC < 2] are light-grey highlighted; Burnham & Anderson, 2002). For full model selection tables and top model coefficients see Table S6. Regional interactions could not be run in some cases because of over-parameterisation issues (insufficient variation in response variable for all category combinations; "—" models not run). The final column indicates whether an effect of AES on conservation grazing score was concluded (i.e. the best model included an AES variable and had substantially more support than the null model: ΔAIC < 2), with the effect direction in parentheses (positive + in favour of AES sites)

| **AES variable (X) Categories/range** | | **Site type Non-AES AES** | | **AES type Non-AES CSS, HLS** | | **Grazing options Non-AES AES+, AES-** | | **Years in AES Continuous: 0–10** | | **AES effect upheld? (direction)** |
|---|---|---|---|---|---|---|---|---|---|---|
| Model specification | ~1 | ~X | ~X*R | ~X | ~X*R | ~X | ~X*R | ~X | ~X*R | |
| (1) Grazing presence (0,1)[a] | 785.5 | 0.1 | 3.4 | 1.8 | 7.6 | 1.7 | 8.3 | 1.4 | 5.9 | No |
| (2) Stock type score (0–2)[b] | 1.1 | 768.6 | — | 2.0 | — | 1.4 | — | 0.8 | — | No |
| (3) Grazing intensity score (0–2)[b] | 4.5 | 5.8 | 1.1 | 7.8 | — | 7.3 | 4.9 | 5.6 | 764.0 | **Yes (+)** |
| (4) Grazing timing score (0–2)[b] | 435.5 | 1.8 | 1.9 | 3.8 | — | 3.7 | 6.1 | 1.5 | 2.1 | No |
| (5) Habitat impact score (0–2)[b] | 426.8 | 0.9 | — | 2.2 | — | 1.2 | — | 2.0 | — | No |
| No. of aspects with optimal score[b] | 670.5 | 2.0 | 1.4 | 3.9 | — | 3.9 | 5.8 | 1.9 | 2.5 | No |

*Notes*: [a] All spatially-paired AES/Non-AES sites: paired-groups = 76, sites = 200, site-visits = 772; binomial error distribution, logit link, Laplace likelihood estimation, lme4 (Bates et al., 2015), optimizer bobyqa (Powell, 2009).

[b] Grazed spatially-paired AES/Non-AES sites only: paired-groups = 33, grazed sites = 90, site-visits = 347; Conway–Maxwell Poisson error distribution, log link, Maximum likelihood estimation, glmmTMB (Magnusson et al., 2017).

To assess whether prescription scores were reflected in the delivery of conservation grazing, we compared site-level conservation grazing scores (continuous response variable: mean score per site) with prescription scores for each of the five grazing aspects separately using linear mixed models (LMMs) containing the random effect of region. For grazing presence, prescription score was categorical (levels: 0,1), for all other aspects prescription score was continuous (range 0–2). Support for an effect of prescription score was assessed by comparing AIC between models with and without this variable (Table S5 for model structures and outcomes).

## 3 | RESULTS

### 3.1 | Is conservation grazing being achieved on English saltmarshes?

At a national level there is a high probability that sites suitable for grazing are being grazed (grazing presence; Table 3, Figure 2a). However, grazed sites scored <1 on average for all other aspects of conservation grazing nationally and regionally (Table 5, Figure 2b), achieving optimal levels for no more than one grazing aspect per site (Figure 2c). Sites are therefore failing to achieve optimal and in many cases suboptimal levels of conservation grazing. Nationally, sites scored the worst in terms of grazing timing and impact on the habitat. Regional differences in scores were supported for stock type, grazing intensity, grazing timing and habitat impact, but the direction of the regional effect differed, with no region scoring higher than other regions overall and all regions scoring <1 on average for all aspects (Table 3, Figure 2b).

### 3.2 | Are AES a successful mechanism for delivering conservation grazing and to what extent is AES agreement wording fit for purpose?

#### 3.2.1 | Assessing AES as a delivery mechanism

At both the national and regional level, the probability that sites suitable for grazing are being grazed was not influenced by the presence of AES, irrespective of AES type, specific grazing options or agreement age (Table 5). The scores achieved for the other aspects of conservation grazing and the number of aspects which were scored as optimal, also did not differ between grazed spatially-paired AES and non-AES sites with the exception of grazing intensity on sites in the East, where older AES sites scored substantially higher and approached optimal levels (Table 5, Figure 3).

#### 3.2.2 | Is AES agreement wording fit for purpose?

Management prescriptions within AES agreements scored very highly for the presence of grazing at a national and regional level (Figure 4a). Conservation grazing scores actually achieved by AES sites for this aspect also largely matched their corresponding management prescription scores (conservation grazing score = 1 where prescription score = 1 in 80% of cases), although overall there was

**TABLE 6** Score definitions for the specificity and level of conservation grazing stipulated in agri-environment scheme management prescriptions for the five aspects of conservation grazing

| Aspect(s) | Prescription score and definition |
|---|---|
| (1) Grazing presence | 0 = Not specific (aspect not specified in prescriptions) 1 = Specific & Optimal (aspect specified at optimal conservation levels) Binary score, range = 0–1 |
| (2) Stock type<br>(3) Grazing intensity<br>(4) Timing of grazing<br>(5) Habitat impact | 0 = Not specific (aspect not specified in prescriptions) 1 = Specific & Suboptimal/ Detrimental (aspect specified but not at optimal levels) 2 = Specific & Optimal (aspect specified at optimal conservation levels) Numeric score, range 0–2 |

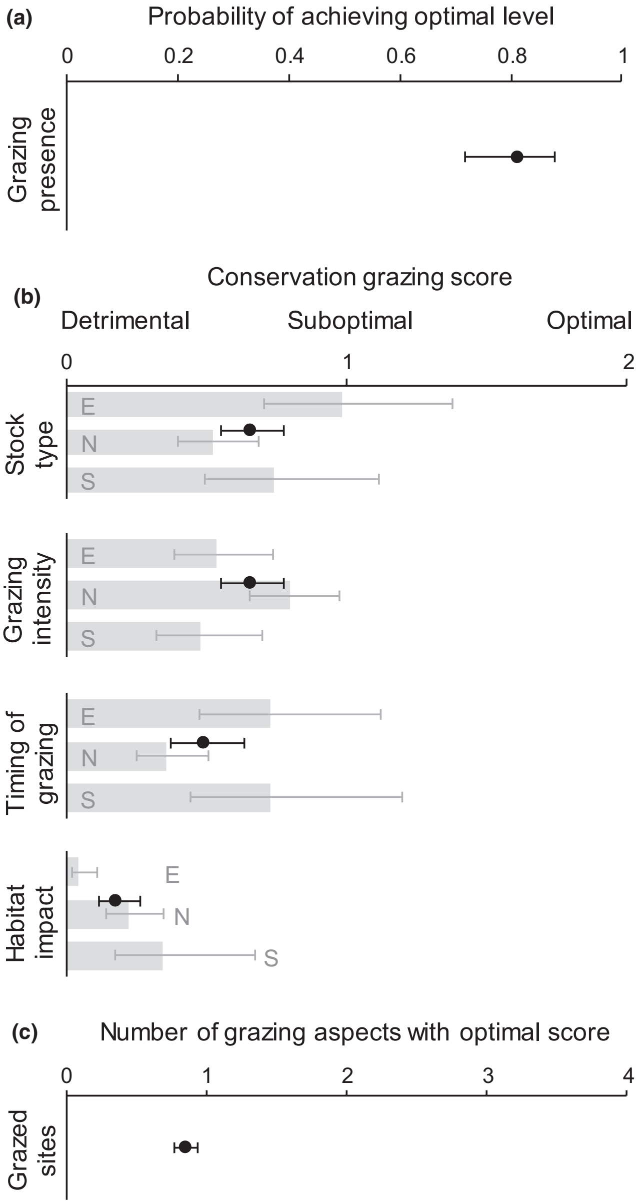


**FIGURE 2** Assessments of conservation grazing on English saltmarshes. Shown are national (point) and regional (bar) mean values estimated by binomial (a) or Conway–Maxwell Poisson (b, c) GLMMs assessing the probability of achieving an optimal grazing presence score (grazing present on suitable sites) across all sites (a) and on grazed sites the scores for the other aspects of conservation grazing (b) and the number of these aspects achieving optimal scores (c). Regional averages are only shown where regional differences were supported by AIC comparisons (East = E, Northwest = N, South = S). Error bars are 95% confidence intervals

no difference in conservation grazing score for either prescription score level for this grazing aspect (Figure 5a; Table S5).

For conservation grazing aspects relevant for grazed sites, AES agreements also achieved high prescription scores in relation to habitat impact both nationally and regionally, indicating that this aspect of conservation grazing is specified more often at optimal conservation levels within management prescriptions (Figure 4b). Prescription scores were low for stock type, grazing intensity and grazing timing at both spatial scales however (Figure 4b). This is reflected in the low total number of grazing aspects with specific and optimal prescription wording (Figure 4c).

There was a shallow but increasing trend in conservation grazing score in relation to prescription score for stock type and grazing timing, but no or shallow-negative relationships for grazing intensity and habitat impact (Figure 5, Table S5). No sites achieved optimal conservation grazing (i.e. conservation grazing score = 2) even when prescriptions specified optimal management (prescription score = 2; Figure 5).

## 4 | DISCUSSION

Our results indicate that although most saltmarsh sites in England that are capable of supporting grazing are grazed by livestock, conservation grazing is not being achieved. Grazing is therefore not being conducted by cattle at “low/moderate” grazing intensity from April or June to October, with variable sward heights and retained standing vegetation crops in the resulting habitat across English sites overall (Table 2; Adnitt et al., 2007; Doody, 2008; Lagendijk et al., 2017; Mandema et al., 2015; Sharps et al., 2017; van Klink et al., 2016). At a national level, the timing of grazing and the impact of grazing on the habitat had the lowest scores, indicating that these two aspects of conservation grazing are where management is failing the most. There were regional differences in scores relating to stock type, grazing intensity, grazing timing and habitat impacts, but no region scored higher than others overall. Additionally, we found that sites with AES agreements were no more likely to be grazed than sites without AES and although AES did marginally influence grazing intensity, the presence of AES did not enable sites to achieve optimal conservation grazing requirements, indicating that AES in their current form are an ineffective conservation grazing delivery mechanism on saltmarsh.

In temperate regions around the world, grazing by domestic livestock is an important component of the management of a range of grassland habitats (Watkinson & Ormerod, 2001). The end goal of grazing can vary from commercial agriculture to biodiversity conservation but, in natural or semi-natural habitats, grazing often has a dual purpose whereby biodiversity areas require sensitive grazing yet only

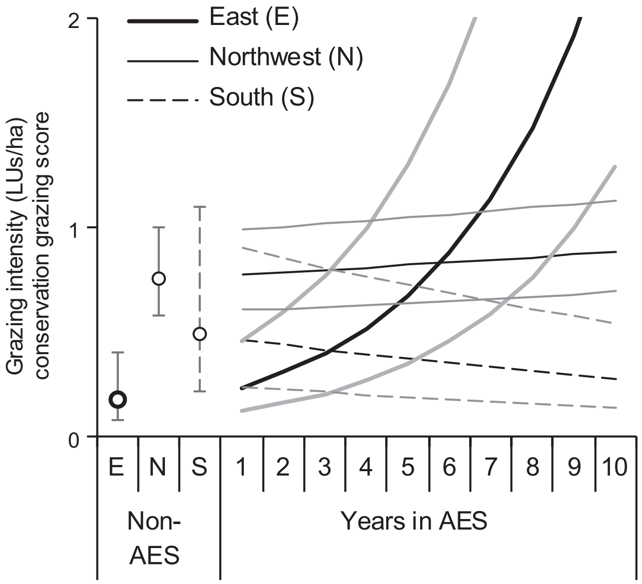


**FIGURE 3** Effects of agri-environment schemes (AES) on grazing intensity conservation grazing score on English saltmarshes (Table 5). Points indicate the regional average score for sites without AES agreements (non-AES; years in AES = 0), lines (±95% CIs) indicate the regional predicted change in score on AES sites with increasing age of AES agreement (years in AES > 0). Error bars are 95% confidence intervals

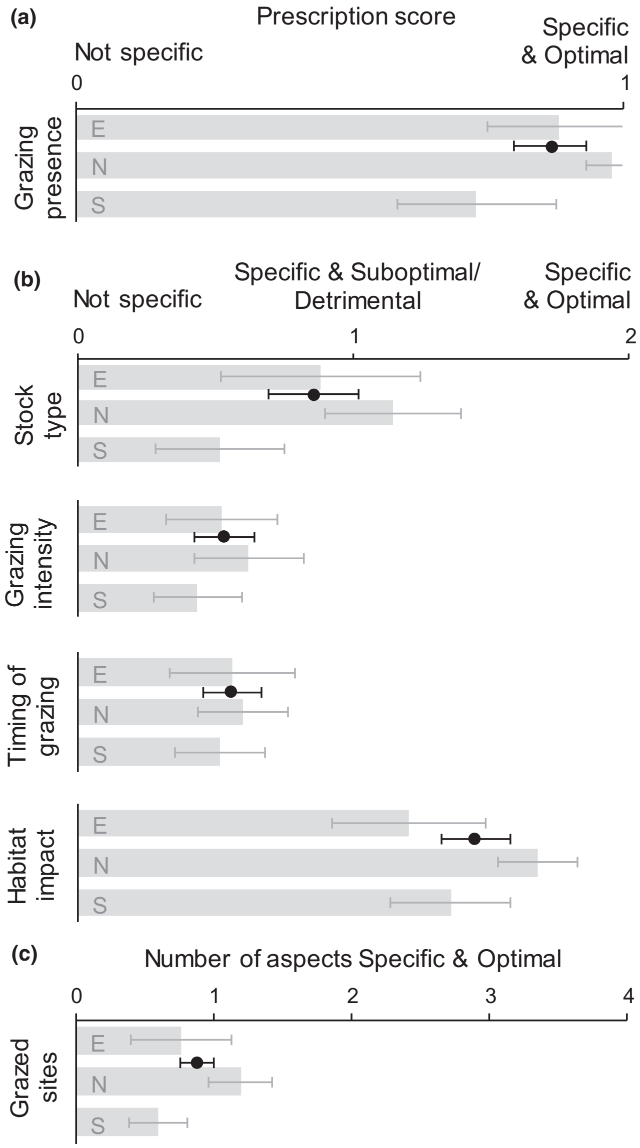


**FIGURE 4** Summary of the agri-environment scheme management prescription scores. Shown are the mean ± 95% confidence interval national (points) and regional (bars: East E, Northwest N, South S) prescription scores for five aspects of conservation grazing (a & b) and (c) the number of aspects where prescription wording was specific and optimal for the aspects relevant to grazed sites (those shown in b)

commercial grazing animals are available for the task. In these situations, payments from AES aim to compensate farmers for loss of income through grazing more sensitively for biodiversity. Here we use a relatively novel approach to assess whether AES delivers grazing that is likely to benefit biodiversity conservation, based on key aspects of conservation grazing reviewed from the literature. This approach is novel in its application to grazing management but was adapted from a similar approach used more widely to score habitat suitability for breeding lapwings *Vanellus vanellus* and to relate those scores to agri-environment management (Smart et al., 2013). We argue that this approach could be more widely adopted in the assessment of the success of any conservation action, not just AES, assuming the specific desired outcomes of management are clear and the success of conservation interventions at achieving those outcomes can be assessed.

The UK supports ~17% of the saltmarsh designated under Natura 2000 (Doody, 2008) but 37% of saltmarsh priority sites are not achieving the target conservation value under the UK Biodiversity Action Plan (JNCC, 2004). Livestock grazing is the main tool by which saltmarsh condition could be improved through direct management intervention and what constitutes optimal conservation grazing is well-studied on European saltmarshes (we found 26 papers 1972–2017 recommending saltmarsh grazing levels: Table S1). However, our results and those from other parts of Europe where saltmarsh condition is declining, show that saltmarsh conservation grazing is not being achieved (Exo, Wellbrock, Sondermann, & Maier, 2017; Haynes, Angus, Scanlan, & Bhatti, 2017; Wolff, Bakker, Laursen, & Reise, 2010), so despite frequent exchanges between researchers (Garbutt et al., 2017) this knowledge is not adequately disseminated to policymakers and managers. The issue therefore is not a lack of evidence about how saltmarshes should be managed, but an issue of the translation of evidence into recommendations for hands-on management and in encouraging land managers to implement recommendations when these go against traditional farming practices and economic gain.

The main way in which research findings can be translated into actions while providing an incentive to land managers is through AES, so the overall failure of English AES in influencing conservation grazing is concerning, particularly if AES sites are already biased towards those where habitat conditions and landowner enthusiasm are more conducive to conservation (Kleijn

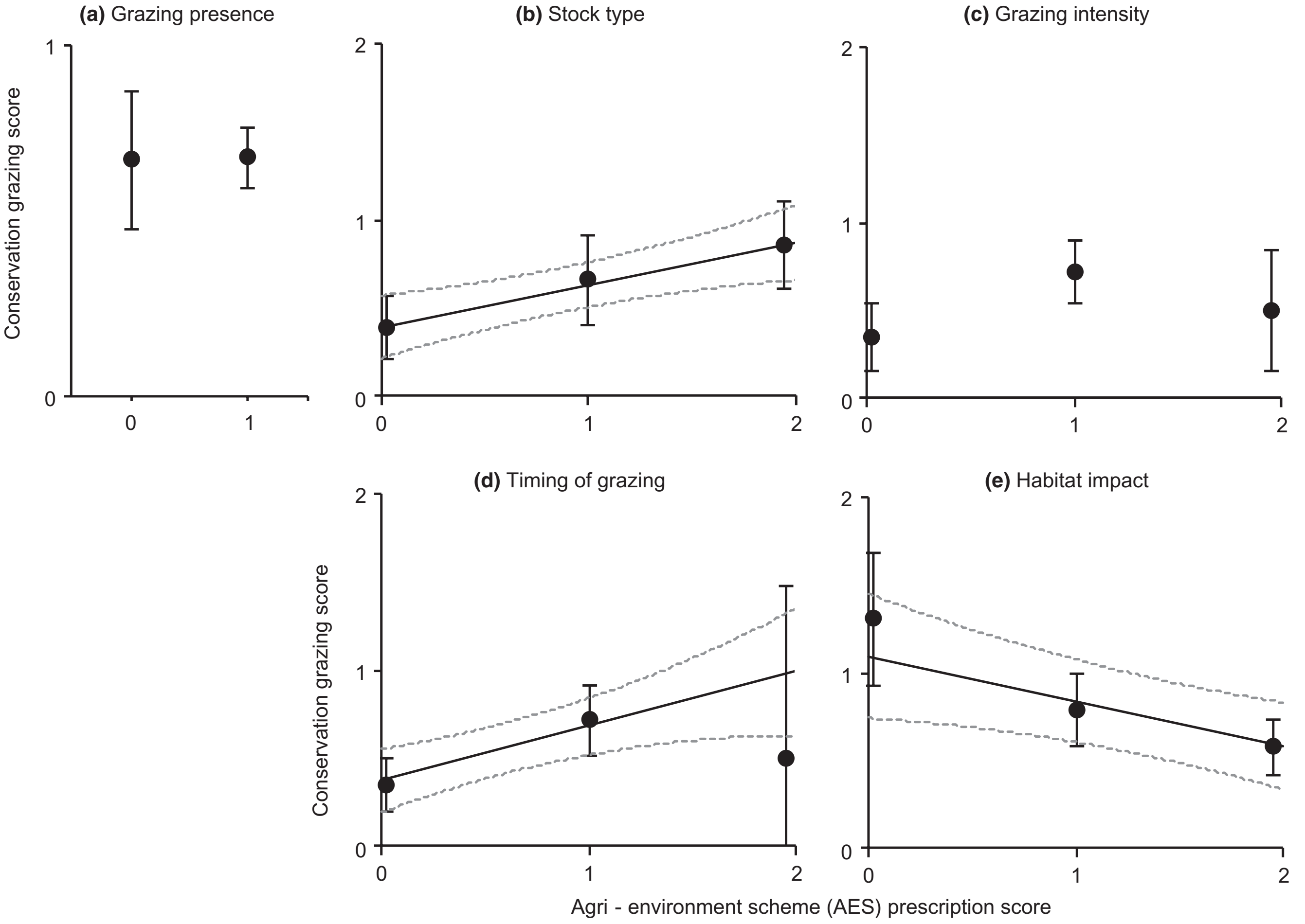


**FIGURE 5** Conservation grazing scores on agri-environment schemes (AES) sites in relation to their prescription scores for five aspects of conservation grazing. All points are means ± 95% confidence intervals predicted by LMMs (a) or from raw data at a given prescription score (b–e). For (b–e) lines show the predicted relationships between conservation grazing and prescription scores from LMM models for aspects where this relationship was supported by AIC comparisons (solid = predicted relationship, dotted = 95% CI; Table S5)

& Sutherland, 2003). We did find some evidence that AES sites improve over time in one region. This is perhaps because older agreements have longer for beneficial management changes to be implemented and take effect or were more prescriptive and provided with better guidance closer to their scheme's start. These findings, both the overall lack of beneficial effects on AES sites and minor positive effects of agreement age are supported by other studies from Europe (e.g. Kleijn, Berendse, Smit, & Gilissen, 2001; Smart et al., 2013).

The annual cost of saltmarsh and grazing management options in the agreements studied was £543,075 for 10,218 ha of saltmarsh, equating to over £5 million spent on saltmarsh management options over the course of 10 years. Livestock grazing is the only active saltmarsh management method available through English AES agreements, but grazing was no more likely on AES sites than non-AES sites and only half (51%) of AES sites were recorded as grazed during our surveys. This implies that many AES sites were paid to maintain saltmarsh by essentially doing nothing, a seemingly uneconomical exercise when 96% of the sites we surveyed were already protected against damaging actions through UK-national and/or European designations (Sites of Special Scientific Interest, Special Protection Areas, Special Areas of Conservation, Ramsar sites; JNCC, 2004). Even if all AES sites had been grazed, the current prescriptions for the grazing management of saltmarsh are clearly not cost effective if the agreements are not delivering the necessary conservation management for this habitat and the species it supports.

The low specificity of AES prescription wording provides one mechanism through which the failure of AES in influencing saltmarsh grazing management could be explained. Prescription wording scored highly for the presence of grazing on sites that have been traditionally grazed. However, the more major areas of failure were grazing intensity, timing and stock type, where management was either not specific or specified suboptimal conservation levels. Agreement-holders are required to follow these prescriptions strictly, so it is perhaps not surprising that the lack of specificity has resulted in a lack of optimal conservation grazing on the ground. In addition, the restricted nature of livestock grazing for conservation management (i.e. lower stocking rates, restrictions on timing and stock type) introduces practical and economic constraints that are likely to influence the management decisions of land managers. Practical constraints include the availability of grazing animals of the appropriate type, capacity to move animals or to restrict their access in space and time, the logistics and economics of operating smaller herds and ensuring that livestock have access to water and safe areas where they can escape from high tides. Economic constraints are also likely to be important and the restricted nature of conservation grazing will undoubtedly reduce income relative to unrestricted grazing. If AES payments are not sufficient to remove these economic constraints, then it is likely that grazing patterns will tend more towards commercial rather than conservation goals. The current grazing management on English saltmarshes is therefore likely to reflect land managers attempting to maximise income while operating within the constraints imposed by their AES prescriptions and the practicalities of grazing saltmarshes.

Conversely, if prescription wording could be improved then on-site grazing management is also likely to improve, as where prescriptions were more specific and optimal, sites implemented better conservation management in terms of stock type and timing of grazing. Being the simplest to define, these are perhaps the easiest aspects to translate into on-site management and subsequently enforce. Grazing intensity and habitat condition are aspects which are more difficult to quantify and therefore enforce, which may explain the lack of translation into on-site grazing even when prescriptions specify optimal management.

Currently, the prescriptions in each agreement are selected by a statutory-agency regional adviser from a pre-defined set of mandatory and elective phrases. The phrases relating to grazing are all elective, lack detail and make no reference to or suggestions for recommended stock types, grazing intensity or timing (although advisers may add additional details if they wish). Agreement wording could therefore be greatly improved if grazing-related prescriptions were made mandatory for livestock-grazed sites and provided specific guidance in terms of stock type, grazing intensity and timing. Improved translation of saltmarsh research findings into recommendations for actual management would be of direct benefit here, as would detailed consultations with researchers and land managers by policymakers when developing new schemes to ensure the incorporation of relevant and recent evidence for beneficial management (Barnett, 2007).

Saltmarsh sites in this study were not achieving conservation grazing and AES sites were grazed no differently than non-AES sites. However, AES are still the only mechanism through which conservation grazing can be implemented nationally on saltmarshes and the large proportion of English saltmarsh already under AES presents a unique opportunity for comprehensive landscape-scale intervention if these AES could be improved to deliver the necessary outcomes (Smart et al., 2013). We propose that the five aspects of saltmarsh conservation grazing be incorporated into AES prescriptions in future to dramatically increase the specificity of AES agreements and their utility for conservation management (Appendix S1). Additionally, a more detailed and reliable system of auditing would be beneficial (http://jncc.defra.gov.uk/; JNCC, 2004), to ensure that management activities take place to the necessary standard prior to payments. Moving to a results-based scheme where payments are made on desirable outcomes rather than on evidence of management may also improve the overall conservation value and economic efficiency of saltmarsh AES options (Armsworth et al., 2012; Hanley et al., 2012; Hasund, 2013; Keenleyside et al., 2014).

Policymakers, researchers and land managers need to work together to ensure that AES effectiveness is improved, particularly through better translation of conservation guidelines into AES, detailed consultations with land managers and researchers when designing new schemes and the increased specificity of prescription wording with detailed rationales to improve mutual understanding of particular grazing management between agreement advisers and managers. In habitats where this process has already been undertaken (e.g. for lowland wet grassland in the UK), bespoke AES in combination with site protection are much more successful in delivering conservation outcomes (e.g. improved breeding habitat for wading birds, Smart et al., 2014). A similar tailoring process on saltmarsh is likely to benefit multiple species and processes within the saltmarsh ecosystem.

## ACKNOWLEDGEMENTS

This study was funded by the RSPB. Many thanks to landowners who allowed site access and Allan Drewitt and regional Natural England staff who provided assistance in arranging this. AES agreement documents, spatial data and locations of management options were provided under Open UK Government License for public sector information by Natural England in 2013. Jenny Gill and two anonymous reviewers provided comments that improved the manuscript.

## AUTHORS' CONTRIBUTIONS

Study conceived by L.R.M. and J.S.; designed by L.R.M. Data acquired by A.F., N.G., C.C.V. and L.R.M. Analyses conducted and paper written by L.R.M.; J.S. provided revisions. All authors approved and are accountable for the final manuscript.

## DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.p3g44gh (Mason, Feather, Godden, Vreugdenhil, & Smart, 2019).

## ORCID

*Lucy R. Mason* https://orcid.org/0000-0001-9567-6262

*Jennifer Smart* https://orcid.org/0000-0003-1789-4461

## REFERENCES

Adnitt, C., Brew, D., Cottle, R., Hardwick, M., John, S., Leggett, D., … Staniland, R. (2007). *Saltmarsh management manual*. Bristol, UK: Environment Agency, DEFRA.

Armsworth, P. R., Acs, S., Dallimer, M., Gaston, K. J., Hanley, N., & Wilson, P. (2012). The cost of policy simplification in conservation incentive programs. *Ecology Letters*, *15*, 406–414. https://doi.org/10.1111/j.1461-0248.2012.01747.x

Ausden, M. (2007). *Habitat management for conservation: A handbook of techniques*. Oxford: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198568728.001.0001

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*, 169–193. https://doi.org/10.1890/10-1510.1

Barnett, A. (2007). Agri-environmental policy: A European overview. *Aspects of Applied Biology*, *81*, 1–6.

Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, *29*, 1006–1016. https://doi.org/10.1111/cobi.12536

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Boorman, L. A. (2003). Saltmarsh review: An overview of coastal saltmarshes, their dynamic and sensitivity characteristics for conservation and management. *JNCC Report, No. 334*.

Burd, F. (1989). The saltmarsh survey of Great Britain. Research and Survey in Nature Conservation, No. 17. Peterborough, UK: Nature Conservancy Council.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Berlin: Springer-Verlag.

Chatters, C. (2004). Grazing domestic animals on British saltmarshes. *British Wildlife*, *15*, 392–400.

Clausen, K. K., Stjernholm, M., & Clausen, P. (2013). Grazing management can counteract the impacts of climate change-induced sea level rise on salt marsh-dependent waterbirds. *Journal of Applied Ecology*, *50*, 528–537. https://doi.org/10.1111/1365-2664.12043

Davidson, K. E., Fowler, M. S., Skov, M. W., Doerr, S. H., Beaumont, N., & Griffin, J. N. (2017). Livestock grazing alters multiple ecosystem properties and services in salt marshes: A meta-analysis. *Journal of Applied Ecology*, *54*, 1395–1405. https://doi.org/10.1111/1365-2664.12892

DEFRA. (2004). *The Countryside Stewardship Scheme (CSS) 2004: Information and how to apply*. UK: DEFRA (Department for Environment, Food and Rural Affairs).

DEFRA. (2010). Definition of terms used in farm business management. LU conversion table located in Appendix 1 p37. Retrieved from http://webarchive.nationalarchives.gov.uk/20130402193300/http://archive.defra.gov.uk/foodfarm/farmmanage/advice/documents/def-of-terms.pdf

Dijkema, K. S. (1990). Salt and brackish marshes around the Baltic Sea and adjacent parts of the North Sea: Their vegetation and management. *Biological Conservation*, *51*, 191–209. https://doi.org/10.1016/0006-3207(90)90151-E

Doody, J. P. (2004). Coastal Squeeze – An historical perspective. *Journal of Coastal Conservation*, *10*, 129–138. https://doi.org/10.1652/1400-0350(2004)010[0129:CSAHP]2.0.CO;2

Doody, J. P. (2007). *Saltmarsh conservation, management and restoration*. Netherlands: Springer Science & Business Media.

Doody, J. P. (2008). Management of Natura 2000 habitats. 1330 Atlantic salt meadows (Glauco-Puccinellietalia maritimae). European Commission. Retrieved from http://ec.europa.eu/environment/nature/natura2000/management/habitats/pdf/1330_Atlantic_salt_meadows.pdf

Environment Agency. (2015). Saltmarsh extents. Retrieved from https://data.gov.uk/dataset/saltmarsh-extents1

European Environment Agency. (2009). Habitats directive article 17 reporting: 1330-Atlantic salt meadows (Glauco-Puccinellietalia maritima). Retrieved from http://ec.europa.eu/environment/nature/knowledge/rep_habitats/

Exo, K.-M., Wellbrock, A. H., Sondermann, J., & Maier, M. (2017). Assessing the impact of mowing on Common Redshanks *Tringa totanus* breeding on saltmarshes: Lessons for conservation management. *Bird Conservation International*, *27*, 440–453. https://doi.org/10.1017/S0959270916000496

FitzGerald, D. M., Fenster, M. S., Argow, B. A., & Buynevich, I. V. (2008). Coastal impacts due to sea-level rise. *Annual Review of Earth and Planetary Sciences*, *36*, 601–647. https://doi.org/10.1146/annurev.earth.35.031306.140139

Garbutt, A., de Groot, A., Smit, C., & Pétillon, J. (2017). European salt marshes: Ecology and conservation in a changing world. *Journal of Coastal Conservation*, *21*, 405–408. https://doi.org/10.1007/s11852-017-0524-6

Gedan, K. B., Silliman, B. R., & Bertness, M. D. (2009). Centuries of human-driven change in salt marsh ecosystems. *Annual Review of Marine Science*, *1*, 117–141. https://doi.org/10.1146/annurev.marine.010908.163930

Hanley, N., Banerjee, S., Lennox, G. D., & Armsworth, P. R. (2012). How should we incentivize private landowners to 'produce' more biodiversity? *Oxford Review of Economic Policy*, *28*, 93–113. https://doi.org/10.1093/oxrep/grs002

Hasund, K. P. (2013). Indicator-based agri-environmental payments: A payment-by-result model for public goods with a Swedish application. *Land Use Policy*, *30*, 223–233. https://doi.org/10.1016/j.landusepol.2012.03.011

Haynes, T. A., Angus, S., Scanlan, C., & Bhatti, N. (2017). Developing a saltmarsh monitoring methodology to meet multiple policy and management objectives in Scotland. *Journal of Coastal Conservation*, *21*, 445–452. https://doi.org/10.1007/s11852-017-0512-x

Hill, M. I. (1988). Saltmarsh vegetation of the Wash: An assessment of change from 1971 to 1985. Research and Survey in Nature Conservation, No. 13. Peterborough: Nature Conservancy Council.

Hughes, R. G. (2004). Climate change and loss of saltmarshes: Consequences for birds. *Ibis*, *146*, 21–28. https://doi.org/10.1111/j.1474-919X.2004.00324.x

JNCC. (2004). *Common standards monitoring guidance for saltmarsh habitats*. Retrieved from http://jncc.defra.gov.uk/pdf/CSM_coastal_saltmarsh.pdf'>http://jncc.defra.gov.uk/pdf/CSM_coastal_saltmarsh.pdf

Jones, L., Angus, S., Cooper, A., Doody, P., Everard, M., Garbutt, A., … Whitehouse, A. (2011). Coastal margins. UK National Ecosystem Assessment Technical Report, pp. 411-615. Cambridge: UNEP-WCMC.

Keenleyside, C., Radley, G., Tucker, G., Underwood, E., Hart, K., Allen, B., & Menadue, H. (2014). Results-based payments for biodiversity guidance handbook: Designing and implementing results-based agri-environment schemes 2014-2020. Prepared for the European Commission, DG Environment, Contract ENV.B.2/ETU/2013/0046. London: Institute for European Environmental Policy.

Kleijn, D., Berendse, F., Smit, R., & Gilissen, N. (2001). Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature*, *413*, 723–725. https://doi.org/10.1038/35099540

Kleijn, D., & Sutherland, W. J. (2003). How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, *40*, 947–969. https://doi.org/10.1111/j.1365-2664.2003.00868.x

Lagendijk, D. D. G., Howison, R. A., Esselink, P., Ubels, R., & Smit, C. (2017). Rotation grazing as a conservation management tool: Vegetation changes after six years of application in a salt marsh ecosystem. *Agriculture, Ecosystems & Environment*, *246*, 361–366. https://doi.org/10.1016/j.agee.2017.05.023

Lynch, H. J., Thorson, J. T., & Shelton, A. O. (2014). Dealing with under- and over-dispersed count data in life history, spatial, and community ecology. *Ecology*, *95*, 3173–3180. https://doi.org/10.1890/13-1912.1

Magnusson, A., Skaug, H. J., Nielsen, A., Berg, C. W., Kristensen, K., Maechler, M., … Brooks, M. E. (2017). glmmTMB: Generalized linear mixed models using template model builder. R package version 0.1.3. Retrieved from https://github.com/glmmTMB

Malpas, L. R., Smart, J., Drewitt, A. L., Sharps, E., & Garbutt, A. (2013). Continued declines of Redshank *Tringa totanus* breeding on saltmarsh in Great Britain: Is there a solution to this conservation problem? *Bird Study*, *60*, 370–383. https://doi.org/10.1080/00063657.2013.781112

Mandema, F. S., Tinbergen, J. M., Ens, B. J., Koffijberg, K., Dijkema, K. S., & Bakker, J. P. (2015). Moderate livestock grazing of salt, and brackish marshes benefits breeding birds along the mainland coast of the Wadden Sea. *The Wilson Journal of Ornithology*, *127*, 467–476. https://doi.org/10.1676/13-133.1

Mason, L. R., Feather, A., Godden, N., Vreugdenhil, C. C., & Smart, J. (2019). Data from: Are agri-environment schemes successful in delivering conservation grazing management on saltmarsh? *Dryad Digital Repository*, https://doi.org/10.5061/dryad.p3g44gh

McOwen, C. J., Weatherdon, L. V., Bochove, J.-W. V., Sullivan, E., Blyth, S., Zockler, C., … Fletcher, S. (2017). A global map of saltmarshes. *Biodiversity Data Journal*, e11764. https://doi.org/10.3897/BDJ.5.e11764

Natural England. (2013). *Higher Level Stewardship: Environmental Stewardship handbook* (4th ed.). Sheffield, UK: Natural England.

Norris, K., Brindley, E., Cook, T., Babbs, S., Forster Brown, C., & Yaxley, R. (1998). Is the density of redshank *Tringa totanus* nesting on saltmarshes in Great Britain declining due to changes in grazing management? *Journal of Applied Ecology*, *35*, 621–634. https://doi.org/10.1046/j.1365-2664.1998.355339.x

Norris, K., Cook, T., O'Dowd, B., & Durdin, C. (1997). The density of redshank *Tringa totanus* breeding on the salt-marshes of the Wash in relation to habitat and its grazing management. *Journal of Applied Ecology*, *34*, 999–1013. https://doi.org/10.2307/2405289

Phelan, N., Shaw, A., & Baylis, A. (2011). *The extent of saltmarsh in England and Wales: 2006–2009*. Bristol: Environment Agency.

Powell, M. J. D. (2009). The BOBYQA algorithm for bound constrained optimization without derivatives. Cambridge NA Report NA2009/06. Cambridge: University of Cambridge.

R Core Team. (2017). R: A language and environment for statistical computing, version 3.4.1. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org

Schekkerman, H., Teunissen, W., & Oosterveld, E. (2008). The effect of 'mosaic management' on the demography of black-tailed godwit *Limosa limosa* on farmland. *Journal of Applied Ecology*, *45*, 1067–1075.

Sharps, E., Smart, J., Mason, L. R., Jones, K., Skov, M. W., Garbutt, A., & Hiddink, J. G. (2017). Nest trampling and ground nesting birds: Quantifying temporal and spatial overlap between cattle activity and breeding Redshank. *Ecology and Evolution*, *7*, 6622–6633. https://doi.org/10.1002/ece3.3271

Smart, J., Bolton, M., Hunter, F., Quayle, H., Thomas, G., & Gregory, R. D. (2013). Managing uplands for biodiversity: Do agri-environment schemes deliver benefits for breeding lapwing *Vanellus vanellus*? *Journal of Applied Ecology*, *50*, 794–804. https://doi.org/10.1111/1365-2664.12081

Smart, J., Wotton, S. R., Dillon, I. A., Cooke, A. I., Diack, I., Drewitt, A. L., … Gregory, R. D. (2014). Synergies between site protection and agri-environment schemes for the conservation of waders on lowland wet grasslands. *Ibis*, *156*, 576–590. https://doi.org/10.1111/ibi.12153

UNEP. (2006). Marine and coastal ecosystems and human wellbeing: A synthesis report based on the findings of the Millennium Ecosystem Assessment(ed. U.U.N.E. Programme)). Nairobi, Kenya.

van Klink, R., Nolte, S., Mandema, F. S., Lagendijk, D. G., WallisDeVries, M. F., Bakker, J. P., … Smit, C. (2016). Effects of grazing management on biodiversity across trophic levels–The importance of livestock species and stocking density in salt marshes. *Agriculture, Ecosystems & Environment*, *235*, 329–339. https://doi.org/10.1016/j.agee.2016.11.001

Watkinson, A., & Ormerod, S. (2001). Grasslands, grazing and biodiversity: Editors' introduction. *Journal of Applied Ecology*, *38*, 233–237.

Wolff, W. J., Bakker, J. P., Laursen, K., & Reise, K. (2010). The Wadden sea quality status report – Synthesis report 2010. Wadden Sea Ecosystem, No. 29. Wilhelmshaven, Germany: Common Wadden Sea Secretariat.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Mason LR, Feather A, Godden N, Vreugdenhil CC, Smart J. Are agri-environment schemes successful in delivering conservation grazing management on saltmarsh? *J Appl Ecol*. 2019;00:1–13. https://doi.org/10.1111/1365-2664.13405

# Supplementary Materials

Supplementary Materials for paper **V** are available online:

http://doi.org/10.1111/1365-2664.13405

**Figure S1**. Site location maps
**Table S1**. Conservation grazing rates
**Table S2**. Study site information
**Table S3**. Livestock Unit conversions
**Table S4**. Prescription scoring
**Table S5**. Prescription analysis results
**Table S6**. Model selection tables
**Appendix S1**. Recommendations for prescription wording

# PAPER VI

# Wader chick condition is not limited by resource availability on wader-friendly lowland wet grassland sites in the UK.

**Mason, L.R.** & Smart, J.

*Wader Study* (2015), **122**: 193–200. http://doi.org/10.18194/ws.00017

**research paper** *Wader Study* 122(3): 193–200. doi: 10.18194/ws.00017

# Wader chick condition is not limited by resource availability on wader-friendly lowland wet grassland sites in the UK

Lucy R. Mason* & Jennifer Smart

*RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK*
**Corresponding author: lucy.mason@rspb.org.uk*

Mason, L.R. & J. Smart. 2015. Wader chick condition is not limited by resource availability on wader-friendly lowland wet grassland sites in the UK. *Wader Study* 122(3): 193–200.

Many wader species breeding on lowland wet grassland in Western Europe are becoming increasingly restricted to wader-friendly protected sites and nature reserves where habitat conditions and management methods are more suitable compared to those in the wider countryside. Breeding success is still low on these protected sites, which often leads site managers and policymakers to ask whether low food availability might be limiting chick survival despite management aimed at providing optimum foraging conditions. Although this question is difficult to answer on a large scale, here we attempt to do so by monitoring and comparing wader chick body condition and rates of growth across a range of UK sites, expecting that chicks in resource-limited areas will grow slower and weigh less than average for their age (be of lower body condition) than those in optimum foraging areas. We demonstrate that, on average, Northern Lapwing *Vanellus vanellus* and Common Redshank *Tringa totanus* chicks achieved growth rates similar to those calculated for larger samples of chicks studied during the past four decades in The Netherlands and the UK, and achieved greater condition than expected based on standardized measures from a previous Dutch study. This suggests that food availability for chicks on well-managed lowland wet grassland sites is unlikely to be the factor limiting chick survival and population recovery of wader species in this habitat. Instead we should be more concerned about other potential causes of chick mortality, such as predation or agricultural activities. The positive message is that if these other causes of chick mortality can be reduced, well-managed wader sites are likely to be successful in producing healthy fledglings to facilitate population recovery.

***Keywords***

Northern Lapwing
*Vanellus vanellus*
Common Redshank
*Tringa totanus*
chick growth
body condition
food availability
habitat management

## INTRODUCTION

Wader species that once commonly bred on lowland wet grassland in Western Europe such as Northern Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa* and Common Redshank *Tringa totanus* are experiencing widespread population declines, largely driven by rates of nest and chick survival that are insufficient to offset adult mortality (BirdLife International 2004, Roodbergen *et al.* 2012). The primary causes of wader nest failure are well known (e.g. nest predation; MacDonald & Bolton 2008) but chick survival is less well studied, despite evidence that this may be the more important demographic parameter (Sharpe *et al.* 2008).

The mechanisms influencing the survival of nidifugous wader chicks include those linked to direct mortality such as predation, agricultural activities (e.g. mowing) or starvation through insufficient invertebrate food availability (Kentie *et al.* 2015, Schekkerman *et al.* 2009, Teunissen *et al.* 2008). Insufficient food availability may also limit chick survival indirectly by reducing their body condition, thereby potentially increasing their susceptibility to death from exposure in cold or wet weather (Beintema & Visser 1989b) or to predation from opportunistic predators (Evans 2004).

The availability of food on lowland wet grassland, both in terms of the abundance and diversity of invertebrates and their accessibility to foraging chicks, will depend on the habitat characteristics relating to soil, sward and hydrology, and the management practices acting on those characteristics. Swards with high structural complexity and species diversity are likely to provide optimum foraging conditions for a range of wader species (Devereux *et al.* 2004, Durant *et al.* 2008a, Kentie *et al.* 2013, McCracken & Tallowin 2004), and moist soils with an abundance of wet features with shallow, muddy edges encourage a high biomass of surface, aerial and aquatic invertebrates (Ausden *et al.* 2003, Eglington *et al.* 2010). Management to provide these characteristics, which are also considered optimum for wader nesting, typically involves: (1) managing swards with extensive cattle or mixed livestock grazing, mowing after the breeding season and control of undesirable plant species (e.g. *Juncus* spp.); (2) raising and maintaining high water levels through to late summer; and (3) creating or managing networks of shallow pools, footdrains and scrapes to provide wet features as foraging areas (Ausden *et al.* 2003, Bellebaum & Bock 2009, Durant *et al.* 2008a,b, Eglington *et al.* 2007, 2010, Kahlert *et al.* 2007, McCracken & Tallowin 2004, Natural England 2013, Smart *et al.* 2006).

Across Western Europe many lowland wet grassland protected areas and reserves employ such management techniques, and wader populations are becoming increasingly restricted to these wader-friendly sites where the habitat is more suitable compared to the wider countryside (Wilson *et al.* 2005). Breeding success is still low on these sites however (e.g. Kahlert *et al.* 2007), and researchers are often asked by site managers and policymakers whether food availability might be limiting chick survival despite management aimed at providing optimum nesting and foraging conditions. This is a difficult question to answer directly on a large scale because the types and energetic benefits of invertebrate prey items available and accessible to a chick are likely to vary both spatially and temporally between sites (Ausden *et al.* 2003, Beintema *et al.* 1991).

Here, we attempt to answer this question in a more indirect way. We monitored Northern Lapwing and Common Redshank chick body condition and growth across a number of managed wet grassland sites in the UK and compared these against standard measures. This method uses the premise that chicks feeding in resource-limited conditions will grow slower and weigh less than average for their age (i.e. be of lower condition) relative to those feeding in optimum foraging conditions (Beintema 1994, Eglington *et al.* 2010, Sharpe *et al.* 2009).

## METHODS

We monitored 627 Northern Lapwing (hereafter, 'Lapwing') and 116 Common Redshank ('Redshank') chicks across 15 lowland wet grassland nature reserves and protected sites in the UK (Lat 51.3–57.1°N, Long 4.2°W–1.7°E; Fig. 1) during 2009, 2010, 2012 and 2013 to determine whether the combined suite of habitat management techniques they used provides sufficient conditions for wader chick foraging and growth (Table 1; 18 site-years studied in total). All sites were managed with the aim of providing optimum conditions for breeding Lapwing and Redshank (both nesting and chick rearing), and although management did not differ substantially our sites represent the range of those that could be described as 'well-managed' for breeding waders in the UK (Table 1).

Chicks were marked with a metal ring and a unique combination of permanent colour rings or temporary leg flags to allow identification on recapture, and a sample were also fitted with 0.4–0.5 g radio-transmitters to help improve brood relocation (Table 2; tags used in 2009/2010: PicoPip, Biotrack, UK and LB-2, Holohil Systems, Canada; 2010/2012/2013: C1, Perdix Wildlife Supplies, UK). Tags were mounted on gauze and glued to the down feathers over the synsacrum and pelvic girdle using water-based latex adhesive.

We measured chick mass (g) and bill length (exposed culmen, mm) on initial capture, after which chicks were recaptured and measured every eight days on average; trapping frequencies higher than this can have adverse effects on survival (Sharpe *et al.* 2009). We used a combination of field observations and manual telemetry to track and recapture tagged chicks and their ringed siblings. We conducted manual telemetry using Telonics TR4 (Telonics, USA) or ATS R2000 (Advanced Telemetry Systems, USA) receivers and handheld Yagi antennas (Biotrack, UK). Of the total sample of chicks monitored, 293 Lapwing and 12 Redshank chicks were captured after hatching in this way (age >0 days). Note that our sample of Redshank chicks was relatively small due to the difficulties of recapturing these chicks which are more cryptic and travel greater distances daily.

We estimated species-specific chick condition indices (CI) for chicks of age >0 days as the ratio of observed body mass to expected mass based on bill length (a reliable indicator of chick age; Beintema & Visser 1989a) each time a chick was recaptured. Expected mass was derived from standardized mean values of mass on bill length calculated from a large sample of Lapwing ($n$ = 5,715) and Redshank ($n$ = 1,048) chicks monitored at various sites in The Netherlands during 1976–1985 (Beintema 1994). Beintema (1994) considered chicks with condition indices of ≥1.0 to be in 'good' condition; i.e. mass greater than the average expected for their age (observed mass ≥ expected mass).

We also fitted species-specific growth curves to the full sample of chick data (mass on chick age in days). The majority of chicks were ringed and radio-tagged on hatching and were of known age, but some chicks of unknown age were also monitored. The age of these chicks (days since hatching) was estimated using site-year specific regression equations of age on bill length from recaptured chicks of known age, or using published equations where site-year data from this study was limited (Beintema 1994, Smart 2005). Growth curves were fitted using nonlinear least-squares models with a self-starting logistic growth function in R (nls, SSlogis; R Core Team 2013) and we included all chicks in this calculation, regardless of their ultimate fates. For comparison, curves were plotted against average trajectories estimated for larger samples of chicks from previous studies, including 5,715 Lapwing and 1,048 Redshank chicks from The Netherlands monitored 1976–1985 (Beintema 1994), 3,174 Lapwing chicks from the UK monitored 1996–2005

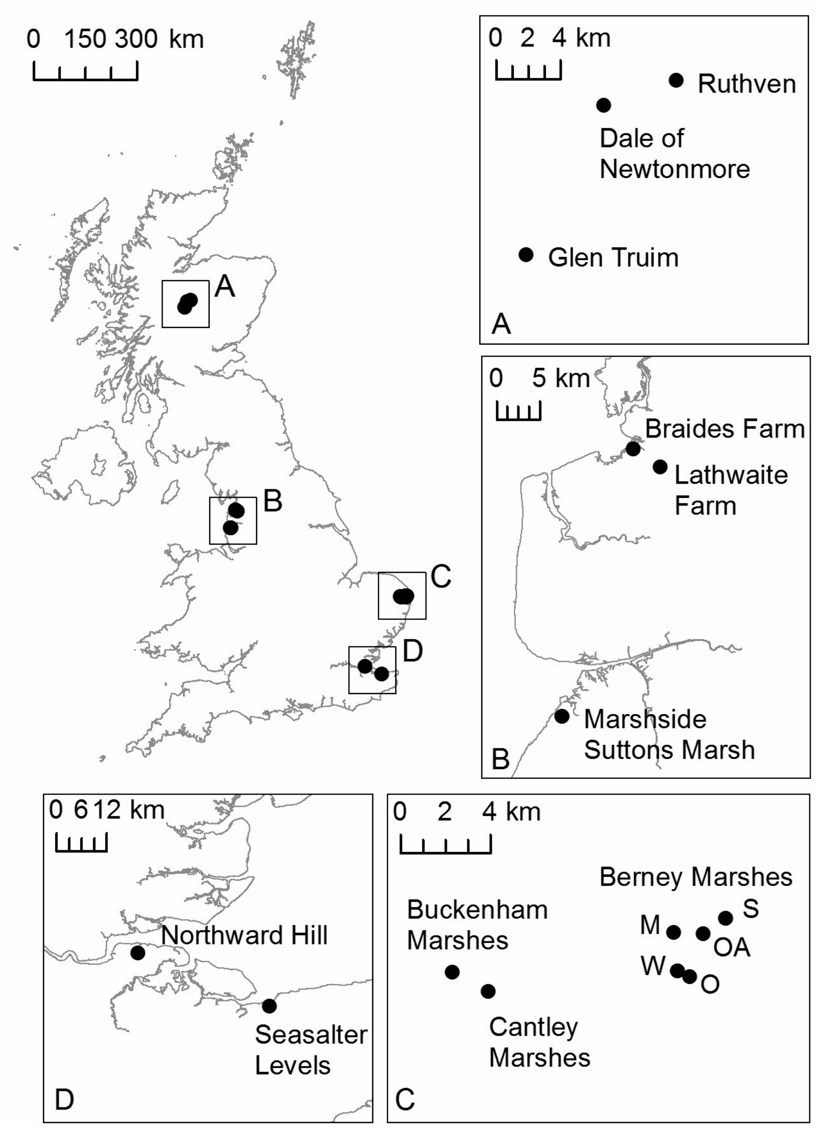


**Fig. 1.** Locations of the 15 UK lowland wet grassland study sites, with boxes A–D showing the locations of sites in more detail. Berney Marshes sites in C are Machete (M), Office (O), Old Arable (OA), Shearmans (S) and Wickhampton (W).

(Sharpe *et al.* 2009) and 1,754 Lapwing measures from 901 chicks from the UK monitored 2005–2007 (Eglington *et al.* 2010).

## RESULTS

Lapwing and Redshank chicks on our study sites attained greater body mass than expected for their age, with average condition indices of 1.2 across all sites in both species (Table 2). In only one site-year (Lapwing chicks at Marshside Suttons Marsh in 2013) was chick condition significantly below 1.0. In both species, the average body condition of tagged chicks did not differ significantly from that of untagged chicks across all site years (Table 2; Lapwing: $F_{1,360} = 2.61$, $P = 0.11$; Redshank: $F_{1,15} = 0.936$, $P = 0.35$), although the number of untagged Redshank chicks was very small ($n = 1$).

Chick growth followed logistic curves that closely matched expected average growth curves previously presented for larger samples of wild Lapwing and Redshank chicks from three studies in European farmland habitats (Fig. 2). These curves were defined by the following relationships between mass (g) and age (days since hatching):

Lapwing mass = 170.19 / (1 + 19.11 x exp (–8.70 x age))
Redshank mass = 127.40 / (1 + 16.48 x exp (–8.63 x age))

The lack of variation in management methods between sites prevented detailed analysis of chick condition in relation to site management. However, chicks on sites managed with high wet feature density, active water management, cattle grazing, mosaic sward, post-breeding mowing and no soil improvement (characteristics and management methods thought to promote optimum chick foraging conditions; 11 sites, Table 1) were of significantly higher condition on average (CI = 1.23 ±0.02 SE, $n = 304$ measures from 249 chicks) than chicks from sites with one or more less-optimum management characteristics (medium or low wet feature density, passive

**Table 1.** Information on site management relating to the habitat features (soil, sward, water) likely to influence food availability or survival of wader chicks on our study sites. Shown are Lapwing nesting densities (nests km$^{-2}$) in each site year, site management type, whether soil improvement took place, target sward structure, breeding season grazing and mowing regimes, methods of maintaining spring/summer surface flooding and wet feature availability (a qualitative indication of relative site wetness). Footnotes define management categories and the references that evidence their importance.

| Site | Year | Wader density | Site type[a] | Soil improvement[b] | Sward management | | | Water management | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | Target structure[c] | Grazing[d] | Mowing[e] | Method[f] | Wet feature availability[g] |
| Berney Marshes: Machete | 2009 | 62 | R+A | None | Mosaic | Cattle (<1 LU ha$^{-1}$) | 1 (Jul–Oct) | Active | High |
| Berney Marshes: Office | 2009 | 61 | R+A | None | Mosaic | Cattle (<1 LU ha$^{-1}$) | 1 (Jul–Oct) | Active | High |
| Berney Marshes: Old Arable | 2009, 2010 | 65, 76 | R+A | None | Mosaic | Cattle (<1 LU ha$^{-1}$) | 1 (Jul–Oct) | Active | High |
| Berney Marshes: Shearmans | 2009, 2010 | 67, 78 | R+A | None | Mosaic | Cattle (<1 LU ha$^{-1}$) | 1 (Jul–Oct) | Active | High |
| Berney Marshes: Wickhampton | 2009, 2010 | 88, 172 | R+A | None | Mosaic | Cattle (<1 LU ha$^{-1}$) | 1 (Jul–Oct) | Active | High |
| Buckenham Marshes | 2010 | 60 | R+A | None | Mosaic | Cattle (<1 LU ha$^{-1}$) | 1 (Jul–Oct) | Active | High |
| Cantley Marshes | 2012 | 42 | R+A | None | Mosaic | Cattle (<1 LU ha$^{-1}$) | 1 (Jul–Oct) | Active | High |
| Northward Hill | 2012 | 117 | R+A | 1, 2 (Jul–Mar) | Mosaic | Mixed (<0.75 LU ha$^{-1}$) | 1 (Jul–Oct) | Active | Medium |
| Seasalter Levels | 2012 | 33 | R+A | None | Mosaic | Mixed (<0.75 LU ha$^{-1}$) | 1 (Jul–Oct) | Passive | High |
| Braides Farm | 2013 | 131 | NR+A | 1 (Jul–Mar) | Mosaic | Cattle (1–2 LU ha$^{-1}$) | None | Passive | Medium |
| Lathwaite Farm | 2013 | 113 | NR+A | 3 (Apr) | Short | None | 2 (Jun–Jul) | Passive | Low |
| Marshside: Suttons Marsh | 2013 | 38 | R+A | None | Mosaic | Cattle (<0.8 LU ha$^{-1}$) | 1 (Jul–Oct) | Active | High |
| Dale of Newtonmore | 2013 | 58 | NR | None | Short | Sheep (<0.5 LU ha$^{-1}$) | None | Passive | Medium |
| Glen Truim | 2013 | 18 | NR | None | Mosaic | Mixed (<0.5–1 LU ha$^{-1}$) | None | Passive | Low |
| Ruthven | 2013 | 23 | R | None | Mosaic | Mixed (0.6–1.2 LU ha$^{-1}$) | 1 (Jul–Oct) | Passive | Medium |

[a] Site type: R = nature reserve; R+A = nature reserve with UK Agri-Environmental Scheme (ESA or HLS); NR = non-reserve; NR+A = non-reserve with Agri-Environmental Scheme management (HLS). (Smart *et al.* 2014)

[b] Soil improvement: 1 = farmyard manure applied at <12.5 tonnes/ha/year; 2 = subsoiling to improve soil structure; 3 = organic soil improver/liming agent (paper pulp) applied and sward rolled to encourage grass growth pre-breeding. (McKeever 2003)

[c] Target sward structure: Short = sward height <10 cm to suit nesting Lapwing; Mosaic = variable height with mixture of short sward (<10 cm), tussocks and/or areas of longer sward (<30 cm, optimum 5–15 cm) to suit a range of wader species. (Kentie *et al.* 2013, McCracken & Tallowin 2004, Milsom *et al.* 2000, Vickery *et al.* 2001)

[d] Livestock type used during breeding season (Cattle, Sheep or Mixed cattle and sheep) and target grazing pressure where known (LU = Livestock Units). (Durant *et al.* 2008b, Hart *et al.* 2002, Smart *et al.* 2006, Vickery *et al.* 2001)

[e] Mowing: None = site never mown; 1 = post-breeding topping to manage sward height and weed species; 2 = post-breeding silage cut. (Schekkerman *et al.* 2009)

[f] Water management method: Active = active maintenance of flooding using system of pumps, sluices, storage reservoirs and abstraction; Passive = rainfall dependent (winter flooding retained as long as possible). (Ausden *et al.* 2003, Eglington *et al.* 2010)

[g] Wet feature availability: High = high density of shallow-edged wet features (footdrains, pools, scrapes, flooded areas) often created and managed specifically for breeding waders; Medium = lower density of wet features but still relatively wet; Low = few wet features, isolated pools or wet areas only, relatively dry compared to High Availability sites (Ausden *et al.* 2003, Eglington *et al.* 2010, Milsom *et al.* 2002, Smart *et al.* 2006)

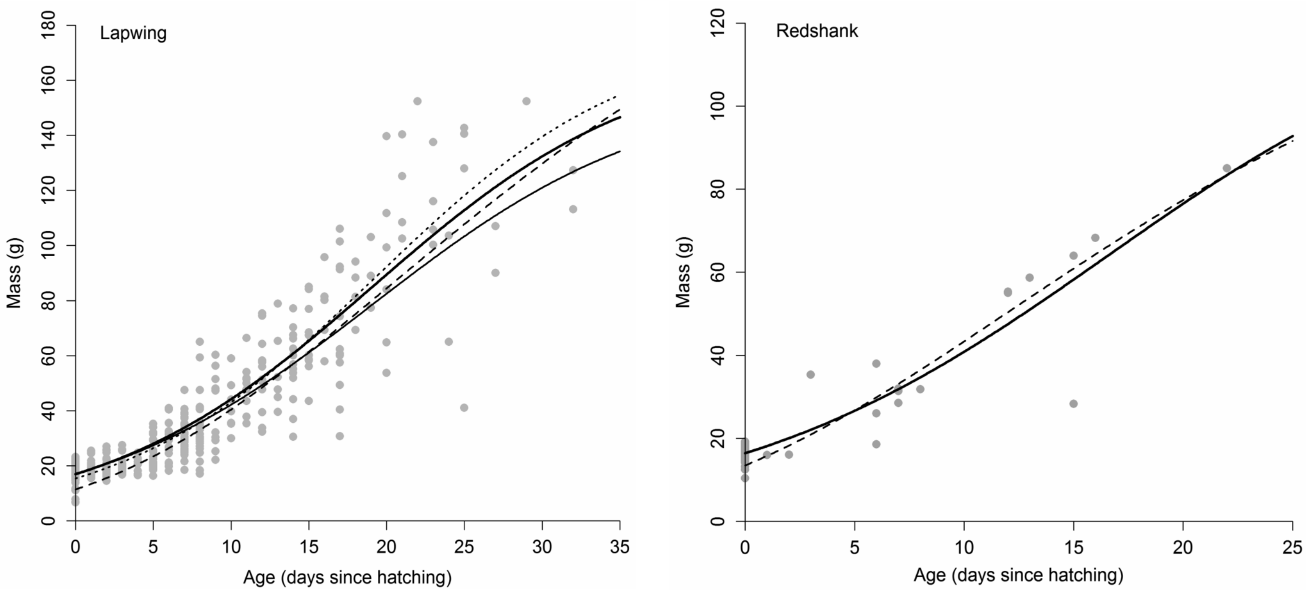


**Fig. 2.** Logistic growth curves (change in mass with age) for Lapwing and Redshank chicks across all sites and years from this study (thick solid lines) compared to published expected average growth curves. Dashed lines: Gompertz growth curves for wild chicks monitored 1976–1985 in The Netherlands (Beintema & Visser 1989a). Thin solid line: logistic growth curve for wild Lapwing monitored 1996–2005 in the UK (Sharpe *et al.* 2009). Dotted line: logistic curve for wild Lapwing monitored 2005–2007 in the UK (Eglington *et al.* 2010). Growth curves for this study were based on 794 measures of 627 individual Lapwing and 130 measures of 116 individual Redshank (note that only 17 measures from 12 Redshank chicks of age >0 were available).

water management, mixed, sheep or no grazing, short sward, no post-breeding mowing and/or soil improvement; 7 sites; CI = 1.05 ±0.04 SE, *n* = 75 measures from 56 chicks, $F_{1,360} = 19.2$, $P < 0.001$).

## DISCUSSION

Our results indicate that Lapwing and Redshank chicks on our study sites are attaining or exceeding the body mass and growth rates expected for their age when compared to average values from other wild populations in Western Europe. This implies that food availability is not the factor limiting chick survival on sites managed to provide suitable habitat conditions for nesting waders in the UK, and that other factors are more likely to be driving current population declines.

Food availability is the most important factor influencing chick growth (Beintema 1994). Invertebrate food must be not only abundant and diverse to supply the dietary needs of different wader species (Ausden *et al.* 2003, Beintema *et al.* 1991), but also accessible to chicks, a factor dependent on sward structure and the availability of wet features (Ausden *et al.* 2003, Eglington *et al.* 2010, McCracken & Tallowin 2004). The ability to forage efficiently is equally important but largely dependent on weather conditions. Low levels of rainfall in late spring can lead to higher chick condition by maintaining water levels and providing higher abundances of invertebrate prey (Beintema 1994). In cold wet weather however, young chicks will require brooding for longer periods, reducing their time available for feeding (Beintema & Visser 1989b, Schekkerman & Visser 2001). High levels of predator activity or other disturbance may also limit foraging efficiency, increasing the time spent hiding or running from threats at the expense of feeding. There is also some concern that attaching radio tags and regularly retrapping chicks might result in reduced body condition through increased weight, hindrance of movement or disturbance (Schekkerman *et al.* 2009, Sharpe *et al.* 2009). The average body condition of tagged chicks did not differ from that of untagged chicks across all site years in this study however, indicating that the tags (representing 2–3% mass of a newly hatched chick) and recapture frequencies we used did not adversely affect chick body condition or growth.

The management methods used on our study sites were successful in providing sward, soil and hydrological conditions that enabled adequate chick growth, but even between these wader-friendly sites, resource availability was affected by management decisions. Chicks were larger and healthier on sites with management methods more likely to provide good foraging opportunities compared to sites with less-optimum management. Although our results for Redshank chick growth and condition are based on a relatively small sample of chick recaptures (Table 2), we found similar values of chick condition to those found for Lapwing. Treated with some caution, these comparable results between species whose chicks employ different foraging strategies (Lapwing specializing on surface-dwelling invertebrates, Redshank gleaning

**Table 2.** Average chick condition indices (CI) for Lapwing and Redshank chicks recaptured after hatching in each site and year with 95% confidence limits. *n* is the number of chick measures used to calculate the mean CI; – indicates sites where 95% confidence limits could not be estimated (*n* = 1). CI values above or equal to 1.0 indicate chick condition above or equal to standard average levels (from Beintema 1994).

| Site | Year | Condition indices | | | | | |
|---|---|---|---|---|---|---|---|
| | | All chicks monitored[1] | | | Radio-tagged chicks only[2] | | |
| | | Mean | 95% CL | *n* | Mean | 95% CL | *n* |
| **Lapwing** | | | | | | | |
| Berney Marshes: Machete | 2009 | 1.2 | (1.04–1.34) | 12 | 1.3 | (1.18–1.32) | 2 |
| Berney Marshes: Office | 2009 | 1.3 | (1.11–1.52) | 15 | 1.2 | (0.95–1.43) | 6 |
| Berney Marshes: Old: Arable | 2009 | 1.3 | (1.20–1.46) | 47 | 1.5 | (1.24–1.85) | 12 |
| Berney Marshes: Old: Arable | 2010 | 1.1 | (0.99–1.18) | 6 | 0.9 | – | 1 |
| Berney Marshes: Shearmans | 2009 | 1.2 | (1.16–1.32) | 42 | 1.3 | (1.18–1.43) | 15 |
| Berney Marshes: Shearmans | 2010 | 1.2 | (1.17–1.27) | 60 | 1.3 | (1.17–1.33) | 29 |
| Berney Marshes: Wickhampton | 2009 | 1.5 | (1.35–1.59) | 39 | 1.6 | (1.31–1.82) | 12 |
| Berney Marshes: Wickhampton | 2010 | 1.2 | (1.12–1.28) | 13 | 1.2 | (1.08–1.24) | 4 |
| Buckenham Marshes | 2010 | 1.1 | (0.94–1.28) | 7 | 1.1 | (0.89–1.37) | 5 |
| Cantley Marshes | 2012 | 1.1 | (1.01–1.18) | 26 | 1.1 | (0.99–1.17) | 19 |
| Northward Hill | 2012 | 1.0 | (0.91–1.02) | 22 | 1.0 | (0.94–1.05) | 11 |
| Seasalter Levels | 2012 | 1.0 | (0.94–1.05) | 2 | 1.0 | (0.94–1.05) | 2 |
| Braides Farm | 2013 | 1.3 | (1.29–1.34) | 4 | 1.3 | (1.29–1.33) | 3 |
| Lathwaite Farm | 2013 | 1.0 | (0.99–1.03) | 7 | 1.0 | (1.00–1.04) | 4 |
| Marshside: Suttons Marsh | 2013 | 0.8 | (0.75–0.88) | 20 | 0.8 | (0.71–0.85) | 16 |
| Dale of Newtonmore | 2013 | 1.1 | (1.04–1.23) | 18 | 1.1 | (1.01–1.24) | 15 |
| Glen Truim | 2013 | 1.1 | (0.92–1.19) | 12 | 1.0 | (0.88–1.10) | 10 |
| Ruthven | 2013 | 1.0 | (0.99–1.08) | 10 | 1.0 | (0.96–1.04) | 7 |
| *All sites and years* | | *1.2* | *(1.16–1.23)* | *362* | *1.2* | *(1.12–1.22)* | *173* |
| **Redshank** | | | | | | | |
| Berney Marshes: Office | 2009 | 1.2 | (1.04–1.45) | 9 | 1.2 | (1.04–1.45) | 9 |
| Berney Marshes: Shearmans | 2009 | 1.3 | (1.08–1.56) | 4 | 1.3 | (1.08–1.56) | 4 |
| Berney Marshes: Shearmans | 2010 | 1.2 | (0.77–1.70) | 2 | 1.5 | – | 1 |
| Berney Marshes: Wickhampton | 2010 | 1.1 | (1.07–1.18) | 2 | 1.1 | (1.07–1.18) | 2 |
| *All sites and years* | | *1.2* | *(1.12–1.37)* | *17* | *1.3* | *(1.13–1.39)* | *16* |

[1] Total individual Lapwing chicks of age >0 monitored = 293, Redshank = 12

[2] Total radio-tagged Lapwing chicks monitored = 119, Redshank = 11

more invertebrates from taller vegetation; Beintema *et al.* 1991) imply that the management techniques and habitat conditions across the study sites were successful in providing sufficient food availability to suit a range of wader species.

Across all sites, the most important management methods are likely to be those related to hydrology. Pools, ditches, footdrains and scrapes have a higher biomass of surface, aerial and aquatic invertebrates compared to surrounding vegetated grassland and are disproportionately utilized by foraging chicks (Ausden *et al.* 2003, Eglington *et al.* 2010). Water levels and the density of wet features are known to have a direct link with chick condition, with chicks found to be in better condition when densities of shallow-edged wet features are actively maintained at high levels into late summer (Eglington *et al.* 2010).

Throughout this study we have made the assumption that comparing observed mass with expected average mass based on chick age is a sufficient metric with which to define chick condition and on which to base inferences on site resource availability ('good' condition and therefore resource availability being defined as observed ≥ expected mass; Beintema 1994). Although this assumption could be flawed if the standardized expected measures on which it is based are not representative of healthy chicks developing in adequate foraging conditions, we do not consider this to be the case. Standardized measures were based on a very large sample of chicks monitored across a wide area in The Netherlands over a 10-year period (Beintema 1994) and are therefore likely to represent a robust estimate of average chick mass over time, controlling for any inter-annual or between-site variation in foraging conditions. Similarly, although comparing growth rates to those from previous studies can provide no absolute conclusions about site suitability (with no knowledge as to the resource-availability on the sites included in these studies), the multiple years of monitoring involved, the large sample sizes and geographical range of sites mean that they are also likely to present robust average estimates of expected chick growth across a range of lowland wet grassland habitat conditions (Beintema & Visser 1989a, Eglington *et al.* 2010, Sharpe *et al.* 2009). The fact that our chicks attained similar growth rates implies that they were at least attaining average expected rates of growth, and were not growing slower than expected (which would have indicated resource limitation).

It is unclear whether 'better than average' growth or 'good' condition is sufficient to allow population recovery. We could find no information on wader population trends in relation to chick condition or growth, and body condition indices are difficult to translate directly into measures of fledging success (Beintema 1994). Chicks with 'good' (better than average) body condition do however have a higher probability of daily survival (Sharpe *et al.* 2009), and might therefore be expected to fledge more successfully and potentially earlier because of their faster growth, leading to higher survival in their first winter through having more time to locate suitable winter habitats and to learn key foraging and roosting behaviours (Gill *et al.* 2014). Our results therefore indicate that on protected lowland wet grassland sites managed for breeding waders, chick growth and condition are sufficient, such that we should expect high rates of fledging.

However, chick survival is not dependent on body condition alone, and is often heavily influenced by unrelated mortality from agricultural activities and predation (Kentie *et al.* 2015, Schekkerman *et al.* 2009, Teunissen *et al.* 2008). The majority of the chicks we monitored in this study were in fact predated before fledging, despite their 'good' body condition (unpublished data). Population declines continue across our sites and elsewhere in Western Europe despite apparently adequate chick condition and growth rates, implying that food availability for chicks is not the primary factor limiting fledging success. The positive message is that if other causes of chick mortality can be reduced, well-managed wader sites are likely to be successful in producing healthy fledglings to facilitate population recovery.

## ACKNOWLEDGEMENTS

We are very grateful to Thomas Bodey, Rebecca Laidlaw, Janine Bicknell, Leila Walker, Maureen Gibson, Andrea Mason, Peadar O'Connell, Jean Roberts and Leah Williams for conducting fieldwork, and to the RSPB staff and landowners who arranged for and allowed access to the reserves and wader breeding sites studied. All ringing and tagging was conducted by trained fieldworkers under license from the British Trust for Ornithology. Licenses to disturb and handle birds were granted by Natural England and Scottish Natural Heritage for scientific research in line with the UK Wildlife and Countryside Act 1981. Jesse Conklin and two anonymous referees provided helpful comments on the manuscript.

## REFERENCES

**Ausden, M., A. Rowlands, W.J. Sutherland & R. James**. 2003. Diet of breeding Lapwing *Vanellus vanellus* and Redshank *Tringa totanus* on coastal grazing marsh and implications for habitat management. *Bird Study* 50: 285–293.

**Beintema, A.J.** 1994. Condition indices for wader chicks derived from bodyweight and bill-length. *Bird Study* 41: 68–75.

**Beintema, A.J., J.B. Thissen, D. Tensen & G.H. Visser**. 1991. Feeding ecology of Charadriiform chicks in agricultural grassland. *Ardea* 79: 31–43.

**Beintema, A.J. & G.H. Visser**. 1989a. Growth parameters in chicks of charadriiform birds. *Ardea* 77: 169–180.

**Beintema, A.J. & G.H. Visser**. 1989b. The effect of weather on time budgets and development of chicks of meadow birds. *Ardea* 77: 181–192.

**Bellebaum, J. & C. Bock**. 2009. Influence of ground predators and water levels on Lapwing *Vanellus vanellus* breeding success in two continental wetlands. *Journal of Ornithology* 150: 221–230.

**BirdLife International**. 2004. *Birds in Europe: population estimates, trends and conservation status.* BirdLife International, Cambridge, UK.

**Devereux, C.L., C.U. McKeever, T.G. Benton & M.J. Whittingham**. 2004. The effect of sward height and drainage on Common Starlings *Sturnus vulgaris* and Northern Lapwings *Vanellus vanellus* foraging in grassland habitats. *Ibis* 146: 115–122.

**Durant, D., M. Tichit, H. Fritz & E. Kernéïs**. 2008a. Field occupancy by breeding lapwings *Vanellus vanellus* and redshanks *Tringa totanus* in agricultural wet grasslands. *Agriculture, Ecosystems & Environment* 128: 146–150.

**Durant, D., M. Tichit, E. Kernéïs & H. Fritz**. 2008b. Management of agricultural wet grassland for breeding waders: integrating ecological and livestock system perspectives – A review. *Biodiversity & Conservation* 17: 2275–2295.

**Eglington, S.M., M. Bolton, M.A. Smart, W.J. Sutherland, A.R. Watkinson & J.A. Gill**. 2010. Managing water levels on wet grasslands to improve foraging conditions for breeding northern lapwing *Vanellus vanellus*. *Journal of Applied Ecology* 47: 451–458.

**Eglington, S.M., J.A. Gill, M. Bolton, M.A. Smart, W.J. Sutherland & A.R. Watkinson**. 2007. Restoration of wet features for breeding waders on lowland wet grassland. *Journal of Applied Ecology* 45: 305–314.

**Evans, K.L.** 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. *Ibis* 146: 1–13.

**Gill, J.A., J.A. Alves, W.J. Sutherland, G.F. Appleton, P.M. Potts & T.G. Gunnarsson**. 2014. Why is timing of bird migration advancing when individuals are not? *Proceedings of the Royal Society B: Biological Sciences* 281: 20132161.

**Hart, J.D., T.P. Milsom, A. Baxter, P.F. Kelly & W.K. Parkin**. 2002. The impact of livestock on Lapwing *Vanellus vanellus* breeding densities and performance on coastal grazing marsh. *Bird Study* 49: 67–78.

**Kahlert, J., P. Clausen, J.P. Hounisen & I.K. Petersen**. 2007. Response of breeding waders to agri-environment schemes may be obscured by effects of existing hydrology and farming history. *Journal of Ornithology* 148: 287–293.

**Kentie, R., J.C.E.W. Hooijmeijer, K.B. Trimbos, N.M. Groen & T. Piersma**. 2013. Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks. *Journal of Applied Ecology* 50: 243–251.

**Kentie, R., C. Both, J.C.E.W. Hooijmeijer & T. Piersma**. 2015. Management of modern agricultural landscapes increases nest predation rates in Black-tailed Godwits *Limosa limosa*. *Ibis* 157: 614–625.

**McCracken, D. & J. Tallowin**. 2004. Swards and structure: the interactions between farming practices and bird food resources in lowland grasslands. *Ibis* 146: 108–114.

**McKeever, C.U.** 2003. *Linking grassland management, invertebrates and Northern Lapwing productivity.* PhD Thesis, University of Stirling, UK.

**MacDonald, M.A. & M. Bolton**. 2008. Predation on wader nests in Europe. *Ibis* 150 (suppl.): 54–73.

**Milsom, T.P., S.D. Langton, W.K. Parkin, S. Peel, J.D. Bishop, J.D. Hart & N.P. Moore**. 2000. Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. *Journal of Applied Ecology* 37: 706–727.

**Milsom, T., J. Hart, W. Parkin & S. Peel**. 2002. Management of coastal grazing marshes for breeding waders: the importance of surface topography and wetness. *Biological Conservation* 103: 199–207.

**Natural England**. 2013. *Wet grassland and breeding waders: Additional guidance for HLS agreements.* Natural England, UK.

**Roodbergen, M., B. van der Werf & H. Hötker**. 2012. Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: review and meta-analysis. *Journal of Ornithology* 153: 53–74.

**Schekkerman, H., W. Teunissen & E. Oosterveld**. 2009. Mortality of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* chicks in wet grasslands: influence of predation and agriculture. *Journal of Ornithology* 150: 133–145.

**Schekkerman, H. & G.H. Visser**. 2001. Prefledging energy requirements in shorebirds: Energetic implications of self-feeding precocial development. *The Auk* 118: 944–957.

**Sharpe, F., M. Bolton, R. Sheldon & N. Ratcliffe**. 2009. Effects of color banding, radio tagging, and repeated handling on the condition and survival of Lapwing chicks and consequences for estimates of breeding productivity. *Journal of Field Ornithology* 80: 101–110.

**Sharpe, F., J. Clark & D. Leech**. 2008. Does variation in demographic parameters account for regional variation in Northern Lapwing *Vanellus vanellus* population declines across Great Britain? *Bird Study* 55: 247–256.

**Smart, J.** 2005. *Strategies of sea-level rise mitigation for breeding redshank.* PhD Thesis, University of East Anglia, UK.

**Smart, J., J.A. Gill, W.J. Sutherland & A.R. Watkinson**. 2006. Grassland-breeding waders: identifying key habitat requirements for management. *Journal of Applied Ecology* 43: 454–463.

**Smart, J., S.R. Wotton, I.A. Dillon, A.I. Cooke, I. Diack, A.L. Drewitt, P.V. Grice & R.D. Gregory**. 2014. Synergies between site protection and agri-environment schemes for the conservation of waders on lowland wet grasslands. *Ibis* 156: 576–590.

**Teunissen, W., H. Schekkerman, F. Willems & F. Majoor**. 2008. Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis* 150: 74–85.

**Vickery, J.A., J.R. Tallowin, R.E. Feber, E.J. Asteraki, P.W. Atkinson, R.J. Fuller & V.K. Brown**. 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology* 38: 647–664.

**Wilson, A.M., J.A. Vickery, R.H.W. Langston, D. Smallshire, S. Wotton & D. Vanhinsbergh**. 2005. Changes in the numbers of breeding waders on lowland wet grasslands in England and Wales between 1982 and 2002. *Bird Study* 52: 55–69.

# PAPER VII

# Tracking day and night provides insights into the relative importance of different wader chick predators

**Mason, L.R.**, Smart, J. & Drewitt, A.L.

*Ibis* (2018), **160**: 71–88. http://doi.org/10.1111/ibi.12523

IBIS
BOU international journal of avian science
*Ibis* (2018), **160**, 71–88
doi: 10.1111/ibi.12523

# Tracking day and night provides insights into the relative importance of different wader chick predators

LUCY R. MASON,[1]* JENNIFER SMART[1] & ALLAN L. DREWITT[2]
[1]*RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire SG19 2DL, UK*
[2]*Natural England, Eastbrook, Cambridge CB2 8DR, UK*

Poor reproductive success driven by nest and chick predation severely limits the population recovery of waders breeding on lowland wet grassland. Managing predation requires knowledge of the predators and because these can be grouped into nocturnal or diurnal hunters, detecting the timing of predation can help assess their relative impacts. Wader nest studies investigating the timing of egg predation have identified nocturnal mammals, primarily Red Foxes *Vulpes vulpes*, as the most important nest predators, but quantifying predator importance for highly mobile wader chicks is more difficult. Manual radiotelemetry can detect whether chicks are alive but cannot detect the time of predation, and predator identity can be determined only in the few cases where remains are recovered. As an alternative we used automatic radio tracking stations (ARTS) to constantly record the signals and predation timing of 179 radiotagged Lapwing *Vanellus vanellus* chicks, combining this with manual telemetry, inference about predator identity from predated remains and site-level Fox, mustelid and avian predator activity monitoring. This approach succeeded in detecting the time of predation for 60% of the 155 chicks that were predated. Diurnal chick predation accounted for a larger number of predation events, but nocturnal predation was more intensive in terms of predation likelihood per hour. Mammalian predation during both day and night had a larger impact on chick survival than did avian predation. Raptors were primarily responsible for predation by birds and Foxes for predation by mammals, with Foxes also having a larger influence on daily chick predation rates than other predators. Chick predation increased seasonally, implying that earlier-hatching breeding attempts are more likely to be successful. Higher Fox, raptor and mustelid activity resulted in higher proportions of chicks being predated by those predators, so quantifying the activity of those three predator groups on a site could be a quicker alternative to studying chicks when investigating which predator species to target with site-specific predation management.

**Keywords:** automatic radio tracking stations, Common Redshank *Tringa totanus*, Fox, lowland wet grassland, mustelid, Northern Lapwing *Vanellus vanellus*, raptor, timing of predation.

Populations of farmland birds once common across Western Europe have declined dramatically in recent decades as a result of agricultural intensification and land-use change (Donald *et al.* 2001, BirdLife International 2004). Wader species breeding on lowland wet grassland are of particular concern (Thorup 2006), suffering range contractions that now restrict declining populations to isolated protected sites (Wilson *et al.* 2005, Balmer *et al.* 2013). On these sites, predation of both nests and chicks limits breeding success, contributing to ongoing declines and preventing population recovery (Peach *et al.* 1994, Langgemach & Bellebaum 2005, MacDonald & Bolton 2008, Teunissen *et al.* 2008, Schekkerman *et al.* 2009, Roodbergen *et al.* 2012). Determining the predators involved and managing their impacts (e.g. through exclusion,

---

*Corresponding author.
Email: lucy.mason@rspb.org.uk

habitat manipulation to reduce impacts, diversionary feeding or lethal control; Bolton *et al.* 2007, Malpas *et al.* 2013, Laidlaw *et al.* 2015) is now a key management necessity.

Predator–prey systems are dynamic and involve multiple interactions between different predator species as well as between predator and prey (Holt 2002, Laidlaw *et al.* 2013). Monitoring the predators as well as the prey in any system in which the survival of the prey species is of interest is therefore an important consideration (MacDonald & Bolton 2008). The predators operating on lowland wet grassland can be characterized by their period of activity; detecting the timing of predation can thus indicate the predator type involved. Nocturnally active predators on wet grassland are usually mammalian (Red Fox *Vulpes vulpes*, European Badger *Meles meles*, European Hedgehog *Erinaceus europaeus* and small mustelids: Stoat *Mustela erminea*, Weasel *Mustela nivalis*, American Mink *Neovison vison*), except in rare circumstances where owls are also present (Barn Owl *Tyto alba*, Long-eared Owl *Asio otus*, Short-eared Owl *Asio flammeus*). Diurnally active predators are primarily avian (raptors, gulls, corvids and herons), although mammalian predators can also be active during the day. Studying the timing of wader nest predation using temperature data-loggers and nest cameras has implicated nocturnal mammals, particularly Foxes, as primarily responsible for wader nest mortality (Teunissen *et al.* 2008, Eglington *et al.* 2009). However, breeding success remains low despite management aimed at reducing nest predation (Bolton *et al.* 2007, Malpas *et al.* 2013), suggesting that chick survival may be the more important demographic parameter (Sharpe *et al.* 2008).

In contrast to nest predation, recent studies indicate that diurnally active avian predators are chiefly responsible for wader chick mortality (Junker *et al.* 2004, 2006, Schoppenhorst 2004, Hönisch *et al.* 2008, Teunissen *et al.* 2008, Schekkerman *et al.* 2009). However, the results of these tracking studies, in which predator types were inferred from chick remains recovered through manual telemetry, are not supported by those of mammalian predator removal and exclusion trials, in which wader nest survival, chick survival and fledging success increased, after nocturnal predation pressure from mammals (Foxes and Badgers) was reduced (Bolton *et al.* 2007, Schifferli *et al.* 2009, Rickenbach *et al.* 2011, Malpas *et al.* 2013). A possible explanation for these different results is that the likelihood of finding prey remains is dependent on the cause of mortality (Schaub 2009) as well as the search intensity, potentially biasing tracking studies towards bird-predated remains, which may be easier to find (e.g., plucked close to the predation site or high up in a nest or plucking post where there are no impediments to tag signals). Mammalian predators, on the other hand, may be more likely to cache remains in thick vegetation or underground and damage tags through chewing or digestion, making them harder to relocate.

A way to remove this potential source of bias is to monitor the timing of chick predation to compare the relative importance of diurnally active avian and nocturnally active mammalian predators. This has been attempted using dawn and dusk manual telemetry surveys to classify predation as nocturnal or diurnal (Rickenbach *et al.* 2011), but such surveys are time-consuming and may result in the misclassification of very early or late predation events. As an alternative, we suggest that automatic radio tracking stations (ARTS), which constantly search for and record signals from radiotags, could be used to determine the timing of predation more accurately. ARTS are a relatively new technology now increasingly used to monitor temporal and spatial movements of birds, mammals and fish in foraging, migration and behavioural studies (e.g. Green *et al.* 2002, Briner *et al.* 2003, Kays *et al.* 2011, Thorstad *et al.* 2013).

In this study, we combine the use of ARTS, manual chick tracking and predator monitoring methods as well as conventional inference based on predated remains to provide insights into the relative importance of different wader chick predators in limiting Northern Lapwing *Vanellus vanellus* chick survival on lowland wet grassland.

## METHODS

### Study sites

We monitored 15 UK lowland wet grassland sites chosen to represent the geographical ranges of lowland wet grassland and breeding waders in the UK and expected to have ≥ 10 breeding wader pairs at varying nesting densities (Fig. 1, Table 1; Jefferson & Grice 1998, Balmer *et al.* 2013). Some sites were monitored in multiple years

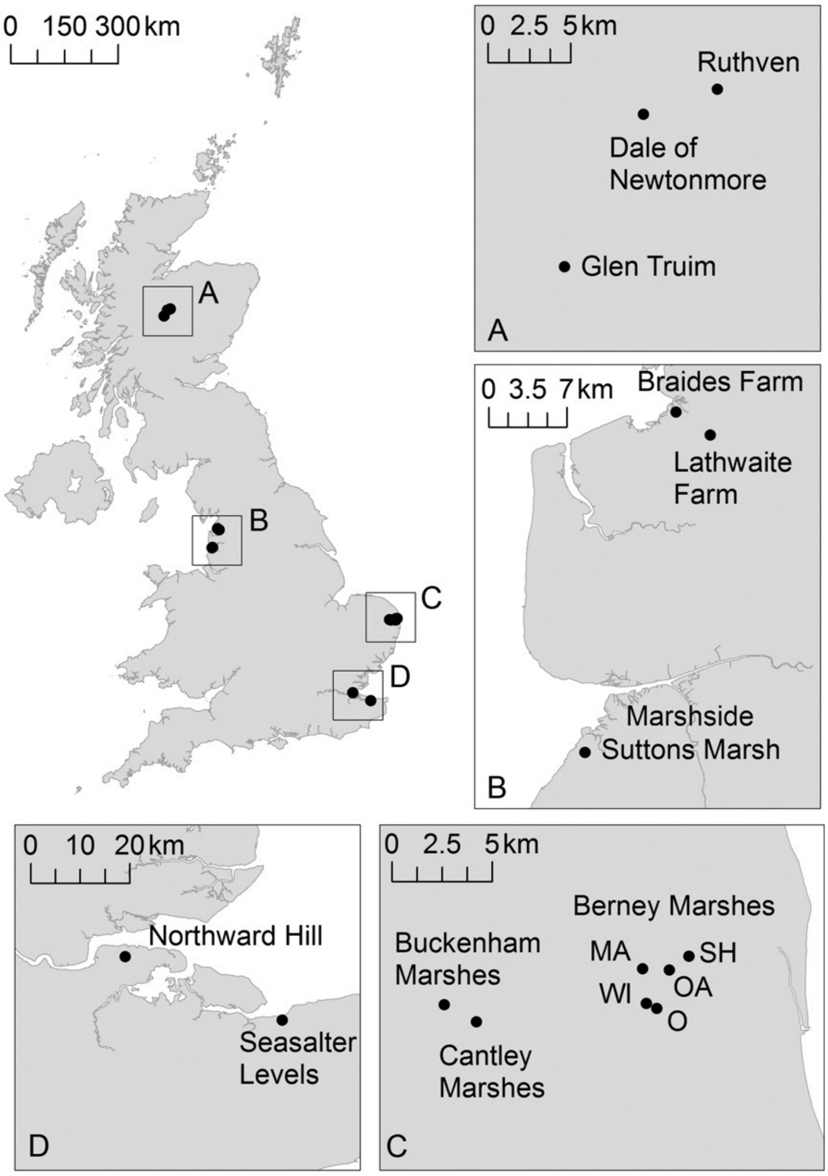


**Figure 1.** Map showing the location of study sites. Insets (A–D) show locations of clustered sites; Berney Marshes sites in C are Machete (MA), Office (O), Old Arable (OA), Shearman's (SH) and Wickhampton (WI). Note that scales vary.

(2009–2013) and because site-specific predation effects were expected to vary annually, we categorized these as independent 'site-years' for analysis (18 site-years, Table 1). All sites were nature reserves or protected areas managed for their breeding wader populations through agri-environment schemes or targeted advisory input from conservation organizations (Smart *et al.* 2006, Eglington *et al.* 2010). Sites comprised multiple fields bounded by wet ditches and accessed by gateways/crossings. No mowing or machinery operations took place during the wader breeding season but lethal control of Foxes (shooting at night by trained marksmen) and Carrion Crows *Corvus corone* (e.g. Larsen cage traps) was conducted on or around most sites before (Foxes) and during (Crows) the wader breeding season following legal welfare requirements (Table 1). Predator management of this kind is now common practice on and around sites managed for breeding waders (Bolton *et al.* 2007). This study therefore represents the levels of chick survival and predator

**Table 1.** Site-years in which Lapwing chick survival and predator activity was monitored (F, Fox; A, avian; M, mustelid; –, no monitoring).

| Site | Year | No. of chicks tagged | Monitoring area (ha) | Lapwing breeding density (nests/km$^2$) | Predator monitoring | Lethal control[a] |
|---|---|---|---|---|---|---|
| Berney Marshes: Machete | 2009 | 5 | 29 | 62.1 | – A – | F & C (on & S) |
| Berney Marshes: Office | 2009 | 11 | 49 | 61.2 | – A – | F & C (on & S) |
| Berney Marshes: Old Arable | 2009 | 10 | 54 | 64.8 | F A M | F & C (on & S) |
| Berney Marshes: Shearman's | 2009 | 16 | 60 | 66.7 | F A M | F & C (on & S) |
| Berney Marshes: Wickhampton | 2009 | 9 | 43 | 88.4 | F A M | F & C (on & S) |
| Berney Marshes: Old Arable | 2010 | 1 | 54 | 75.9 | F – M | F & C (on & S) |
| Berney Marshes: Shearman's | 2010 | 24 | 60 | 78.3 | F A M | F & C (on & S) |
| Berney Marshes: Wickhampton | 2010 | 11 | 43 | 172.1 | F A M | F & C (on & S) |
| Buckenham Marshes | 2010 | 10 | 40 | 60.0 | F A M | F & C (on & S) |
| Marshside: Suttons Marsh | 2011 | 9 | 68 | 19.1 | – A M | F* (S) |
| Cantley Marshes | 2012 | 17 | 48 | 41.7 | F A M | F & C (on & S) |
| Northward Hill | 2012 | 14 | 18 | 116.7 | F A M | F & C (on) |
| Seasalter Levels | 2012 | 3 | 27 | 33.3 | F A M | F & C (on) |
| Braides Farm | 2013 | 6 | 13 | 130.8 | F A M | F (S) |
| Dale of Newtonmore | 2013 | 9 | 19 | 57.9 | F A M | F* & C* (S) |
| Glen Truim | 2013 | 8 | 39 | 17.9 | F A M | F* & C* (S) |
| Lathwaite Farm | 2013 | 4 | 8 | 112.5 | F A M | F (S) |
| Ruthven | 2013 | 12 | 44 | 22.7 | F A M | F* & C* (S) |

[a] Lethal predator control: F = Fox; C = Carrion Crow; on = lethal control conducted on chick monitoring site if necessary to control predation in breeding season; S = control conducted on land immediately adjacent to site; * = control likely but not confirmed.

activity characterizing typical lowland wet grasslands managed for breeding waders in the UK.

## Wader chick monitoring

The relatively abundant and easy-to-monitor Northern Lapwing was chosen as a study species. Lapwings often nest in close proximity to other wader species (e.g. Common Redshank *Tringa totanus*, Black-tailed Godwit *Limosa limosa*), and although their nesting ecology and adult predator defence behaviours differ (Cramp & Simmons 1983, Kis *et al.* 2000), their nests are subject to similar predation rates (MacDonald & Bolton 2008). We also expected Lapwing chicks to be subject to similar predation pressures to those of other wader species, as they congregate around the same wet features (Beintema *et al.* 1991, Smart *et al.* 2006, Eglington *et al.* 2010) and have similar responses to predators (crouching when young, running when older; Walters 1990).

In all, 179 Lapwing chicks (Table 1) were ringed and fitted with unique combinations of permanent colour rings or temporary leg flags and a 0.4–0.5 g radio tag 10–15 mm in length with a 12–15 cm hair-thin whip antenna (2009–2010: Biotrack, Wareham, UK; Holohil Systems, Ontario, Canada. 2010–2013: Perdix Wildlife Supplies, Kenilworth, UK). Tags were mounted on gauze with Araldite or Superglue adhesive and attached to the down feathers over the pelvic girdle using water-based latex adhesive (Copydex). Down feathers were folded over the gauze and tag on adhesion to reduce visibility. This method has commonly been used in similar chick predation studies with no reported negative effects (Hönisch *et al.* 2008, Teunissen *et al.* 2008, Schekkerman *et al.* 2009). Tags pulsed at individual frequencies of 173.001–173.999 MHz with an average beeps rate of 33 beeps per minute (BPM).

Chicks were manually tracked and captured to re-glue tags if necessary every 8 days (the minimum recommended by Sharpe *et al.* 2009 to prevent recapture-related mortality) using Telonics TR4 or ATS R2000 receivers and handheld Yagi antennas (receivers: Telonics, Mesa, AZ, USA and Advanced Telemetry Systems, Isanti, MN, USA; antennas: Biotrack). Brood size and location observations were made from a suitable distance to minimize disturbance. Tags had an expected battery life of 30 days, similar to the fledging period for Lapwing (35–40 days; Cramp & Simmons 1983) and were removed just before this battery end date if predation did not occur and if the chick could be recaptured. The majority of chicks were ringed and tagged on hatching (164/179). This sometimes resulted in a tag life shorter than the duration of the fledging period, so part-grown chicks from broods of unknown hatch date (15/179) were also tagged to account for any age-dependence in survival from hatching to fledging (Bolton *et al.* 2007). The age of part-grown chicks (days) was estimated using site-year specific regression equations of age on bill length (mm) from recaptured chicks of known age, or using published equations where site-year data from this study were limited (Mason & Smart 2015). In some cases, up to three chicks per brood were tagged to increase the sample size of chicks for analysis (one-chick broods, $n = 79$; two-chick broods, $n = 47$; three-chick broods $n = 2$).

## Tracking day and night

Each ARTS was a multi-directional antenna mounted on a 4 m pole and connected to a logging receiver and 12 V battery (Receiver: DataSika B; Biotrack. Antenna: Base Station Antenna BS3; RW Badland, Stourbridge, UK). Up to two ARTS per site-year were either placed near the centre of areas where tagged wader broods congregated or set to target individual broods, and could detect tag signals optimally within a 250 m radius (Figs 2 and S1). ARTS scanned for up to 20 tag frequencies on a cyclical 24 h basis, scanning each frequency for 30 s and recording the date, time to nearest second, BPM and relative signal strength from each tag pulse detected. Tag signal strength and therefore ARTS detection rate were lowest when chicks were being brooded, hiding or dead (adults or vegetation impeding tag signals) and strongest when chicks were active and moving. Daily fluctuations in tag signal strength were recorded for some Lapwing chicks (signal peaking at night); these could hypothetically result from temperature-induced tag frequency drift, diel patterns of chick activity or a reduction in ambient noise interference at night (see Appendix S1 for a discussion of these effects). These fluctuations did not affect the detection of mortality events, which always manifested as

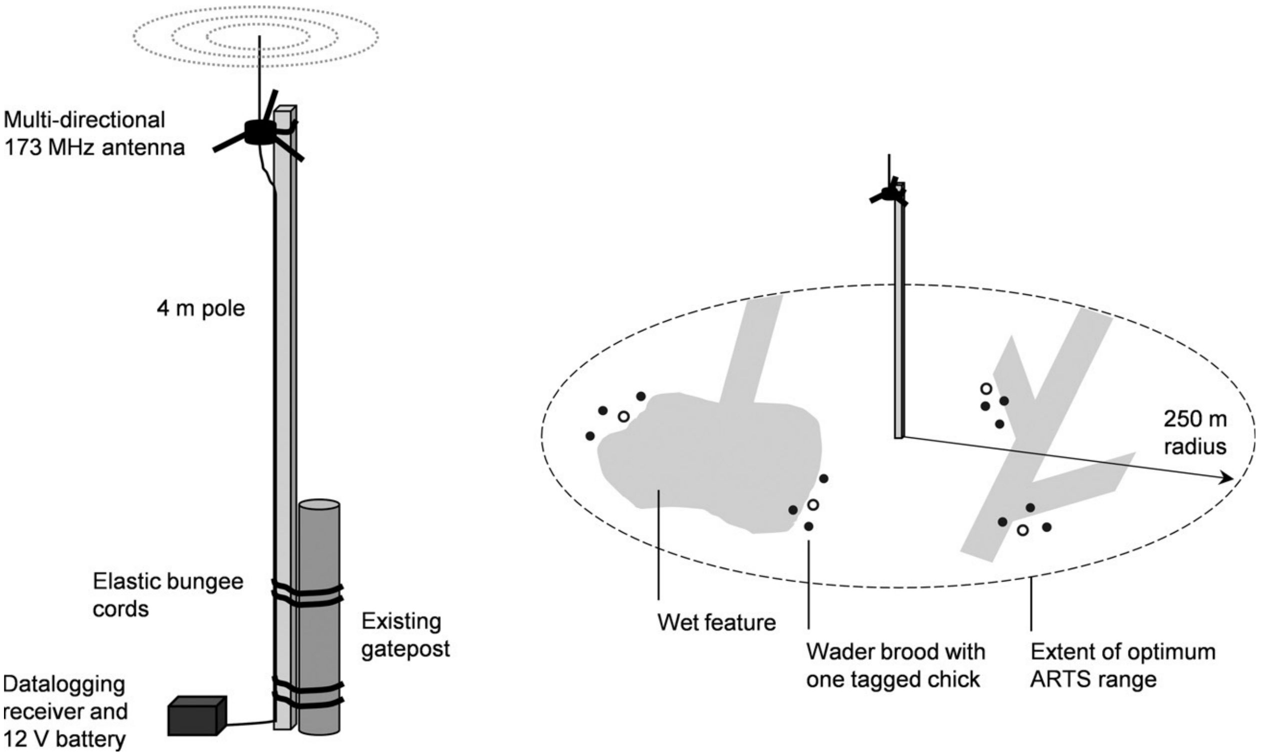


**Figure 2.** Diagrammatic representation of a typical automatic radio tracking station (ARTS) set up to follow a congregation of wader broods on lowland wet grassland wader breeding fields.

signal disappearances or suspicious changes in the usual fluctuation pattern.

Data were exported from the receiver to a laptop computer every 2–3 days using the DataSika Host Application (Biotrack, 2009) and visually examined in Microsoft Excel (2007) for any suspicious changes in tag output that might indicate a mortality event (usually the sudden disappearance of a tag signal or an unexpected reduction or increase in signal strength out-with daily signal fluctuations; Appendix S1). Any suspicious ARTS data changes were then investigated using manual telemetry, surveying in ever-widening circles from locations in which chicks were last observed up to a distance of 2 km. Chicks were recorded as predated if ARTS data indicated a distinct change in tag signal followed by the recovery of predated remains, or if the tag signal and chick disappeared before the expected date of tag battery failure/fledging and its parents were no longer chick calling or alarming. Chicks found dead with no visible signs of trauma (easy to find with manual telemetry as tags were undamaged and remains were in the last-known brood location) were recorded as dying of causes other than predation based on visual observations (starvation, exposure or drowning; Teunissen *et al.* 2008) irrespective of ARTS evidence. Tag failure was assumed when tag signals disappeared but the tagged chick was still observed alive in the expected brood location (in these cases, chick fate was classed as unknown). Chicks were considered to have survived the 30 day monitoring period if tags were removed from well-feathered chicks (Bolton *et al.* 2011) at the end of tag battery life or if chicks were observed to have fledged before tags could be removed. If signal changes resulted from tagged chicks moving out of ARTS range, ARTS stations were moved to ensure all broods were adequately covered (this did not influence predation detection from ARTS data).

On confirmation of chick predation, ARTS data were examined to identify the exact time at which the tag signal disappeared or changed suspiciously as above, accurate from 2 s to 10 min depending on the number of programmed tag frequencies. Detection of predation timing in this way was clear and reliable (Appendix S1) unless ARTS data were intermittent due to chicks moving out of range before predation, in which case predation time was classed as unknown. Predation events were attributed to day or night based on how timings compared to morning and evening UK Civil Twilight (CT): diurnal predation events occurred between morning and evening CT; nocturnal events between evening CT and morning CT the following day.

## Identifying predators from timing of predation and remains

Predator types were inferred from both the timing of predation and the location and characteristics of remains following example criteria in Table 2 and Teunissen *et al.* (2008). All nocturnal predation was attributed to mammals, as these were the only nocturnal chick predators present on our sites. Only one nocturnal avian predator was ever observed (Barn Owl, 2 site-years only) and there was no evidence of it being perceived as a threat by waders, or of it predating chicks (Table S1). Both mammalian and avian predators were active on our study sites during the day, so diurnal predation was attributed to predator species based on inference from recovered remains. Inferring predator type from predation timing in this way is a common method used in wader nest survival studies (Teunissen *et al.* 2008, Eglington *et al.* 2009).

Inference regarding the importance of individual predator species was based on characteristics of remains compared with the outcomes and characteristics of observed predation events (Table 2). Full written histories of chick fates, timing of predation and remain characteristics were additionally examined by one person at the end of the project to ensure consistency in predator inference between site-years.

## Predator monitoring

We used rapid assessment methods to monitor the activity of three predator groups known to predate lowland wader nests and chicks (Junker *et al.* 2004, Schoppenhorst 2004, Hönisch *et al.* 2008, Teunissen *et al.* 2008, Schekkerman *et al.* 2009, Rickenbach *et al.* 2011) during the same period as chicks were monitored in each site-year (Table 1).

To assess Fox activity, faecal (scat) transects were conducted at the beginning (April–late May) and end (May–June) of the wader chick monitoring period in each site-year when wader chicks were most active (Webbon *et al.* 2004). Transects

**Table 2.** Examples of the location and characteristics of recovered predated radiotagged chick remains used to infer the identity of chick predators. Also see Teunissen *et al.* (2008).

| Predator | Timing, location and state of remains |
|---|---|
| Unknown | ARTS data and chick disappearance suggest predation but timing of predation not clear, remains not recovered or characteristics of remains not specific enough to suggest predator species |
| Avian | |
| Unknown avian | Daytime predation and remains characteristic of avian predator (e.g. tag plucked not bitten) but not specific enough to suggest species |
| Unknown raptor | Tag with plucked feathers torn out not bitten; tag found plucked a long way (> 500 m) from where chick last seen (>500 m), antenna bent sharply by bill |
| Marsh Harrier *Circus aeruginosus* | Predation event observed; remains suggest raptor predation (above) and spp. observed hunting in vicinity of chick 5 mins either side predation time |
| Common Buzzard *Buteo buteo* | Tag found in or underneath nest; remains suggest raptor predation and spp. observed hunting in vicinity of chick at time of predation |
| Common Kestrel *Falco tinnunculus* | Tag found in nest; remains suggest raptor predation and spp. observed hunting in vicinity of chick at time of predation |
| Peregrine Falcon *F. peregrinus* | Tag at plucking site |
| Mammalian | |
| Unknown mammal | Nocturnal predation and/or remains characteristic of mammalian predator (chewed, bite marks, cached, limbs bitten off) |
| Unknown mustelid | Small bite marks to the back of neck or head; carcass cached in grass tussock |
| Red Fox *Vulpes vulpes* | Tag or ring in scat; tag in or around burrow; legs, rings and tag found chewed or bitten off next to fox scat; whole broods predated in quick succession |
| Weasel *Mustela nivalis* | Predation event observed; bite marks to back of head and carcass partially eaten leaving the skin, head and legs intact |

followed linear features encompassing access routes and the inner circumference of chick monitoring fields. The first visit aimed to clear scat deposited the previous winter; the second recorded scats deposited by Foxes active during the monitoring period. Our measure of Fox activity was the relative Fox density (scat/km/day) based on the number of scat recorded on the second visit, the length of transect walked (km; MAPINFO PROFESSIONAL v6 2000) and the number of days since the first transect.

Mustelid activity was monitored using tracking tunnels. In 2009/2010 these consisted of wooden tunnels over a clay tracking cartridge built following the specifications of the Game and Wildlife Conservancy Trust mink raft (Reynolds *et al.* 2007). Mink raft tracking cartridges were modified for use on land by replacing baskets with 150 × 100 × 45 mm plastic food containers which could be filled with water and sunk level with the ground. In 2010–2013 this design was replaced by black corrugated plastic tunnels with a wooden base and ink and paper tracking cartridge as described in Laidlaw *et al.* (2013). This change in tunnel design was made to increase fieldwork efficiency (plastic tunnels were lighter, so were easier to store, transport and set up) rather than concerns over wooden tunnel efficacy. In all site-years an average of 0.5 tunnels per hectare were placed around the circumference of chick monitoring fields in positions most likely to intercept mustelids (long vegetation, gateways, ditch crossing points). Tunnels were activated in the first week of chick monitoring in each site-year (late April–early May) and checked weekly for 3 weeks. On each visit the tracking medium was examined for the presence/absence of mustelid prints and the tracking cartridge refreshed. Mustelid activity (mustelid presence/tunnel/day) was calculated for each visit by dividing the number of tunnels with mustelid prints by the total number of tunnels on site, and then dividing this by the number of days since the tunnels were last checked. This was then averaged across the three tunnel visits to provide a mustelid activity estimate for the chick monitoring period for that site-year. Although we have no validation data to compare the two tunnel designs directly, anecdotally we encountered no differences in tunnel-use by mustelids nor in the ease with which mustelid prints could be identified between the two designs, and mustelid activity rates averaged across site-years using each method did not significantly differ (mean mustelid presence/tunnel/day wood = 0.003 ± 0.004 95% CI,

$n = 4$ site-years; plastic = 0.002 ± 0.001, $n = 12$; $t = 0.79$, $P = 0.48$).

Avian species with the potential for chick predation are numerous in lowland wet grassland landscapes and could include many raptors, corvids, gulls, herons and egrets. As some may never predate wader chicks on a site-specific basis, automatically assuming predator effects would result in biased and meaningless estimates of predator activity. Rather than assume that all species actively predated waders in all site-years, we therefore used the predator deterrence behaviour of wader adults to inform our definition of a perceived avian predator in each site-year, considering that only species which waders perceived as a threat were likely to be actively involved in predation (Walters 1990). Lapwing adults actively deterred all raptor species present in all site-years but deterrence of other species (corvids, gulls, herons, egrets) was site-specific and dependent on individual predator behaviours (Table S1).

To estimate the activity of avian predators defined above during the period wader chicks were active, timed watches were conducted during the wader chick monitoring period in each site-year, from the date of first chick tagging to the date of final chick predation or fledging (mean start date 13 May, end date 11 June). In 2009 and 2011, watches were of varying frequency and duration (mean watch frequency per site-year = 10, range = 2–16; mean duration = 2.2 h, range = 1.4–2.9; mean total hours watched = 22 h, range 3–31) but in 2010, 2012 and 2013, watch length and frequency were standardized (minimum 2 h weekly) to allow time for other monitoring activities (mean frequency = 5, range = 2–10; mean duration = 2.2 h, range = 2.0–4.2; mean total hours watched = 11 h, range = 4–21). During timed watches in all site-years, all separate predatory passes by individual avian predators over the wader monitoring area were recorded, a pass defined as a potential predation event, i.e. any flight or strike exhibiting hunting behaviour (raptor species) or any flight, strike or foraging activity to which wader adults reacted with deterrence behaviour (corvids, gulls, herons, egrets). The total number of predatory passes/hour was calculated for each watch and averaged across all watches at a site to provide a site-year level estimate of avian predator activity, thus controlling for differences in watch frequency, watch duration and total number of watches (due to the difference in chick monitoring period length) between site-years. The activity of all avian predators combined (all raptors, gulls, corvids, herons and egrets combined) and raptor activity were correlated (Pearson's $r = 0.39$, $t = 17.24$, df = 1615, $P < 0.0001$).

## Drivers of chick survival

We used an extension of Mayfield logistic regression to investigate the effects of predator activity on daily chick predation probability (DPP; Aebischer 1999). This analysis method is still common in both chick and nest predation studies (Sharpe *et al.* 2009, Laidlaw *et al.* 2015, Dunn *et al.* 2016, MacDonald *et al.* 2016, Setchfield & Peach 2016) and is in this case preferable to other survival analysis methods (e.g. 'Survival-Time analysis', Nur *et al.* 2004) because it facilitates clearer interpretation of continuous covariate effects and better allows for the control of data non-independence where survival over time is not inherently of interest. We ran binomial generalized linear mixed models (GLMMs) in R (glmer, lme4: R Core Team 2013, Bates *et al.* 2014), with the daily predation outcome of each chick as a response variable (1 = predated, 0 = alive or dead for reasons other than predation) from the date of tagging to the date of predation, death, disappearance or tag removal up to 30 days after tag attachment. Models used a logit link, Laplace likelihood approximation and the random effects of chick identity nested within brood nested within site-year (to account for non-independence of chick-days from the same chick, multiple chicks from the same brood, and variation in predator abundance and chick survival between site-years). We were interested in testing the main effects of Fox activity, mustelid activity, all-avian predator activity and monitoring date (seasonal variation in survival; 1 April = day 1), and also included chick age (hatch day = age 0) as a control variable to account for any age-dependent effects on mortality (e.g. Bolton *et al.* 2007, Sharpe *et al.* 2009). Although two-way interactions between predator activity variables were biologically plausible, we only included main effects in our models, as including interactions would have resulted in model overspecification due to our relatively small dataset (full model parameters $n = 9$; binomial datapoints: success/predation $n = 133$, failure/survival $n = 1484$;

Harrell 2015). Variance inflation factors for variables were close to 1 in all cases (maximum = 1.14), indicating no multicollinearity. Model convergence was improved by first centring all variables (standardized $x = x$ – mean $(x)$/sd $(x)$), and by using 'bobyqa' as the optimizer (Bates & Maechler 2009, Powell 2009). Only site-years with available Fox, avian and mustelid data were included (14 site-years, 153 chicks from 106 broods, Table 1). All assumptions of the Mayfield logistic regression method were fulfilled (Nur *et al.* 2004).

Model selection was based on AIC$_c$ (Akaike information criterion with correction for small sample sizes), which selects the model best approximating the 'true' model (Burnham & Anderson 2002) but favours model complexity (Arnold 2010). We compared models with all possible combinations of covariate main effects, maintaining a constant random effect structure and conforming to marginality assumptions (dredge, MuMIn: Barton 2014). Top AIC$_c$ models were selected as those with $\Delta$AIC$_c \leq 6$ that were not more complex versions of a model with a lower AIC$_c$ (excluding models with uninformative parameters: Arnold 2010, Richards *et al.* 2011). Standardized regression coefficients ($\beta$; Schielzeth 2010) for all covariates retained in top models were compared to determine relative effect sizes.

## RESULTS

Of the 179 chicks tagged, 155 (87%) were predated, nine (5%) died from other causes (drowning, exposure) and 13 (7%) survived (Fig. 3). Only two chicks (1%) had unknown fates attributable to tag failure. These results represent very low survival rates, with a probability of chicks surviving predation beyond 30 days of monitoring across all site-years between 5.4% (−2.0/+3.1% 95% confidence interval (CI); Mayfield 1961) and 5.6% (−2.5/+4.4%; Kaplan & Meier 1958) depending on the method used (see Table S2 for site-year specific estimates).

### Timing of predation

The timing of predation could be determined for 93 (60%) of the 155 predated chicks (Fig. 4). A higher proportion were predated during the day (54 chicks: 58% of chicks where timing known, 35% of all predated) than at night (39: 42% of chicks where timing of predation known, 25% of all predated). The number of chicks predated at night was, however, disproportional to the number of hours of darkness. Daylight was 7–12 h longer than darkness during April–July on our study sites (www.timeanddate.com; Fig. 4). Comparing the ratios of the proportion of chicks predated by

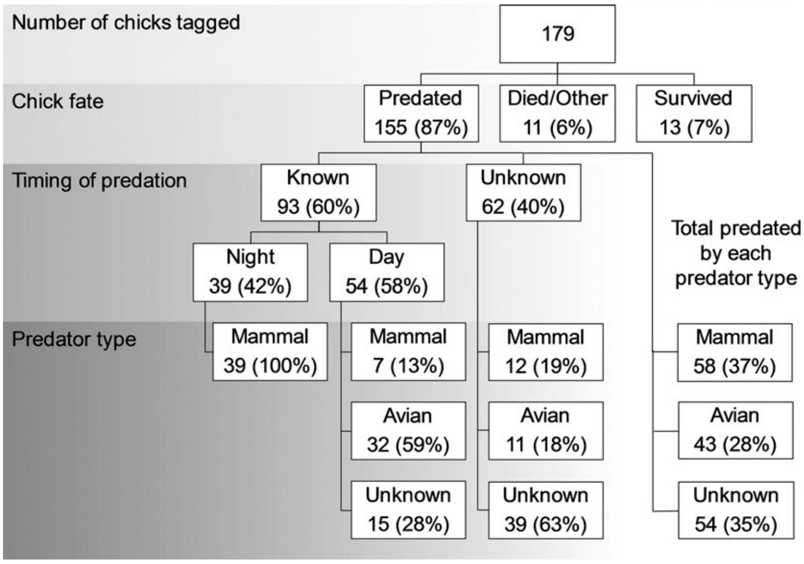


**Figure 3.** Summary of Lapwing chick survival results. From top to bottom, the diagram shows the proportions of radiotagged chicks that were predated, survived the 30-day monitoring period, or died or disappeared from other causes, followed by the timing of predation and the main predator types (inferred from timing of predation and predated remains). Boxes show the numbers of chicks in each category and this number as a percentage of the total one flow-level above it.

night (pN) or day (pD) with the proportion of hours of darkness (hN) or daylight (hD), nocturnal predation was 1.91 times more intensive than diurnal predation (nocturnal pN/hN = 1.53, diurnal pD/hD = 0.80).

## Predator identification

Predated remains were recovered from 38% of chicks overall, although this varied between site-years (site-year mean = 42%; Table S3). Timing of predation information was available for 58% of those never recovered, although again this varied between site-years (mean = 61%). For all chicks where predator type could be determined, mammalian predation accounted for 10% more predation events than avian predation and was similar in terms of biological significance to diurnal predation (49 chicks predated by mammals, 54 predated diurnally; Fig. 3). All nocturnal predation was attributed to mammals (as mammals were the only nocturnal chick predators active on our sites), whereas both mammals and avian predators contributed to predation in daylight hours (Fig. 3, Tables 3 and S4). Where the timing of predation could not be determined, mammalian and avian predators were identified in almost equal proportions (Fig. 3), indicating that ARTS data were unbiased towards particular predation events (no over-representation of either predator type in the undetected category). Foxes were the most frequently identified mammalian predator, active both night and day, and raptors were the most frequent avian predator. Foxes and raptors accounted for equal proportions of predation events (20%) and together contributed to 40% of predation mortality (Table 3).

It took longer to find mammal-predated (median time 4.5 days, range = 0–23 days) than avian-predated remains (median time 1 day, range = 0–9 days; Mann–Whitney $W = 158.5$, $P = 0.02$, 15 site-years). However, knowing the timing of predation did not significantly increase our ability to detect mammalian predation (59% of chicks predated by mammals where timing of predation was known, 52% where timing was unknown, $\chi^2_1 = 0.27$, $P = 0.61$, all site-years) nor were predated remains taken further away by avian predators (avian median distance from last chick location to predated remains = 194 m, range = 43–3702; mammalian median = 155 m, range = 0–1099; Mann–Whitney $W = 326.5$, $P = 0.277$, 14 site-years).

## Drivers of chick survival

Monitoring date was the best predictor of DPP, being retained in all best fit models (Tables 4 and S5). The magnitude of the effect of date on DPP was relatively high (top model $\beta = 0.39 \pm 0.14$ se),

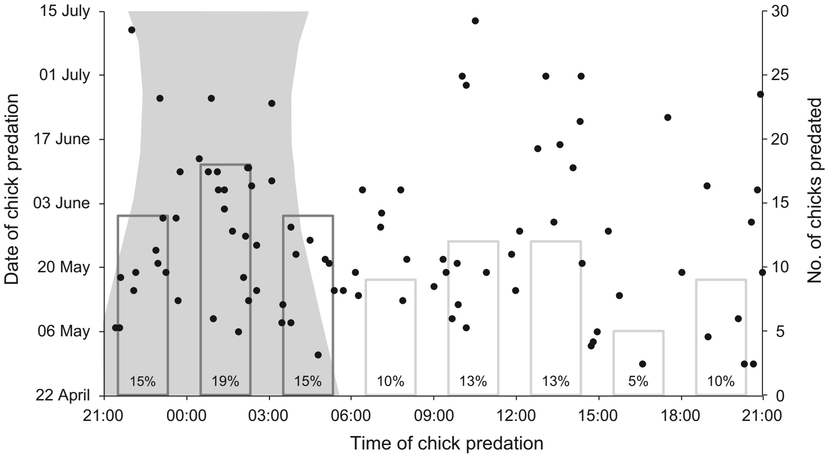


**Figure 4.** The timing of predation of Lapwing chicks. Columns indicate the numbers and percentage of chicks predated during 3-h time intervals (right-hand axis); points show the temporal distribution of predation events throughout the monitoring period (left-hand axis). Each point represents a predated chick ($n = 93$); overlapping points have been jittered by 20 min for clarity. Darker grey columns and grey shading indicate hours of darkness.

**Table 3.** Avian and mammalian predators identified as important in limiting Lapwing chick survival and the time at which predation occurred.

| | | | Timing of predation | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Total | | Day | | Night | | Unknown | |
| Inferred predator type | Number | % | Number | % | Number | % | Number | % |
| Mammalian predator | 58 | 37.4 | 7 | 4.5 | 39 | 25.2 | 12 | 7.7 |
| Unknown mammal | 16 | 10.3 | 0 | 0 | 14 | 9.0 | 2 | 1.3 |
| Red Fox *Vulpes vulpes* | 34 | 21.9 | 7 | 4.5 | 21 | 13.5 | 6 | 3.9 |
| Mustelid (Weasel *Mustela nivalis*, unknown spp.) | 8 | 5.2 | 0 | 0 | 4 | 2.6 | 4 | 2.6 |
| Avian predator | 43 | 27.7 | 32 | 20.6 | 0 | 0 | 11 | 7.1 |
| Unknown bird | 9 | 5.8 | 3 | 1.9 | | | 6 | 3.9 |
| All Raptors | 34 | 21.9 | 29 | 18.7 | | | 5 | 3.2 |
| Unknown raptor spp. | 21 | 13.5 | 18 | 11.6 | | | 3 | 1.9 |
| Common Buzzard *Buteo buteo* | 5 | 3.2 | 3 | 1.9 | | | 2 | 1.3 |
| Common Kestrel *Falco tinnunculus* | 5 | 3.2 | 5 | 3.2 | | | 0 | 0 |
| Marsh Harrier *Circus aeruginosus* | 1 | 0.6 | 1 | 0.6 | | | 0 | 0 |
| Peregrine Falcon *F. peregrinus* | 2 | 1.3 | 2 | 1.3 | | | 0 | 0 |

Shown are numbers of chicks predated and percentages of the total 155 chicks predated (Fig. 3). Avian and mammalian predators with the largest contribution to predation are shaded grey.

with chicks more likely to be predated each day as the monitoring period progressed (Fig. 5a), equating to a 30.2% probability of a chick surviving 30 days at the start of the season compared with a 0% probability at the end (22 April–13 July; 30 day fledging success = $[1 - \text{daily predation probability}]^{30}$; Mayfield 1961). Fox activity was also a good predictor of DPP, being retained in the top model with an effect magnitude of 0.31 ± 0.12 se. DPP increased as Fox activity increased (Fig. 5b), with a 19.6% chance of surviving 30 days on sites with low Fox activity compared with 1.6% on sites with high Fox activity at the average date when chicks hatch (15 May). Chick age as a control factor was also included in the top model with a positive effect on DPP ($\beta = 0.28 \pm 0.16$ se).

The proportion of Fox-, mustelid- and raptor-specific (though not all-avian predator) predation events was positively related to the activity of each predator group on a site-year level (linear regression on percentage of chicks predated by a predator transformed using arcsin($\sqrt{x}$): Fig. 6; all-avian: $F_{1,15} = 0.004$, $P = 0.95$). As predator activity increased on a site, the proportion of chicks predated by that predator also increased.

## DISCUSSION

Our results demonstrate that although diurnal predation was biologically more significant than nocturnal predation, it was less intensive, and mammalian rather than avian predators had the highest impact on wader chick survival. Mammalian predation was of equal biological significance to diurnal predation because mammals were active both nocturnally and diurnally, whereas avian predators were only active by day. Foxes were most commonly implicated in mammalian predation events, whereas raptors were mainly responsible for avian predation. ARTS were a cost-effective tool for monitoring predation (Appendix S2) and should be considered for use in future predation studies. Detecting timing of predation was possible for 60% of chicks, and where timing could not be determined accurately this was largely because chicks moved out of range and were predated before ARTS could be moved. Importantly, the timing of predation could be determined for 58% of all tags that were never recovered and for which all predator inference information would otherwise have been lost (Table S3). This, combined with remain recoveries (Tables S3 and S4), made predator inference possible for 65% of all predation events (Table 3).

The predation mortality we recorded (87% of chicks) is higher than that reported by other studies in similar habitats (Table S6). We also found similarly high predation mortality (83%) attributed to the same predator species groups for 23 Common Redshank chicks we monitored

**Table 4.** Model selection results from binomial GLMMs testing for effects of predator activity (Fox, avian, mustelid), chick age and monitoring date on the daily probability of chick predation.

| Variable inclusion and coefficients of best fit models | | | | | | Model selection | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| (Intercept) | Fox | Avian | Mustelid | Date | Age | AICc | ΔAICc | *w* | logLik (df) | $R^2$m | $R^2$c |
| −2.45 ± 0.13 | 0.31 ± 0.12 | | | 0.39 ± 0.14 | 0.28 ± 0.16 | 910.3 | 0.0 | 0.24 | −448.1 (7) | 0.00006 | 0.00006 |
| x | x | x | | x | x | 910.7 | 0.4 | 0.19 | −447.3 (8) | 0.00008 | 0.00008 |
| x | x | | x | x | x | 911.4 | 1.1 | 0.14 | −447.7 (8) | 0.00008 | 0.00008 |
| x | x | x | x | x | x | 912.1 | 1.8 | 0.10 | −447.0 (9) | 0.00016 | 0.00033 |
| −2.48 ± 0.11 | 0.28 ± 0.10 | | | 0.36 ± 0.11 | | 912.1 | 1.8 | 0.10 | −450.0 (6) | 0.04883 | 0.05715 |
| x | x | x | | x | | 912.8 | 2.5 | 0.07 | −449.4 (7) | 0.04540 | 0.04540 |
| x | x | | x | x | | 913.5 | 3.2 | 0.05 | −449.7 (7) | 0.04477 | 0.04477 |
| −2.42 ± 0.16 | | | | 0.41 ± 0.15 | 0.29 ± 0.15 | 914.2 | 3.9 | 0.03 | −451.1 (6) | 0.00004 | 0.00004 |
| x | x | x | x | x | | 914.3 | 4.0 | 0.03 | −449.1 (8) | 0.04555 | 0.04555 |
| x | | x | | x | x | 915.8 | 5.5 | 0.02 | −450.9 (7) | 0.00004 | 0.00004 |
| x | | | x | x | x | 916.2 | 5.9 | 0.01 | −451.1 (7) | 0.00004 | 0.00004 |

ΔAICc, difference in AICc between a model and the model with the lowest AICc; *w*, AICc weight; logLik, log likelihood; df, number of estimable parameters. Shown are models within 6 ΔAICc units of that with the lowest AICc, with the best fit models (those which are not more complex versions of a simpler nested model of lower AICc value; Richards *et al.* 2011) highlighted grey, darker shading indicating the top model (that with lowest AICc). x denotes variables inclusion in each model, with standardised regression coefficients (betas ± se) presented for variables included in the best fit models. Marginal ($R^2$m) and conditional ($R^2$c) estimates of model fit are calculated following Nakagawa and Schielzeth (2013). See Table S5 for results from the full model set.

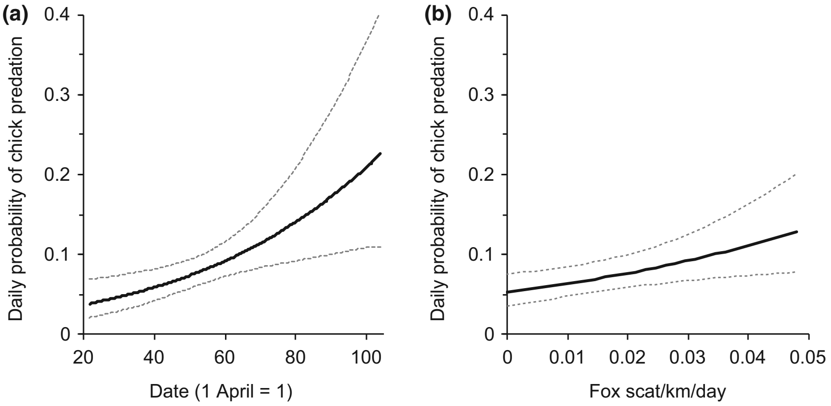


**Figure 5.** Relationships between the daily probability of chick predation (DPP) and (a) monitoring date and (b) Fox activity at the average chick hatch date based on coefficients reported by the top model (Table 4). Solid lines are back-transformed logit predictions assuming a constant value (mean chick age, mean Fox activity or mean hatch date) for model covariates not represented in each plot. Dotted lines are 95% confidence intervals estimated using the delta method.

using the same methods as for Lapwing (five site-years; Table S7). These high predation rates are unlikely to result from misclassification resulting from scavenging or tag failure. Evidence of scavenging would have been present in ARTS data, exhibiting an unexpected tag signal reduction or disappearance after death when signals are impeded by vegetation, followed by a sharp increase and eventual disappearance upon scavenging when tagged remains were moved, lifted, removed from site or destroyed. Tag failures were unlikely to have been misclassified as predation events: few tags failed before the full 30 days of monitoring (1% of 179 tags) and no additional tag failure went undetected because in all other cases any loss of tag signal from ARTS or manual telemetry was accompanied by observations of last known brood locations which confirmed true disappearance of an active chick, and therefore predation or death.

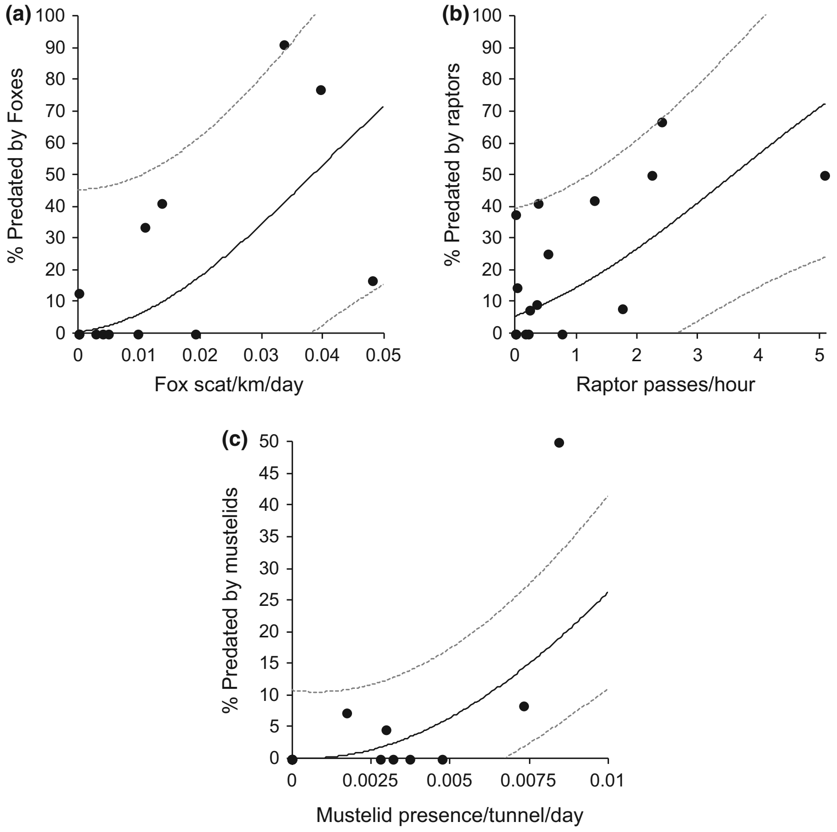


**Figure 6.** Relationships between the percentage of predated wader chicks predated by Foxes, raptors and mustelids and the activity of (a) Foxes ($F_{1,13}$ = 12.02, $P$ = 0.004), (b) raptors ($F_{1,15}$ = 8.68, $P$ = 0.01) and (c) mustelids ($F_{1,14}$ = 16.65, $P$ = 0.001), respectively, in each site-year. Solid lines are back-transformed predictions from univariate linear regression models on response variables transformed using arcsin($\sqrt{x}$). Dotted lines are 95% confidence intervals estimated using the delta method. Note that scales vary.

It is also unlikely that the use of ARTS themselves inflicted any additive predation mortality. The antenna and pole were too thin to provide a viable perch for avian predators and, when erected, the equipment was visually unobtrusive and unlikely to cause disturbance to breeding waders (Fig. S1). Frequent visits to download ARTS data (every 2–3 days) may have influenced mortality through human disturbance, although visits were no more frequent than during a conventional manual telemetry study (e.g. 1–5 days: Teunissen *et al.* 2008). However, further research would be needed to exclude completely any ARTS effects.

Radiotagging and repeated trapping have the potential to influence chick mortality by encouraging poor body condition, increasing detection by predators or reducing the ability to escape. Sharpe *et al.* (2009) found that frequent disturbance associated with tracking and recapturing chicks, rather than the attachment of a tag itself, affected body condition, but that a recapture frequency of greater than 8 days was sufficient to reduce this effect. By following this recommendation the chicks we monitored attained body condition equal to or better than expected for their age, and there was no significant difference in condition between tagged and untagged chicks (Table S8; Beintema 1994, Mason & Smart 2015). Tags and mounting methods themselves could have directly hindered movement or increased visibility to predators, although other studies found no effects on the predation probability of tagged vs. untagged chicks (Hönisch *et al.* 2008, Schekkerman *et al.* 2009), and we expect these effects to be minimal due to tags being small, light, covered with feathers to reduce visibility and with very thin, black pliable antennae. Despite the potential negative effects, radiotagging is still the only practical method of studying causes of wader chick mortality. Our tagging and recapture methods matched those used by other studies (Table S7), meaning that the high predation rates we detected are at least likely to be valid in the context of existing wader chick predation research.

Nocturnal mammalian predation was attributed mainly to Foxes, whose increasing activity reduced the probability of daily chick survival. Foxes are also responsible for the majority of wader nest predation (e.g. Teunissen *et al.* 2008) and if Fox predation pressures are reduced on a site through exclusion or lethal control, both wader nest and chick survival increase (Bolton *et al.* 2007, Schifferli *et al.* 2009, Rickenbach *et al.* 2011, Malpas *et al.* 2013). The impact of Foxes on lowland wet grassland is perhaps unsurprising given the 'honeypot' nature of these sites for generalist predators (Seymour *et al.* 2003), attracting high densities of other common prey species (rodents, lagomorphs, galliforms) as a result of better habitat conditions and less intensive hunting and agricultural pressure. Lethal Fox control is now ubiquitous on or around lowland wet grassland sites managed for breeding waders in the UK, so the fact that Foxes still account for a high proportion of chick predation indicates that the current lethal control methods or the implementation of those methods is largely ineffective. Electric fencing or encouraging ecosystem resilience through the provision of habitats for alternative prey are likely to be more successful alternatives (Laidlaw *et al.* 2013, 2015, Malpas *et al.* 2013).

Generalist raptors (Buzzard, Marsh Harrier, Kestrel, Peregrine) were equal in importance to Foxes in the proportion of chicks predated, but the activity of all avian predators combined did not affect daily predation rates. We found no evidence of corvid or gull predation and little evidence these species were perceived as predation threats by waders on our study sites, despite their presence in higher numbers compared with raptors (mean passes per hour: corvids = 2.2 ± 0.68 se, gulls = 0.4 ± 0.17, raptors = 0.9 ± 0.32; Table S1). It is also unlikely that predation events from these species occurred but went undetected, as no chick remains were ever recovered from typical areas of high gull or corvid activity (e.g. colonies or nesting locations). The validity of managing avian predation of chicks by direct means (lethal or non-lethal) therefore needs careful consideration, as any corvid or gull control is unlikely to influence wader chick survival (although lethally controlling crows can successfully improve wader nest survival at high crow densities; Bolton *et al.* 2007). Raptors are legally protected in the UK (Redpath *et al.* 2001) so non-lethal or indirect predation management methods would be the only options to manage unsustainable predation from these species.

We recorded a higher proportion of nocturnal, mammalian predation, particularly by Foxes, than did other chick-tracking studies, where avian predation was more important (Junker *et al.* 2004, Schoppenhorst 2004, Teunissen *et al.* 2005, 2006, 2008, Schekkerman *et al.* 2009). A limitation of these studies is the potential for a bias towards relocating avian-predated chicks (Teunissen *et al.* 2008, Schekkerman *et al.* 2009), which we found were easier (required less time) to locate than those predated by mammals. By recording the timing of predation, we were able to infer at least some predator-type information from the proportion of chicks whose remains were never found, which may explain the higher proportion of mammalian predation overall. These results also support the findings of predator control or exclusion studies which implicate mammals as more important chick predators (Bolton *et al.* 2007, Schifferli *et al.* 2009, Rickenbach *et al.* 2011, Malpas *et al.* 2013).

Another reason for the disparity may be differences in the activity of different predator types between regions. The studies where avian predation was found to be important were based in areas where Fox abundance may be low (grasslands along the North Sea coasts of The Netherlands and Germany; J. Bellebaum pers. comm.) while raptor abundance may be high. In contrast, studies which implicate mammals as important chick predators largely originate from areas where Fox abundance may be high while raptor abundance is low (UK, Switzerland: Bolton *et al.* 2007, Schifferli *et al.* 2009, Rickenbach *et al.* 2011, Malpas *et al.* 2013). Given the relationship we found between the proportions of chicks predated by Foxes and raptors and their respective activity (Fig. 6), the contrasting Fox and raptor predation results from these different regions may not be surprising. The higher level of mammalian predation found in this study is likely to be more representative of levels of mammalian predation on wet grassland sites managed for breeding waders in the UK.

Nevertheless, caution is required when interpreting the relative importance of predator types due to the possibility of misclassifying predated remains. However, the fact that the high proportion of nocturnal, mammalian predation we detected by recording timing of predation information also matches the known importance of nocturnal, mammalian predation in limiting wader nest survival in the same habitat (Teunissen *et al.* 2008, Eglington *et al.* 2009) gives further weight to the validity of our results, despite the disparity with previous chick predation studies.

The predator monitoring methods we used are cheaper and quicker than monitoring wader chicks themselves. Site managers could use such monitoring as a basis for rapid assessment of the likely importance of Foxes, mustelids and raptors in limiting wader chick survival on a site based on the relationships we found between the activity of these predator groups and the proportion of chicks predated by those predators (Fig. 6). Interpreting these relationships requires caution, however, due to the possibility of expectation-driven bias from observers who collected both predator activity and interpreted predated remains. We attempted to lessen such a bias by collating and inspecting the interpretation of chick histories and predated remain characteristics at the end of the project, although some possibility of bias still remains. It is also important to note that these relationships were found specifically for Foxes, small mustelids and raptors, which were the predator groups most active in predating waders and which elicited an anti-predator response from Lapwing adults on our study sites: they are unlikely to be relevant for or extendable to other predator species.

Chick mortality increased as the breeding season progressed, with later-hatching chicks susceptible to a higher daily risk of predation. Predation pressures are likely to increase seasonally as predators start to provision their own young, despite simultaneous increases in alternative prey. Over 50% of wader chicks monitored during this study hatched between 18 April and 15 May, the same period in which Fox cubs are developing (born March–April; e.g. Webbon *et al.* 2004) and raptor chicks hatch (May onwards for Marsh Harrier, Kestrel, Buzzard; Ferguson-Lees & Christie 2001). Early wader breeding attempts may be more likely to evade predation at the chick stage, and may be more likely to result in successful fledging. Juveniles fledging earlier in the season will also have a longer period in which to increase their body weight before winter, and may be more likely to survive to recruit to future breeding populations by having more time to locate suitable winter habitats and to learn key foraging and roosting behaviours (Gill *et al.* 2014). Habitat and predation management methods that encourage successful early nesting attempts are therefore more likely to maintain populations and promote more rapid wader population recovery.

Managing chick predation is only likely to be advantageous on sites where this is the main mortality factor and where additional mortality has been minimized through good habitat management (Bolton *et al.* 2007, Eglington *et al.* 2010, Mason & Smart 2015). Even on well-managed sites, we highlight the need for accurate knowledge about the timing of predation and activity of all wader chick predator groups to make meaningful inferences about the relative importance of different predators. The previously unproven importance of difficult-to-detect mammalian predation in wader chick mortality emphasizes the need to avoid making assumptions about predation based on visual observations of predator abundance or predation events alone. Predation pressures from key predator groups are likely to increase as predators increase across Europe (Foxes: Chautan *et al.* 2000, raptors: PECBMS 2014). A positive message is that the relationships we found between the proportions of chicks predated by Foxes, raptors and mustelids and the activity of these groups could be used with caution to indicate the likely relative importance of these predators on sites similar to those we studied.

We thank Thomas Bodey, Janine Bicknell, Tessa Cole, Maureen Gibson, Rebecca Laidlaw, Andrea Mason, Peadar O'Connell, Jean Roberts, Andrew Robertson, Leila Walker, Leah Williams and RSPB staff/volunteers for fieldwork, and Braides Farm, Lathwaite Farm, Gavin Thomas, Richard Storton and Karen Birkby for site access. All ringing and tagging was conducted under licence from the British Trust for Ornithology. Licences to disturb and handle birds were granted by Natural England and Scottish Natural Heritage for scientific research in line with the UK Wildlife and Countryside Act 1981. Adam Butler and Mark Brewer (BIOSS) provided statistical guidance, and Jochen Bellebaum, Christian Rutz, Ruedi Nager and three anonymous referees provided constructive comments on the manuscript. This study was jointly funded by the RSPB and Natural England through the Action for Birds in England Partnership.

## REFERENCES

**Aebischer, N.J.** 1999. Multi-way comparisons and generalised linear models of nest success: Extensions of the Mayfield method. *Bird Study* **46**: S22–S31.

**Arnold, T.W.** 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wildl. Manage.* **74**: 1175–1178.

**Balmer, D.E., Gillings, S., Caffrey, B.J., Swann, R.L., Downie, I.S. & Fuller, R.J.** 2013. *Bird Atlas 2007–11: The Breeding and Wintering Birds of Britain and Ireland*. Thetford: BTO Books.

**Barton, K.** 2014. *MuMIn: Multi-model inference*. R package version 1.10.5. Available at: http://CRAN.R-project.org/package=MuMIn

**Bates, D. & Maechler, M.** 2009. *lme4: Linear mixed-effects models using S4 classes*. R package version 0.999375-32.

**Bates, D., Maechler, M., Bolker, B. & Walker, S.** 2014. *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-7. Available at: http://CRAN.R-project.org/package=lme4

**Beintema, A.J.** 1994. Condition indices for wader chicks derived from bodyweight and bill-length. *Bird Study* **41**: 68–75.

**Beintema, A.J., Thissen, J.B., Tensen, D. & Visser, G.H.** 1991. Feeding ecology of Charadriiform chicks in agricultural grassland. *Ardea* **79**: 31–43.

**BirdLife International** 2004. *Birds in the European Union: A Status Assessment*. Wageningen: BirdLife International.

**Bolton, M., Tyler, G., Smith, K. & Bamford, R.** 2007. The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *J. Appl. Ecol.* **44**: 534–544.

**Bolton, M., Bamford, R., Blackburn, C., Cromarty, J., Eglington, S., Ratcliffe, N., Sharpe, F., Stanbury, A. & Jennifer, S.** 2011. Assessment of simple survey methods to determine breeding population size and productivity of a plover, the Northern Lapwing *Vanellus vanellus*. *Wader Study Group Bull.* **118**: 141–152.

**Briner, T., Airoldi, J.-P., Dellsperger, F., Eggimann, S. & Nentwig, W.** 2003. A new system for automatic radiotracking of small mammals. *J. Mammal.* **84**: 571–578.

**Burnham, K.P. & Anderson, D.R.** 2002. *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Berlin: Springer-Verlag.

**Chautan, M., Pontier, D. & Artois, M.** 2000. Role of rabies in recent demographic changes in red fox (*Vulpes vulpes*) populations in Europe. *Mammalia* **64**: 391–410.

**Cramp, S. & Simmons, K.E.L.** 1983. *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic. Vol. III: Waders to Gulls*. Oxford: Oxford University Press.

**Donald, P.F., Green, R.E. & Heath, M.F.** 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B* **268**: 25–29.

**Dunn, J.C., Gruar, D., Stoate, C., Szczur, J. & Peach, W.J.** 2016. Can hedgerow management mitigate the impacts of predation on songbird nest survival? *J. Environ. Manage.* **184**: 535–544.

**Eglington, S.E., Gill, J.A., Smart, M.A., Sutherland, W.J., Watkinson, A.R. & Bolton, M.** 2009. Habitat management and patterns of predation of Northern Lapwings on wet grasslands: the influence of linear habitat structures at different spatial scales. *Biol. Conserv.* **142**: 314–324.

**Eglington, S.M., Bolton, M., Smart, M.A., Sutherland, W.J., Watkinson, A.R. & Gill, J.A.** 2010. Managing water levels on wet grasslands to improve foraging conditions for breeding Northern Lapwing *Vanellus vanellus*. *J. Appl. Ecol.* **47**: 451–458.

**Ferguson-Lees, J. & Christie, D.A.** 2001. *Raptors of the World*. London: Christopher Helm.

**Gill, J.A., Alves, J.A., Sutherland, W.J., Appleton, G.F., Potts, P.M. & Gunnarsson, T.G.** 2014. Why is timing of bird migration advancing when individuals are not? *Proc. R. Soc. Lond. B* **281**: 20132161.

**Green, M., Piersma, T., Jukema, J. & De Goeij, P.** 2002. Radio-telemetry observations of the first 650 km of the migration of Bar-tailed Godwits *Limosa lapponica* from the Wadden Sea to the Russian Arctic. *Ardea* **90**: 71–80.

**Harrell, F.** 2015. *Regression Modeling Strategies: With Applications to Linear Models, Logistic and Ordinal Regression, and Survival Analysis*. New York: Springer.

**Holt, R.D.** 2002. Food webs in space: on the interplay of dynamic instability and spatial processes. *Ecol. Res.* **17**: 261–273.

**Hönisch, B., Artmeyer, C., Melter, J. & Tüllinghoff, R.** 2008. Telemetrische Untersuchungen an Küken vom Großen Brachvogel Numenius arquata und Kiebitz *Vanellus vanellus* im EU-Vogel-schutzgebiet Düsterdieker Niederung [In German with English summary]. *Vogelwarte* **46**: 39–48.

**Jefferson, R.G. & Grice, P.V.** 1998. The conservation of lowland wet grassland in England. In Joyce, C.B. & Wade, P.M. (eds) *European Wet Grasslands: Biodiversity, Management and Restoration*: 31–48. Chichester: Wiley.

**Junker, S., Krawczynski, R., Ehrnsberger, R. & Düttmann, H.** 2004. Habitat use and chick mortality of radio-tagged Lapwings *Vanellus vanellus* and Black-tailed Godwits *Limosa limosa* in the Stollhammer Wisch, Lower Saxony. *Wader Study Group Bull.* **103**: 14.

**Junker, S., Düttmann, H. & Ehrnsberger, R.** 2006. Schlupferfolg und Kükenmortalität beim Kiebitz (*Vanellus vanellus*) auf unterschiedlich gemanagten Grünlandflächen in der Stollhammer Wisch (Landkreis Wesermarsch, Niedersachsen) [In German with an English abstract]. *Osnabr. Natwiss. Mitt.* **32**: 111–122.

**Kaplan, E.L. & Meier, P.** 1958. Nonparametric estimation from incomplete observations. *J. Am. Stat. Assoc.* **53**: 457–481.

**Kays, R., Tilak, S., Crofoot, M., Fountain, T., Obando, D., Ortega, A., Kuemmeth, F., Mandel, J., Swenson, G. & Lambert, T.** 2011. Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest. *Comput. J.* **54**: 1931–1948.

**Kis, J., Liker, A. & Szekely, T.** 2000. Nest defence by Lapwings: Observations on natural behaviour and an experiment. *Ardea* **88**: 155–163.

**Laidlaw, R.A., Smart, J., Smart, M.A. & Gill, J.A.** 2013. Managing a food web: impacts on small mammals of managing grasslands for breeding waders. *Anim. Conserv.* **16**: 207–215.

**Laidlaw, R.A., Smart, J., Smart, M.A. & Gill, J.A.** 2015. The influence of landscape features on nest predation rates of grassland-breeding waders. *Ibis* **157**: 700–712.

**Langgemach, T. & Bellebaum, J.** 2005. Prädation und der Schutz bodenbrütender Vogelarten in Deutschland [in German with an English abstract]. *Vogelwelt* **126**: 259–298.

**MacDonald, M.A. & Bolton, M.** 2008. Predation on wader nests in Europe. *Ibis* **150**: 54–73.

**MacDonald, E.C., Camfield, A.F., Martin, M., Wilson, S. & Martin, K.** 2016. Nest-site selection and consequences for nest survival among three sympatric songbirds in an alpine environment. *J. Ornithol.* **157**: 393–405.

**Malpas, L.R., Kennerley, R.J., Hirons, G.J.M., Sheldon, R.D., Ausden, M., Gilbert, J.C. & Smart, J.** 2013. The use of predator-exclusion fencing as a management tool improves the breeding success of waders on lowland wet grassland. *J. Nat. Conserv.* **21**: 37–47.

**Mason, L.R. & Smart, J.** 2015. Wader chick condition is not limited by resource availability on wader-friendly lowland wet grassland sites in the UK. *Wader Study* **122**: 193–200.

**Mayfield, H.** 1961. Nesting success calculated from exposure. *Wilson Bull.* **73**: 255–261.

**Nakagawa, S. & Schielzeth, H.** 2013. A general and simple method for obtaining R2 from generalised linear mxed-effects models. *Methods Ecol. Evol.* **4**: 133–142.

**Nur, N., Holmes, A.L. & Geupel, G.R.** 2004. Use of survival time analysis to analyze nesting success in birds: an example using Loggerhead Shrikes. *Condor* **106**: 457–471.

**Peach, W.J., Thompson, P.S. & Coulson, J.C.** 1994. Annual and long-term variation in the survival rates of British Lapwings *Vanellus vanellus*. *J. Anim. Ecol.* **63**: 60–70.

**PECBMS** 2014. Trends of common birds in Europe, 2014 update.

**Powell, M.J.D.** 2009. *The BOBYQA algorithm for bound constrained optimization without derivatives*. Cambridge NA Report NA2009/06. Cambridge: University of Cambridge.

**R Core Team** 2013. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: http://www.R-project.org/ version 3.0.2.

**Redpath, S., Thirgood, S. & Leckie, F.M.** 2001. Does supplementary feeding reduce predation of Red Grouse by Hen Harriers? *J. Appl. Ecol.* **38**: 1157–1168.

**Reynolds, J., Short, M., Porteus, T., Rodgers, B. & Swan, M.** 2007. *The GWCT Mink Raft*. Fordingbridge: The Game and Wildlife Conservation Trust UK. Available at: www.gwct.org.uk

**Richards, S.A., Whittingham, M.J. & Stephens, P.A.** 2011. Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. *Behav. Ecol. Sociobiol.* **65**: 77–89.

**Rickenbach, O., Grüebler, M.U., Schaub, M., Koller, A., Naef-Daenzer, B. & Schifferli, L.** 2011. Exclusion of ground predators improves Northern Lapwing *Vanellus vanellus* chick survival. *Ibis* **153**: 531–542.

**Roodbergen, M., van der Werf, B. & Hötker, H.** 2012. Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: review and meta-analysis. *J. Ornithol.* **153**: 53–74.

**Schaub, M.** 2009. Evaluation of bias, precision and accuracy of mortality cause proportion estimators from ring recovery data. In Thompson, D.L., Cooch, E.G. & Conroy, M.J. (eds) *Modeling Demographic Processes in Marked Populations*: 1081–1097. New York: Springer.

**Schekkerman, H., Teunissen, W. & Oosterveld, E.** 2009. Mortality of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* chicks in wet grasslands: Influence of predation and agriculture. *J. Ornithol.* **150**: 133–145.

**Schielzeth, H.** 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**: 103–113.

**Schifferli, L., Rickenbach, O., Koller, K. & Grüebler, M.** 2009. Massnahmen zur Förderung des Kiebitzes *Vanellus vanellus* im Wauwilermoos (Kanton Luzern): Schutz der Nester vor Landwirtschaft und Prädation [In German with an English summary: Nest protection from agriculture and predation to improve nest and chick survival of the Northern Lapwing *Vanellus vanellus* in Swiss farmland]. *Ornithol. Beob.* **106**: 311–326.

**Schoppenhorst, A.** 2004. Breeding success and clutch loss of grassland birds in the wet grassland area of the Bremer Becken – initial results of the breeding season 2002. *Wader Study Group Bull.* **103**: 15.

**Setchfield, R.P. & Peach, W.J.** 2016. The influence of crop tiller density on the breeding performance of a cereal-nesting specialist. *J. Appl. Ecol.* **53**: 1430–1439.

**Seymour, A.S., Harries, S., Ralston, C. & White, P.C.L.** 2003. Factors influencing the nesting success of Lapwings *Vanellus vanellus* and behaviour of Red Fox *Vulpes vulpes* in Lapwing nesting sites. *Bird Study* **50**: 39–46.

**Sharpe, F., Clark, J. & Leech, D.** 2008. Does variation in demographic parameters account for regional variation in Northern Lapwing *Vanellus vanellus* population declines across Great Britain? *Bird Study* **55**: 247–256.

**Sharpe, F., Bolton, M., Sheldon, R. & Ratcliffe, N.** 2009. Effects of color banding, radio tagging, and repeated handling on the condition and survival of Lapwing chicks and consequences for estimates of breeding productivity. *J. Field Ornithol.* **80**: 101–110.

**Smart, J., Gill, J.A., Sutherland, W.J. & Watkinson, A.R.** 2006. Grassland-breeding waders: identifying key habitat requirements for management. *J. Appl. Ecol.* **43**: 454–463.

**Teunissen, W., Schekkerman, H. & Willems, F.** 2005. *Predatie bij Weidevogels: Op Zoek Naar de Mogelijke Effecten van Predatie op de Weidevogelstand* (in Dutch With an English Summary). Wageningen: Sovon Vogelonderzoek Nederland.

**Teunissen, W., Schekkerman, H. & Willems, F.** 2006. Predation on meadowbirds in the Netherlands – results of a four-year study. *Osnabr. Natwiss. Mitt.* **32**: 137–143.

**Teunissen, W., Schekkerman, H., Willems, F. & Majoor, F.** 2008. Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis* **150**: 74–85.

**Thorstad, E.B., Rikardsen, A.H., Alp, A. & Økland, F.** 2013. The use of electronic tags in fish research: an overview of fish telemetry methods. *Turk. J. Fish. Aquat. Sci.* **13**: 881–896.

**Thorup, O.** 2006. *Breeding Waders in Europe 2000*. UK International Wader Studies 14: International Wader Study Group.

**Walters, J.R.** 1990. Anti-predatory behavior of Lapwings: field evidence of discriminative abilities. *Wilson Bull.* **102**: 49–70.

**Webbon, C., Baker, P.J. & Harris, S.** 2004. Faecal density counts for monitoring changes in red fox numbers in rural Britain. *J. Appl. Ecol.* **41**: 768–779.

**Wilson, A.M., Vickery, J.A., Langston, R.H.W., Smallshire, D., Wotton, S. & Vanhinsbergh, D.** 2005. Changes in the numbers of breeding waders on lowland wet grasslands in England and Wales between 1982 and 2002. *Bird Study* **52**: 55–69.

Received 19 May 2015;
revision accepted 26 July 2017.
Associate Editor: Christian Rutz.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1**. Photographs of a typical ARTS set-up.

**Table S1.** Avian predators found on lowland wet grassland.

**Table S2.** Site-year specific chick survival estimates.

**Table S3.** Recovery rates of remains from predated chicks.

**Table S4**. Percentages of recovered tags attributed to different predator types.

**Table S5**. Full results of AICc model selection.

**Table S6.** Mortality statistics compared between wader chick survival studies.

**Table S7.** Predation summary for Redshank chicks monitored with Lapwing chicks.

**Table S8.** Body condition indices for tagged and untagged Lapwing chicks.

**Appendix S1**. Detection of predation and diel patterns of signal strength in ARTS data.

**Appendix S2**. Cost-benefit analysis of ARTS.

# Supplementary Materials

Supplementary Materials for paper **VII** are available online:

http://doi.org/10.1111/ibi.12523

Figure S1

Tables S1–S8

Appendix S1–S2

# PAPER VIII

## The use of predator-exclusion fencing as a management tool improves the breeding success of waders on lowland wet grassland

**Malpas, L.R.**, Kennerley, R.J., Hirons, G.J.M., Sheldon, R.D., Ausden, M., Gilbert, J.C. & Smart, J.

*Journal for Nature Conservation* (2013)*,* **21**: 37–47.

http://doi.org/10.1016/j.jnc.2012.09.002

© Graham Hirons

Journal for Nature Conservation 21 (2013) 37–47

Contents lists available at SciVerse ScienceDirect

Journal for Nature Conservation

journal homepage: www.elsevier.de/jnc

# The use of predator-exclusion fencing as a management tool improves the breeding success of waders on lowland wet grassland

Lucy R. Malpas*, Rosalind J. Kennerley, Graham J.M. Hirons, Rob D. Sheldon, Malcolm Ausden, Joanne C. Gilbert, Jennifer Smart

*The Royal Society for the Protection of Birds, UK Headquarters, The Lodge, Sandy, Beds. SG19 2DL, UK*

ARTICLE INFO

*Article history:*
Received 16 August 2012
Received in revised form
14 September 2012
Accepted 22 September 2012

*Keywords:*
Anti-predator fencing
Badger
Fox
Lapwing
Mammalian predation
Nest survival
Non-lethal methods
Predator control

ABSTRACT

Waders breeding on lowland wet grassland have undergone dramatic declines across Europe in recent decades. Few species now achieve the levels of breeding success required for population stability and recovery, with predation from large mammals acting as a key compounding factor limiting nest survival and productivity. Predator management through lethal control is often controversial, yet alternative non-lethal methods are little tested in the context of grassland breeding waders. Excluding predators through the use of electric fences has led to improvements in nest and chick survival in other habitats. To test the applicability of this method to lowland wet grassland we constructed predator-exclusion fences on sites across the UK and, with Lapwing *Vanellus vanellus* as a study species, used historical and contemporary data to test whether excluding large mammalian predators leads to an increase in wader nest survival and productivity, and whether effects differ between fence designs. Lapwing nest survival was significantly higher in the presence of any type of predator-exclusion fence, with significantly fewer nests predated each day. Overall productivity also improved, with significantly higher numbers of chicks fledged per pair in years when fences were operational. Different designs and methods of powering fences resulted in different levels of success, with combination design fences and those powered by mains electricity performing best. Excluding large mammalian predators from areas of lowland wet grassland with predator-exclusion fencing successfully improves Lapwing nest survival and productivity, allowing breeding success to exceed the levels required for population recovery. Other wader species breeding in the same habitat are also likely to benefit from the increased protection from predation provided by fences. Predator-exclusion fencing is therefore an effective management tool for protecting restricted and declining populations of breeding waders on lowland wet grassland.

## Introduction

Many waders breeding on lowland wet grassland in Britain and Europe (Lapwing *Vanellus vanellus*, Redshank *Tringa totanus*, Curlew *Numenius arquata*, Black-tailed Godwit *Limosa limosa* and Snipe *Gallinago gallinago* L. in particular) have undergone significant breeding population declines and range contractions in recent decades (Donald et al. 2006; Henderson et al. 2002; PECBMS 2012; Wilson et al. 2005). Historical declines were driven largely by the substantial degradation and loss of suitable breeding areas through wetland drainage and agricultural intensification (e.g. Fuller et al. 1995; Taylor & Grant 2004), and nature reserves or land managed by agri-environmental schemes are now increasingly important refuges for these species in lowland UK (Ausden & Hirons 2002; Wilson et al. 2004). There has been much research into the management of lowland wet grassland reserves to increase habitat favourability for nesting waders (Eglington et al. 2010, 2009b, 2007; Smart et al. 2006). However, despite evidence that improvements in habitat management have benefitted wader populations (Ausden & Hirons 2002), such measures have so far failed to facilitate population recovery (Wilson et al. 2005). It is thought that predation, predominantly from mammalian predators, acts as a compounding factor on wader populations, particularly those restricted to small areas of suitable breeding habitat, and may prevent populations from recovering even when habitat conditions are favourable (Ausden et al. 2009; MacDonald & Bolton 2008a).

Predation is a key factor in determining wader breeding success (Bellebaum & Bock 2009; Eglington et al. 2009a; Grant et al. 1999; Grimm 2005; Teunissen et al. 2008) and experimental studies

---

* Corresponding author at: Conservation Science, The Royal Society for the Protection of Birds, UK Headquarters, The Lodge, Sandy, Beds. SG19 2DL, UK.
Tel.: +44 07736 793292; fax: +44 01493 700645.
*E-mail addresses:* lucy.malpas@rspb.org.uk (L.R. Malpas), rosalindkennerley@hotmail.com (R.J. Kennerley), graham.hirons@rspb.org.uk (G.J.M. Hirons), robert.sheldon@rspb.org.uk (R.D. Sheldon), malcolm.ausden@rspb.org.uk (M. Ausden), jo.gilbert@rspb.org.uk (J.C. Gilbert), jennifer.smart@rspb.org.uk (J. Smart).

1617-1381/$ – see front matter © 2012 Elsevier GmbH. All rights reserved.
http://dx.doi.org/10.1016/j.jnc.2012.09.002

indicate beneficial effects of reducing the abundance of avian and mammalian predators on the subsequent survival of wader nests (Bolton et al. 2007; Fletcher et al. 2010; Nordström et al. 2003; Smith et al. 2010; Tharme et al. 2001). Lethal control methods are however time-consuming, highly skilled and often controversial activities, and rarely succeed in lowering target predator densities to an extent that completely removes the threat of predation from these species (Bolton et al. 2007; Smith et al. 2010), partly due to rapid immigration from surrounding populations (Rushton et al. 2006). The removal of top predators may also result in mesopredator-release, where the relaxation of prey competition or direct predation pressure allows populations of other predator species to increase (Crooks & Soulé 1999; Ellis-Felege et al. 2012; Latham 1952; Ritchie & Johnson 2009).

Alternative non-lethal control methods may involve habitat manipulation to channel predator activity away from breeding birds and to encourage them to nest at higher densities (Bodey et al. 2010; Gibbons et al. 2007; Seymour et al. 2003), or methods which directly prevent predators from reaching colonies or individual nests (predator-exclusion fencing or nest exclosures, e.g. Isaksson et al. 2007; Mayer & Ryan 1991). Techniques to protect individual nests are successful in increasing hatching success for small populations of waders such as Lapwing (Isaksson et al. 2007), Dunlin *Calidris alpina* L. (Pauliny et al. 2008) and Piping Plover *Charadrius melodus* Ord. (Murphy et al. 2003a) but are unsuitable for species that rely on nest crypsis, where nest exclosures result in high levels of adult mortality (Isaksson et al. 2007; Murphy et al. 2003b; Smith et al. 2011). Individual nest protection is also impractical for sites with large wader populations, and cannot improve the survival of precocial chicks when predation is a key cause of mortality (Smith et al. 2011). In contrast, predator-exclusion fencing – which can be used to enclose large areas and can deter large mammalian predators in two ways: either by presenting a physical barrier or by modifying behaviour through the use of unpleasant stimuli such as a small electric shock (Poole & McKillop 2002) – may be a more practical management tool for localised populations (Jackson 2001; LaGrange et al. 1995; Mayer & Ryan 1991; Rickenbach et al. 2011). A recent review of multiple species and habitats identified a significant 92% increase in avian hatching success with the use of predator-exclusion fencing (Smith et al. 2011). Fencing has also led to improvements in overall wader breeding success (i.e. the number of fledglings produced) in arable and mixed farmland habitats (Rickenbach et al. 2011; Schifferli et al. 2009). The applicability of this method to the protection of waders breeding on lowland wet grassland is however unknown.

In this trial, we test the effect of erecting predator-exclusion fencing on lowland grassland wader nesting success and overall productivity, using Lapwing as a study species. Lapwing breeding ecology is well-studied and the species is relatively easy to locate and monitor as it nests in short, open vegetation. Although other waders nesting in lowland wet grassland habitats have different nesting requirements (preferring to nest in longer vegetation; Durant et al. 2008), all are subject to similar predation rates (Green 1988; MacDonald & Bolton 2008b; Mason & Macdonald 1976). These factors mean that Lapwing is an ideal study species to use as an indicator of whether the exclusion of large mammalian predators could facilitate lowland wader population recovery.

## Methods

### Study sites

Ten lowland wet grassland sites managed as extensive grazing marshes in England, Wales and Northern Ireland were selected to test the general applicability of predator-exclusion fencing over multiple years across lowland habitats (Fig. 1 and Table 1). All sites were nature reserves or protected areas, selected for inclusion based on the presence of high levels of large predatory mammal activity (predominantly red fox *Vulpes vulpes*, but also European badger *Meles meles*) and the identification of mammalian predation as the major cause of low wader breeding success (nest camera images of 141 predated wader nests on these sites plus five other UK lowland wet grassland reserves between 2003 and 2009 indicated 63% of nests predated by foxes, 13% predated by badgers; RSPB unpublished data).

At some sites lethal control of foxes before the wader breeding season (late winter–early spring) and/or carrion crows *Corvus corone* during the wader breeding season (March–June) was conducted in addition to fencing to protect vulnerable breeding populations outside of the fenced area (Table 1, "additional control"). Fox control was conducted at night by trained marksmen and carrion crows were trapped with Larsen cage traps, both operating according to legal welfare requirements. Badgers are protected by law in the UK, so no lethal control of this species was performed.

Routine habitat management was also conducted at each site to maintain sward structures and hydrological conditions required by breeding Lapwing and other waders (see Eglington et al. 2010, 2007; Smart et al. 2006 for the evidence informing these management guidelines). This trial is therefore a practical evaluation of predator-exclusion fencing as a non-lethal predator control technique in the presence of additional lethal control of foxes and crows and ongoing habitat management practises characterising lowland wet grassland areas managed for breeding waders in the UK.

### Fence specifications

Predator-exclusion fences were constructed by trained site staff or specialist contractors and were of two designs: stranded electrical fencing (hereafter 'stranded' fencing); and, a combination of electric and standard stock fencing (hereafter 'combination' fencing; Table 1, see Appendix 1 for fence specifications). Stranded fencing was the design of choice used at the majority of sites as it was less expensive (£1.50–£3.50 per m, compared to GBP£10–£12 per m for combination fencing; Ausden et al. 2011), less time consuming to erect and more flexible in design. It was however less durable (lasting c.10 years) and was limited when enclosing large areas. Combination fencing, by providing a more formidable and durable barrier (>20 years lifetime), was used at sites where previous monitoring indicated the presence of badgers as a predator of Lapwing nests, and/or where stranded fencing would have presented an insufficient barrier to grazing stock.

Fence structures were permanent and operational February–July, with the exception of Greylake where a stranded fence was only in place for the wader breeding season. Some permanent fences were deactivated or intentionally breached by opening gateways in the winter to allow movements of non-target species (brown hare *Lepus europaeus*, otter *Lutra lutra*). Electricity was supplied via battery or mains power from the UK National Grid (Table 1).

Fences were checked weekly for signs of damage: fault-finding devices were used to identify any voltage loss, in which case the entire fence length was checked to determine the source (most often vegetation that had fallen against live wires). Vegetation under and adjacent to the fence line was controlled either by cattle or sheep grazing, the placement of weed-control matting, the application of a broad-spectrum systemic herbicide (glyphosate) or regular mowing.

**Fig. 1.** Locations of ten lowland wet grassland sites where predator-exclusion fences were constructed and where Lapwing breeding success was monitored for this study.

Foxes or signs of foxes were encountered within fenced areas at Greylake in 2010 and Morfa Dinlle in 2011. These intrusions were attributed to errors during fence set-up (foxes present inside the fenced area when the temporary fence was erected at Greylake) or oversights during fence maintenance (gate left open for one night at Morfa Dinlle). Of the three foxes that breached the fence at Greylake in 2010, one was lethally controlled and the other two were chased out. One fox entered through the open gate at Morfa Dinlle, but was only present for one night (not present the next morning when the gate was shut, but prints found in soft mud). All intrusions were dealt with promptly before Lapwing nests were predated. Any management of fox intrusions was considered part of the regular maintenance of the fenced area and was not counted as additional control.

### *Monitoring Lapwing breeding success*

A large number of fieldworkers were involved in the collection of data for this trial due to the number of years involved and geographical distribution of sites. To standardise field procedures and data collection, fieldworkers were provided with a detailed manual prior to the onset of fieldwork which described the methods and included standard reporting forms.

#### *Nest survival*

Lapwing nests were intensively monitored to determine survival rates and causes of nest failure, with study sites split into two groups for analysis (Table 1). At Group 1 sites, fences enclosed a proportion of the lowland wet grassland habitat suitable for wader

**Table 1**

Summary of sites where predator-exclusion fences were erected, showing the type of fence (Str = stranded, Com = combination), power supply (Bat = battery, Mns = mains) and the area of wader breeding habitat enclosed by fences (the area un-enclosed is also indicated for Group 1 sites). Most fences were continuous around the area shown, but for some sites a barrier to continuous construction (e.g. a ditch) meant that multiple adjacent enclosures were required (areas of separate enclosures shown in parentheses). Also shown are site groupings for the nest survival analysis (Group 1 = within year comparisons of inside versus outside fenced area, Group 2 = between year comparisons of before versus after fence construction), the years of nest survival data available for each site, the number of nests monitored, the years of productivity data available for each site and the number of Lapwing pairs present. Years range from 2004 (04) to 2011 (11). No nest survival data was available for Portmore Lough (na). Years in which fences were operational are highlighted in bold; years in which additional predator control was conducted are indicated by *.

| Site | Type:power | Area (ha) | | Analysis | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Fenced | Unfenced | Group | Nest survival | No. nests[a] | Productivity | Pairs[b] |
| Elmley Marshes | Str:Bat | 65 (26 + 39) | 178 | 1 | **09***,**10***,**11*** | **64**/140 | 07*,08*,**09***,**10***,**11*** | 67 |
| Morfa Dinlle | Com:Bat | 28 | 42 | 1 | **10**,**11** | **30**/8 | 09,**10**,**11** | 25 |
| Otmoor | Com:Mns | 43 | 257 | 1 | **10***,**11*** | **54**/67 | 07*,08*,09*,**10***,**11*** | 55 |
| Ouse Washes | Str:Mns | 44 (22 + 22) | 32 | 1 | **08*** | **30**/7 | **08*** | 21 |
| Ynys-Hir | Str:Mns | 14 | 204 | 1 | **08**,**09**,**10** | **88**/58 | 04,05,**06**,**07**,**08**,**09**,**10**,**11** | 71 |
| Greylake | Str:Bat | 50 | 58 | 1 | **10**,**11*** | **51**/9 | 05*,06*,07*,**08***,**09***,**10**,**11*** | 13 |
| | | | | 2 | 05*,06*,07*,**08***,**09*** | 45/**21** | | |
| Newton Marsh | Com:Mns | 65 | | 2 | 08,09,**10**,**11** | 31/**28** | 08,09,**10**,**11** | 31 |
| Old Moor | Str:Bat | 7 | | 2 | 08,**09**,**10** | 18/**17** | 08,**09**,**10** | 16 |
| Valley Wetlands | Com:Bat | 3.5 | | 2 | 09*,10*,**11*** | 10/**2** | 09*,10*,**11*** | 5 |
| Portmore Lough | Com:Mns | 25 (10 + 15) | 15 | na | na | na | 06,07,08,**09**,**10**,**11** | 10 |

[a] Total number of nests monitored inside (bold)/outside fences (normal text) for Group 1 sites, and before (normal text)/after (bold) fence construction for Group 2 sites.

[b] Mean annual number of Lapwing pairs breeding on each site during the productivity years listed.

breeding, with an area of similar habitat left unfenced. Lapwing nests were monitored both inside and outside the fenced area to allow within year comparisons (Table 1). At Group 2 sites, the entire area of lowland wet grassland supporting breeding waders was enclosed by fencing, so only between-year comparisons of Lapwing nest survival (before versus after fence construction) were possible. Different years of monitoring data from Greylake were included in both analysis groups (Table 1) as although Lapwing nested outside the fence in 2010 and 2011, all pairs nested within the fenced area in 2008 and 2009. Across all sites and years a total of 778 nests were monitored: 317 inside fences and 289 outside fences on Group 1 sites; 68 before fence construction and 104 after fence construction on Group 2 sites.

Nests were located from a distance (usually from a vehicle) by observing adult Lapwing behaviour, and were marked with a cane placed >20 paces away to aid relocation but avoid attracting predators (Galbraith 1987). Active nests were monitored remotely every 3–4 days to determine the presence of incubating adults, in the absence of which nests were checked in person and the number and temperature of eggs (warm or cold to touch), or the number of hatched chicks recorded. Clutch fate and the cause of failure for unsuccessful nests (predation, flooding, trampling or desertion) were determined with reference to standard criteria defined within the methods manual provided to all fieldworkers.

For the purposes of this trial, nest predation was classified as a binary outcome, with nests recorded as failing due to predation or not failing due to predation (the latter including successful nests and nests failing due to flooding, trampling or desertion; Eglington et al. 2009a). Although high predation pressures may act to increase nest desertion, only 2% of the total nests monitored were classed as having been abandoned and there was no substantial difference in desertion rates between fenced and unfenced areas (% nests deserted inside fence = 2%, outside fence = 2% for Group 1 sites, before fence = 0%, after fence = 4% for Group 2 sites). Nests were considered successful if at least one egg hatched (Bolton et al. 2007). Nest exposure days (Mayfield 1961, 1975) were calculated as the interval from the date the nest was found to the date it failed, rounded to the nearest whole day. Where the exact date of failure was uncertain, the failure date was estimated as being halfway between the last known active date and the date when the nest was first known to have failed (Manolis et al. 2000).

### *Productivity*

Deterministic population modelling by MacDonald and Bolton (2008b) indicates that 0.6–0.8 fledged chicks per Lapwing pair are required to maintain a stable population. To examine whether excluding large mammalian predators enabled breeding Lapwing to reach these levels of productivity, annual surveys were conducted at each site to estimate overall breeding success (Table 1). Lapwing productivity (no. of chicks fledged per pair) was estimated using methods described in detail by Bolton et al. (2011). Following this method, the total number of adults and the growth stage of visible chicks was assessed from vantage points during 4–5 survey visits made to each site between mid-March and early-July. Productivity was calculated as the total number of well-grown and fledged chicks recorded across all visits divided by the number of breeding pairs (half the maximum number of adults recorded on visits between mid-April and the end of May). Surveys were conducted at the site scale for both Group 1 and Group 2 sites, as the mobility of adult Lapwing and fledged chicks prevented the identification of original nesting or hatching locations. Therefore, only comparisons of Lapwing productivity between years when fences were present and years before fences were possible (no. years studied before fences = 1–3, no. years studied after fence construction = 1–6; Table 1).

## *Statistical analysis*

### *Nest survival*

The daily predation rate of nests (daily probability of predation) was modelled following the principles outlined by Aebischer (1999), using generalised linear mixed models (GLMMs) with binomial error distributions, logit link functions and the Laplace approximation of likelihood (Bolker et al. 2009), fitted using the lme4 package in R (Bates & Maechler 2009; R Development Core Team 2009). For both Group 1 and Group 2 sites, the random terms of study year nested within site were included to control for the non-independence of nests in each year at each site.

For Group 1 sites, four models were fitted in addition to the null model, each including one of the nested explanatory variables listed in Table 2 singly. These variables were created to test for the interactions between e.g. fence presence/absence and fence type, where the type of fence was only relevant for nests inside the fenced area. A variable testing for the interaction between the

**Table 2**
Nested explanatory variables combining the effects of fence presence or absence, fence type, fence power method and the presence or absence of additional predator control outside the fence, used in analysis of Lapwing nest survival and annual Lapwing productivity. Shown are variable names, category levels and the inclusion of variables in each analysis: NS1 = nest survival Group 1 sites (inside versus outside fences); NS2 = nest survival Group 2 sites (before versus after fence construction); PR = productivity (before versus after fence construction, all sites). Category levels in square brackets replace "Outside" and "Inside" for NS2 and PR analyses. The first category listed for each variable is the reference category used in analysis.

| Variable | Category levels | Analysis |
|---|---|---|
| FENCE | 1: Outside [before] fence<br>2: Inside [after] fence | NS1, NS2, PR |
| FENCE:TYPE | 1: Outside fence<br>2: Inside fence, stranded design<br>3: Inside fence, combination design | NS1 |
| FENCE:POWER | 1: Outside fence<br>2: Inside fence, battery powered<br>3: Inside fence, mains electricity powered | NS1 |
| FENCE:CONTROL | 1: Outside [before] fence, no additional predator control<br>2: Outside [before] fence, additional predator control<br>3: Inside [after] fence, no additional predator control<br>4: Inside [after] fence, additional predator control | NS1, PR |

presence or absence of fencing and additional predator control (FENCE:CONTROL; Table 2) was included to allow for the possibility of additional lethal control artificially increasing the effectiveness of fences and/or the survival of nests outside fences. Pairwise chi-squared likelihood ratio tests were conducted between models of differing complexity to test the contribution of additional levels of nesting. The best fit model was then identified as the model which was a significantly better fit to the response variable than the null model, and where increasing levels of complexity did not improve the model fit. Due to the smaller sample size of sites available in Group 2 and the lack of suitable variation in fence type, power method and additional control at these sites, analysis was limited to the investigation of whether fence presence or absence had any effect on nest survival. One model containing a factor indicating whether nests were monitored before or after fence construction (Table 2) was compared against the null model, using the methods described above. Tukey HSD post hoc tests were preformed for both Group 1 and Group2 site analyses to examine differences between multiple category levels of nested explanatory variables supported by the best fit models using the glht function from the multcomp package in R (Hothorn et al. 2008).

Hatching successes of less than 50% are likely to be unsustainable for Lapwing populations given plausible levels of chick survival (MacDonald & Bolton 2008b: deterministic modelling, assuming 25% chick survival). The predation-dependent hatching success of nests from this study – the probability of a nest surviving predation during the incubation period (31 days; Galbraith 1988) – was calculated as the daily survival rate (DSR) raised to the power of 31, where DSR = 1 − daily probability of predation.

*Productivity*

The effect of the presence of fencing on annual Lapwing productivity (fledged chicks per pair) at both Group 1 and Group 2 sites together was investigated using linear models in R (R Development Core Team 2009), with the response variable (site-level Lapwing productivity) transformed with $\ln[x+1]$ to conform to assumptions of normality. Two models were run in addition to the null model and included each of the nested explanatory variables shown in Table 2 singly. As in the Group 1 nest survival analysis, the FENCE:CONTROL variable (Table 2) was included to allow for the possibility of additional lethal control artificially increasing the effectiveness of fences and/or the breeding success of Lapwing pairs outside fences. The effects of fence type and power method were not considered relevant for inclusion in this site-level analysis. Model selection involved pairwise chi-squared likelihood ratio tests and followed methods outlined for the nest survival analysis above. The inclusion of study site as a random term (i.e. the use of linear mixed models) was not considered necessary, as this term was found to explain negligible amounts of variation in the response variable during initial analyses (null linear mixed model run in R using the lme4 package: variance of site as random effect = <0.001; residual variance = 0.096). In this situation the effect estimates and standard errors calculated by linear mixed models will equate to those reported by linear models.

## Results

### *The impact of predator-exclusion on Lapwing nest survival*

There were two best fit nest survival models for Group 1 sites, one examining the difference in daily predation rate between nests outside fences and inside fences of different types, the other examining the difference in daily predation rate between nests outside fences and inside fences powered by different methods (Tables 2 and 3). Average daily predation rates for Lapwing nests were significantly lower inside fences of any type (stranded: $z = -4.96$, $P < 0.001$, combination: $z = -5.21$, $P < 0.001$) and any power method (battery: $z = -2.95$, $P < 0.01$, mains-electricity: $z = -7.03$, $P < 0.001$) compared to outside fences (Table 3 and Fig. 2a, b). However, nests inside stranded fences were significantly more likely to be predated compared to nests inside combination fences ($z = 2.63$, $P < 0.05$; Fig. 2a), and nests inside battery powered fences were significantly more likely to be predated compared to nests inside mains-electricity powered fences ($z = 3.15$, $P < 0.01$; Fig. 2b). Results of the nest survival analysis for Group 2 sites were similar, with the daily predation rate for nests significantly lower in years after fence construction compared to years prior to construction (Table 3 and Fig. 2c).

Models comparing daily predation rates inside and outside fences in the presence or absence of additional predator control at Group 1 sites were not supported (Table 3), indicating that lethal predator control did not increase fence effectiveness nor did it reduce the probability of predation for nests outside fenced areas.

The values shown in Fig. 2a and b relate to predation-dependent hatching success estimates on Group 1 sites of 90% (+4/−6% SE) inside combination and 69% (+7/−9% SE) inside stranded fence types compared to 34% (+11/−10% SE) outside fences, and 86% (+4/−6% SE) inside mains-electricity powered and 63% (+9/−11% SE) inside battery powered fences compared to 37% (±11% SE) outside fences. Predation dependent hatching success estimates for Group 2 sites (values from Fig. 2c), equate to 84% (+6/−10% SE) after fence construction compared to 34% (±11% SE) before. Nests within predator-exclusion fences of any type and power method therefore consistently exceeded the 50% minimum sustainable level of predation-dependent hatching success necessary for population recovery given plausible levels of chick survival, whilst predation-dependent hatching success outside fences or before construction was substantially lower than this minimum sustainable level.

### *The impact of predator-exclusion on annual Lapwing productivity*

Lapwing productivity in years before predator-exclusion fences averaged 0.23 chicks fledged per pair (+0.07/−0.07 SE,

**Table 3**

Results of binomial errors GLMMs of factors affecting nest survival for Group 1 and Group 2 sites, with each model containing a single nested explanatory variable from Table 2. Shown are the log likelihood (logLik) values with associated degrees of freedom (df) for each model. Chi-squared statistics ($\chi^2$) and degrees of freedom (df) of pairwise likelihood ratio (LR) tests are shown for comparisons between nested models listed in the first column and simpler models listed under 'Model comparisons'. Blank cells for model comparisons indicate models were not nested so LR tests were not performed. Significant differences between models are highlighted in bold, with the better model being that with the higher (less negative) logLik value. Results are reported from the best fit model for each analysis (shaded grey).

| **GROUP 1** | | | Model comparisons | |
|---|---|---|---|---|
| | | | NULL | FENCE |
| Model | logLik | df | $\chi^2$ (df) | $\chi^2$ (df) |
| NULL | -318.8 | 3 | | |
| FENCE | -289.6 | 4 | **58.5 (1)**$^{***}$ | |
| FENCE:TYPE | -285.4 | 5 | **66.8 (2)**$^{***}$ | **8.3 (1)**$^{**}$ |
| FENCE:POWER | -284.5 | 5 | **68.6 (2)**$^{***}$ | **10.1 (1)**$^{**}$ |
| FENCE:CONTROL | -288.0 | 6 | **61.6 (3)**$^{***}$ | 3.1 (2) $^{ns}$ |

| Best fit model results | Category level | Estimate | SE | Wald *Z* |
|---|---|---|---|---|
| FENCE:TYPE | Outside fence *(intercept)* | **-3.34** | **0.292** | **-11.42**$^{***}$ |
| | Inside fence, stranded design | **-1.06** | **0.215** | **-4.96**$^{***}$ |
| | Inside fence, combination design | **-2.38** | **0.456** | **-5.21**$^{***}$ |
| Random effect: YEAR:SITE, variance = 0.313; SITE, variance = 0.269 | | | | |
| FENCE:POWER | Outside fence *(intercept)* | **-3.42** | **0.296** | **-11.58**$^{***}$ |
| | Inside fence, battery powered | **-0.76** | **0.259** | **-2.95**$^{**}$ |
| | Inside fence, mains electricity powered | **-1.94** | **0.276** | **-7.03**$^{***}$ |
| Random effect: YEAR:SITE, variance = 0.375; SITE, variance = 0.250 | | | | |

| **GROUP 2** | | | Model comparisons |
|---|---|---|---|
| | | | NULL |
| Model | logLik | df | $\chi^2$ (df) |
| NULL | -84.08 | 3 | |
| FENCE | -79.87 | 4 | **8.4 (1)**$^{**}$ |

| Best fit model results | Category level | Estimate | SE | Wald *Z* |
|---|---|---|---|---|
| FENCE | Before fence *(intercept)* | **-3.33** | **0.314** | **-10.62**$^{***}$ |
| | After fence | **-1.87** | **0.573** | **-3.27**$^{**}$ |
| Random effect: YEAR:SITE, variance = 0.557; SITE, variance < 0.001 | | | | |

*P*-values: not significant ($^{ns}$), <0.05 ($^{*}$), <0.01 ($^{**}$), <0.001 ($^{***}$).

**Table 4**

Results of linear models of factors affecting annual Lapwing productivity across all sites. Shown are the log likelihood (logLik) values with associated degrees of freedom (df) for each model and the results of chi-squared likelihood ratio (LR) tests between nested models, with significant differences between models highlighted in bold (the better model being that with the higher, less negative logLik value). Annual productivity was transformed with ln[$x$ + 1] prior to analysis to conform to normality assumptions. Other details as in Table 3.

| | | | Model comparisons | |
|---|---|---|---|---|
| | | | NULL | FENCE |
| Model | logLik | df | $\chi^2$ (df) | $\chi^2$ (df) |
| NULL | -10.6 | 2 | | |
| FENCE | -0.4 | 3 | **20.3 (1)**$^{***}$ | |
| FENCE:CONTROL | 1.2 | 5 | **23.6 (3)**$^{***}$ | 3.3 (2) $^{ns}$ |

| Best fit model results | Category level | Estimate | SE | *t value* |
|---|---|---|---|---|
| FENCE | Before fence *(intercept)* | **0.21** | **0.057** | **3.65**$^{***}$ |
| | After fence | **0.37** | **0.075** | **4.96**$^{***}$ |

*P*-values: not significant ($^{ns}$), <0.05 ($^{*}$), <0.01 ($^{**}$), <0.001 ($^{***}$).

back-transformed from ln[$x$ + 1]): substantially lower than the estimated 0.6–0.8 chicks per pair required to maintain population stability (Table 4 and Fig. 3). After fence construction however, mean annual productivity increased significantly to 0.79 chicks per pair (+0.14/−0.13 SE; Fig. 3).

The model comparing productivity in the presence or absence of fences and additional predator control was not supported (Table 4), again indicating that lethal predator control did not influence fence effectiveness nor did it increase the breeding success of Lapwing pairs in the absence of fencing.

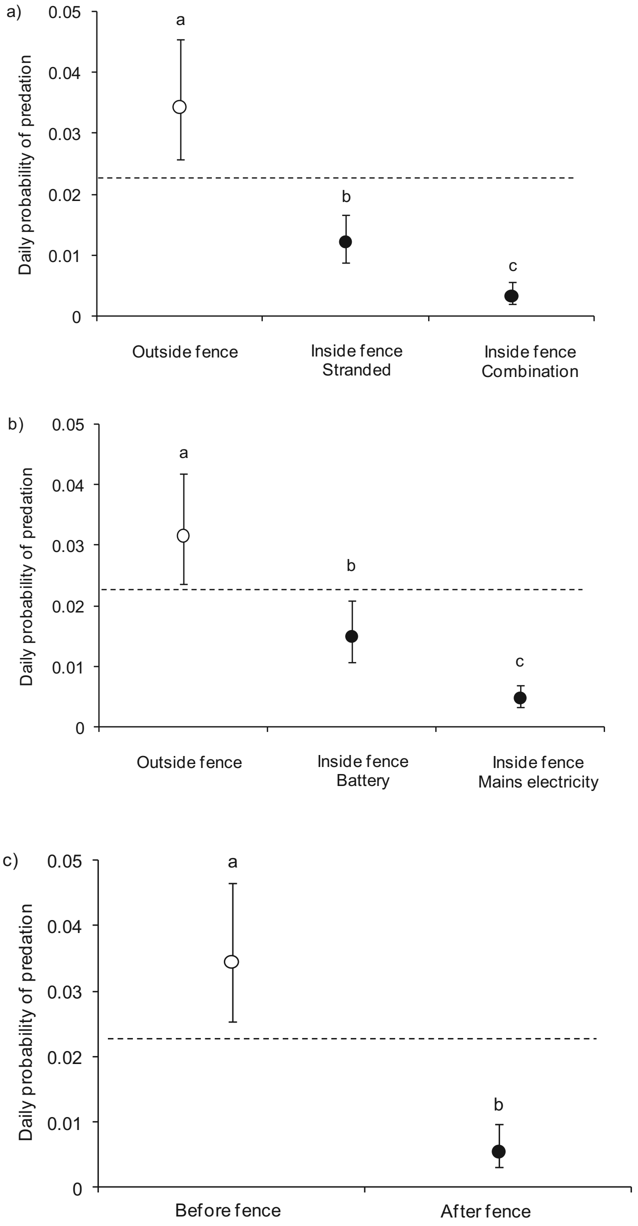


**Fig. 2.** Mean daily probability of predation ± standard error (SE) calculated from best fit models and back-transformed from logits for Lapwing nests (a) outside fenced areas and inside fenced areas enclosed by stranded or combination fence types on Group 1 sites, (b) outside fenced areas and inside fenced areas enclosed by battery or mains-electricity powered fence types on Group 1 sites, and (c) before and after fence construction for Group 2 sites. Dotted lines indicates the optimum daily predation probability (0.022), values above which result in predation-dependent hatching successes of <50% (unsustainable for Lapwing populations given plausible levels of chick survival; MacDonald & Bolton 2008b). Different letters indicate significant differences.

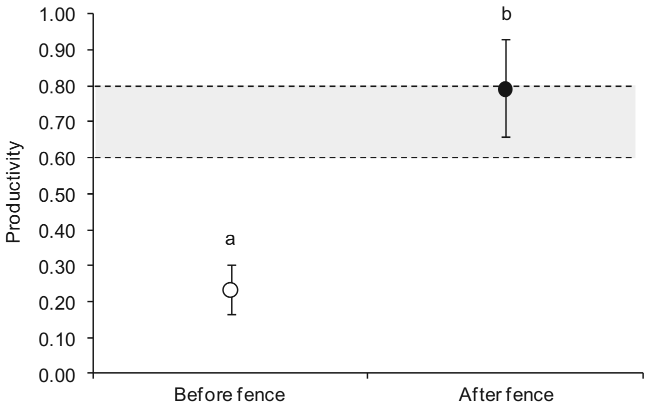


**Fig. 3.** Mean Lapwing productivity (no. fledged chicks per pair) ± SE across all sites for years before and after fence construction, calculated from best fit model estimates and back-transformed from $\ln[x+1]$. The dotted lines and shaded area indicate the minimum productivity range (0.6–0.8 fledged chicks per pair) necessary for population stability (MacDonald & Bolton 2008b). Different letters indicate significant differences.

## Discussion

Low breeding success is the main demographic factor driving the decline of Lapwing (Peach et al. 1994), and predation is widely accepted to be a major cause of low wader nest and chick survival on lowland wet grassland (Green 1988; Grimm 2005; MacDonald & Bolton 2008b; Teunissen et al. 2008). The results of this trial show that predator-exclusion fences offer considerable protection against the larger mammalian predators (foxes and badgers) in this habitat, enabling colonies of breeding waders to reach and exceed sustainable levels of nesting success and productivity that may facilitate population recovery. Daily predation rates were significantly lower for nests both inside fences and in years after fence construction (Table 3 and Fig. 2), and the number of chicks fledged by each Lapwing pair was significantly higher in years when fences were present (Table 4 and Fig. 3).

Improvements in annual productivity on sites with operational fences may indicate that not only do more nests survive the incubation period, but more chicks survive to fledge. Although avian predators are often implicated as the predators of chicks in mixed farming systems (Schekkerman et al. 2009; Teunissen et al. 2008), excluding large mammalian predators is known to reduce chick mortality in arable farmland (Rickenbach et al. 2011). Little is known about the relative contributions of different predator species to wader chick mortality on lowland grazing marshes, but higher Lapwing productivity in years when fences were present may indicate that large mammals, particularly foxes, may play a role in limiting chick survival. If fences play a role in protecting chicks as well as nests, it is important that habitat suitable for chick foraging, as well as for nesting, is provided within fenced areas so that broods do not move outside the protective barrier (Eglington et al. 2007).

There may be other, indirect, benefits of large predator exclusion, such as an increase in wader adult or chick fitness through a perceived release from predation pressure. Zanette et al. (2011) found that the perception of increased predation risk alone significantly reduced the number and fitness of songbird offspring. Excluding predators may reduce the need for predator defence behaviours, thus allowing breeding waders to incubate nests for longer periods (Cervencl et al. 2011) and increase the time in which chicks and adults are able to feed. The protection offered by fenced areas may also encourage pairs to nest at higher densities which may increase the effectiveness of predator defence behaviours and help to deter avian or smaller predators not excluded by the fence (Berg et al. 1992; Elliot 1985; Šálek & Šmilauer 2002). Although we have no data to support these hypotheses, there is evidence that waders may choose to nest within fenced areas. In 2008 and 2009 at Greylake all Lapwing nested within the fence, despite the presence of an adjacent suitable area of wet grassland.

The exclusion of large mammals is unlikely to result in 100% breeding success if other predators or other causes of nest or chick mortality operate within fenced areas. However, conservation management need not achieve a completely predation-free area, but rather an average productivity well above the minimum level required for a self-sustaining population. Across all sites, 16% of nests inside fences were still recorded as failing due to predation. Although the specific nest predators could not be identified, it is likely that these nests were taken by avian predators (e.g. corvids) or small mustelids such as stoats *Mustela erminea* and weasels *Mustelia nivalis* which are known to predate small numbers of wader nests and chicks in addition to large mammals (Ausden et al. 2009; Teunissen et al. 2008). Nests of waders in lowland wet grassland habitats may also fail due to reasons such as flooding, desertion or trampling by livestock. The proportions of nests failing due to these reasons were comparable between fenced and unfenced areas (9% of nests inside/after construction, 16% of nests outside/before construction). Despite these latent levels of nest failure and predation from alternative sources, predator-exclusion fencing still reduced the failure rate of nests enough that over 50% of nests survived predation, and productivity exceeded the 0.6–0.8 chicks per pair required to ensure population stability.

### *Trade-offs in fence design and effectiveness*

The effectiveness of fences as protective barriers was strongly dependent upon their structural design and power method. Combination fences and those powered by mains-electricity offered the greatest protection from predation (Fig. 2a, b), with stranded and battery powered fences less effective. There are a number of possible reasons for this:

(1) Stranded fences pose a less formidable barrier to predator movement than combination fences and may also be less reliable. It is possible for large mammals to force their way through stranded fences, whereas combination fences can rarely be breached other than by tunnelling or climbing. Stranded fences are also more easily blown down, damaged by livestock and susceptible to loss of tension than combination fences, which are usually supported by a base structure of permanent stock fencing.

(2) Stranded fences are often temporary and removed outside of the wader breeding season. This may allow predators to become accustomed to hunting within the fenced area so that they are more likely to attempt to breach the fence when it is re-erected. Removing fences may also allow predators to settle in the area during the non-breeding season.

(3) Fence batteries are less reliable than mains electricity because their electrical charge decreases over time. Although solar panels can be used to trickle-charge batteries to increase their longevity, they must still be recharged and replaced regularly. Battery-powered wires are also less able to burn off small pieces of vegetation so are more likely to short-circuit than mains-powered wires. The risk of a fence becoming ineffective is therefore higher when it is battery powered, meaning that predator intrusions are more likely.

(4) The results for stranded and battery powered fences are based on nest survival data from a small number of sites only (Table 1). It is possible that predation rates inside fences are artificially high at these sites due to very high large predator populations or pressures from other predator groups, such as raptors, corvids or mustelids, although we have little evidence to support this.

Despite the lower protection offered by stranded and battery powered fences, in some situations these designs are the only feasible option. The presence of mobile non-target species or the need for visually un-intrusive structures may demand the use of temporary stranded fencing. Battery power may be the only option where supplying mains electricity to isolated or very wet sites is impractical. Battery powered and stranded designs also have a lower initial construction cost, although their higher maintenance requirements and shorter lifespan mean that overall their cost is comparable to that of combination designs and mains power. Site managers wishing to include predator-exclusion fences in their management toolkit must therefore make trade-offs in the practicality, logistics, cost and time required for maintenance, against the effectiveness of the fence as a protective barrier for breeding waders. Fencing may not be suitable for use in all situations, such as where the vulnerable target species is dispersed over large areas.

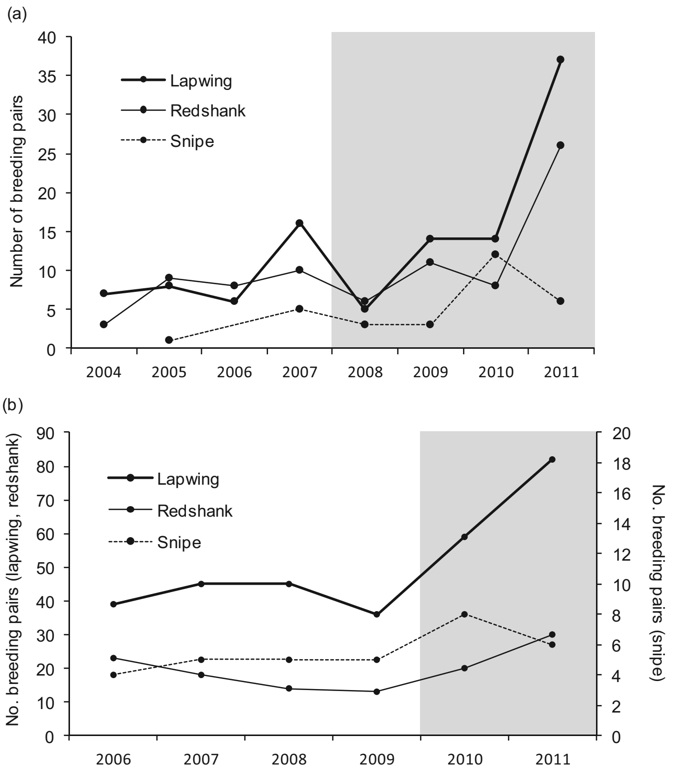


**Fig. 4.** Trends in the number of breeding pairs of Lapwing, Redshank and Snipe recorded at (a) Greylake and (b) Otmoor, with years with operational predator-exclusion fencing shaded grey.

### *Predator-exclusion fences as a management tool*

This trial shows that predator-exclusion fences are a successful and effective tool for managing unsustainable levels of large mammalian predation on vulnerable populations of waders breeding on lowland wet grassland. Although this study focussed on Lapwing, other waders (Redshank, Snipe, Curlew, Black-tailed Godwit, Oystercatcher *Haematopus ostralegus*, Avocet *Recurvirostra avosetta* and Ruff *Philomachus pugnax* L.) suffer comparable rates of predation from large mammalian predators (MacDonald & Bolton 2008b) and are likely to benefit from the protection offered by exclusion fencing. Although there are few studies comparing breeding success inside and outside fences for these other species, at some sites the numbers of breeding pairs of Redshank and Snipe have increased in years following fence construction (Fig. 4).

Lethal predator control in addition to exclusion fencing was not found to improve the effectiveness of fences, nor the nest survival or productivity of waders breeding outside. Predator-exclusion fencing may therefore provide a suitable alternative to lethal control in situations where such management is undesirable, although it may not provide a completely non-lethal solution if predators that breach the fence cannot be removed in any other way (Smith et al. 2011). Fencing is also a cost-effective alternative to intensive, prolonged lethal control, with the cost per year for a 50 ha area approximately GBP£1700 for combination fencing and GBP£1240 for stranded fencing (assuming a fenced perimeter of 700 m × 715 m, one combination fence at GBP£12 per m lasting 20 years or two stranded fences at GBP£3.50 per m lasting 10 years). Comparatively, lethal control of foxes over a typical 250–300 ha lowland wet grassland site would be GBP£3600 per year (assuming two visits per week for 18 weeks from mid-February to mid-June at £100 per visit; Bolton et al. 2007). Control over this larger area would be necessary to prevent immediate recolonisation by foxes. Predator-exclusion fencing could therefore cost GBP£1900–£2360 less per year, but benefit waders 2.4 times more than intensive lethal control of foxes by conferring a greater increase in nest survival (max increase in Lapwing nesting success with fencing = 56%, Group 1 sites, combination design; max increase where lethal control is undertaken = 24%, Berney Marshes TG466055, Bolton et al. 2007).

There is however the potential for fenced areas to become prey "hotspots" during the wader breeding season if larger numbers of nests and chicks survive and remain active inside the fence compared to outside. Such prey hotspots could become the focus of increased activity by other predator species not excluded by the fence (Stephens & Krebs 1986; e.g. raptors, corvids or small mustelids: Ausden et al. 2009; Teunissen et al. 2008), resulting in predation pressures that increase over time and limit the net benefit of the fenced area for breeding waders. Evidence from other predator-prey systems suggests that interference competition between predators is likely to limit the extent of this effect however (López-Bao et al. 2011; Rohner & Krebs 1998), and we observed no significant increase in the daily probability of nest predation inside fences nor a decline in Lapwing productivity in the presence of fences in successive years (paired *t*-tests of site specific yearly comparisons, later minus earlier year after fence construction: Group 1 sites, mean difference in predation probability = $-0.007 \pm 0.008$ SE, $n = 7$, $t = -0.87$, $P = 0.417$; Group 2 sites, mean difference = $0.001 \pm 0.009$ SE, $n = 3$, $t = 0.15$, $P = 0.896$; all sites mean difference in productivity = $-0.08 \pm 0.193$ SE, $n = 16$, $t = -0.4$, $P = 0.692$). Nevertheless, it is important that continued monitoring of any fenced area is conducted to ensure that potential negative effects are identified as soon as possible.

The management toolkit for areas of lowland wet grassland supporting breeding waders currently comprises sensitive habitat management (e.g. Eglington et al. 2010, 2009b, 2007; Smart et al. 2006), with lethal control used to manage unsustainable levels of predation from large mammals (Bolton et al. 2007). Predator-exclusion fencing is an important addition to this toolkit, providing a successful non-lethal alternative to lethal predator control that may be less time-consuming and more cost-effective. Ultimately however, predator-exclusion fencing is only likely to be successful in situations where habitat conditions and management are optimum for wader breeding, but where predation from large mammals prevents populations from responding positively. On sites where high levels of avian predation limit chick survival and overall productivity, fencing is unlikely to provide a successful conservation management solution. Decisions as to whether exclusion fencing is suitable for the protection of a vulnerable species should therefore be made on a site-by-site basis.

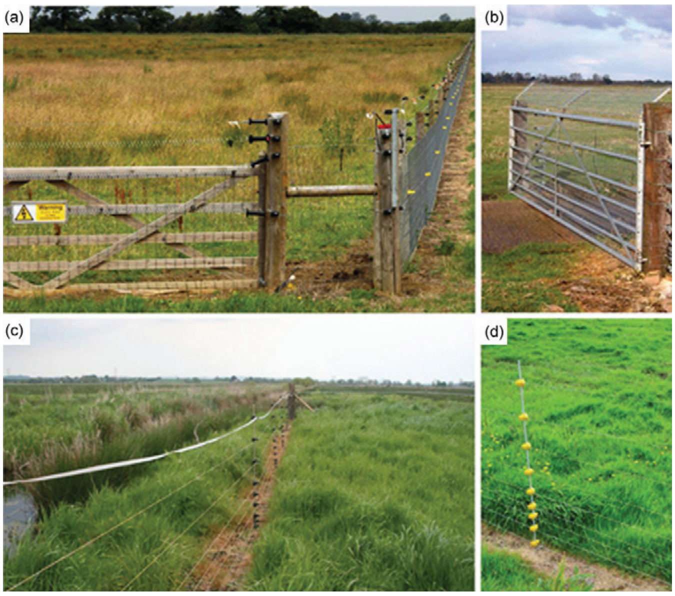
## Acknowledgements

This work was funded by The Royal Society for the Protection of Birds (RSPB). We thank the many reserve staff and volunteers who provided historical records and collected data on nest survival and productivity, and are grateful to the Newton Marsh owners group who allowed access to this site. Two anonymous referees provided constructive suggestions for improving the manuscript.

## Appendix 1. Fence specifications

Stranded fencing was 1.1 m high and had nine strands of wire alternating between earthed (E) and live (L), placed at heights of 6 (E), 13 (L), 20 (E), 28.5 (L), 38.5 (E), 51.5 (L), 69 (E), 89.5 (L) and 110 (E) cm – a design modified from recommendations given by McKillop et al. (1999). Combination fencing consisted of 1 m high livestock fencing (high tensile steel wire and 8 cm wire mesh buried 25 cm into the ground) either with two live wires 10 and 20 cm above the fence and one offset 20 cm from the fence, 65 cm off the ground, or with electrified pig-netting (65 cm high lattice with horizontal wire spacing 0, 10, 10, 10, 10, 12.5, 12.5 cm and vertical wire spacing 16.5 cm) secured along the fence line (Valley Wetlands only). These designs were adapted at some sites by supplementing additional wires or by changing the configuration of live wires. Existing gateways into field compartments were incorporated into both stranded and combination fence designs using non-electrified metal wire mesh to cover the gate, with either an outward-facing wire mesh overhang >30 cm wide or with live wires above and across the gateway, up to the height of the fence.

**Fence design examples:** Combination design predator-exclusion fence and electrified gateway at Otmoor (a), non-electrified gateway with wire mesh overhang at Ouse Washes (b), and stranded design predator-exclusion fences at Greylake (c) and Ynys-Hir (d). Photographs by Graham White and Rosalind Kennerley.



## References

Aebischer, N. J. (1999). Multi-way comparisons and generalised linear models of nest success: Extensions of the Mayfield method. *Bird Study*, *46*, S22–S31.

Ausden, M., Bolton, M., Butcher, N., Hoccom, D. G., Smart, J., & Williams, G. (2009). Predation of breeding waders on lowland wet grassland – Is it a problem? *British Wildlife*, October 2009, 29–38.

Ausden, M., Hirons, G., & Kennerley, R. (2011). Using anti-predator fences to increase wader productivity. *Conservation Land Management*, *9*, 5–8.

Ausden, M., & Hirons, G. J. M. (2002). Grassland nature reserves for breeding wading birds in England and the implications for the ESA agri-environment scheme. *Biological Conservation*, *106*, 279–291.

Bates, D., & Maechler, M. (2009). *lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-32*.

Bellebaum, J., & Bock, C. (2009). Influence of ground predators and water levels on Lapwing *Vanellus vanellus* breeding success in two continental wetlands. *Journal of Ornithology*, *150*, 221–230.

Berg, A., Lindberg, T., & Kallebrink, K. G. (1992). Hatching success of Lapwings on farmland – Differences between habitats and colonies of different sizes. *Journal of Animal Ecology*, *61*, 469–476.

Bodey, T. W., Smart, J., Smart, M. A., & Gregory, R. D. (2010). Reducing the impacts of predation on ground-nesting waders: A new landscape-scale solution? *Aspects of Applied Biology*, *100*, 167–174.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., et al. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*, 127–135.

Bolton, M., Bamford, R., Blackburn, C., Cromarty, J., Eglington, S., Ratcliffe, N., et al. (2011). Assessment of simple survey methods to determine breeding population size and productivity of a plover, the Northern Lapwing *Vanellus vanellus*. *Wader Study Group Bulletin*, *118*, 141–152.

Bolton, M., Tyler, G., Smith, K., & Bamford, R. (2007). The impact of predator control on Lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *Journal of Applied Ecology*, *44*, 534–544.

Cervencl, A., Esser, W., Maier, M., Oberdiek, N., Thyen, S., Wellbrock, A., et al. (2011). Can differences in incubation patterns of Common Redshanks *Tringa totanus* be explained by variations in predation risk? *Journal of Ornithology*, *152*, 1033–1043.

Crooks, K. R., & Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, *400*, 563–566.

Donald, P. F., Sanderson, F. J., Burfield, I. J., & van Bommel, F. P. J. (2006). Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agriculture Ecosystems & Environment*, *116*, 189–196.

Durant, D., Tichit, M., Kerneıs, E., & Fritz, H. (2008). Management of agricultural wet grassland for breeding waders: Integrating ecological and livestock system perspectives – A review. *Biodiversity and Conservation*, *17*, 2275–2295.

Eglington, S. M., Bolton, M., Smart, M. A., Sutherland, W. J., Watkinson, A. R., & Gill, J. A. (2010). Managing water levels on wet grasslands to improve foraging conditions for breeding northern Lapwing *Vanellus vanellus*. *Journal of Applied Ecology*, *47*, 451–458.

Eglington, S. M., Gill, J. A., Bolton, M., & Smart, M. A. (2009). Reversion of arable land to wet grassland for breeding waders. *Conservation Land Management*, *7*, 5–9.

Eglington, S. M., Gill, J. A., Bolton, M., Smart, M. A., Sutherland, W. J., & Watkinson, A. R. (2007). Restoration of wet features for breeding waders on lowland wet grassland. *Journal of Applied Ecology*, *45*, 305–314.

Eglington, S. E., Gill, J. A., Smart, M. A., Sutherland, W. J., Watkinson, A. R., & Bolton, M. (2009). Habitat management and patterns of predation of Northern Lapwings on wet grasslands: The influence of linear habitat structures at different spatial scales. *Biological Conservation*, *142*, 314–324.

Elliot, R. D. (1985). The exclusion of avian predators from aggregations of nesting Lapwings (*Vanellus vanellus*). *Animal Behaviour*, *33*, 308–314.

Ellis-Felege, S. N., Conroy, M. J., Palmer, W. E., & Carroll, J. P. (2012). Predator reduction results in compensatory shifts in losses of avian ground nests. *Journal of Applied Ecology*, *49*, 661–669.

Fletcher, K., Aebischer, N. J., Baines, D., Foster, R., & Hoodless, A. N. (2010). Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *Journal of Applied Ecology*, *47*, 263–272.

Fuller, R. J., Gregory, R. D., Gibbons, D. W., Marchant, J. H., Wilson, J. D., Baillie, S. R., et al. (1995). Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology*, *9*, 1425–1441.

Galbraith, H. (1987). Marking and visiting Lapwing *Vanellus vanellus* nests does not affect clutch survival. *Bird Study*, *34*, 137–138.

Galbraith, H. (1988). Effects of agriculture on the breeding ecology of Lapwings *Vanellus vanellus*. *Journal of Applied Ecology*, *25*, 487–503.

Gibbons, D. W., Amar, A., Anderson, G. Q. A., Bolton, M., Bradbury, R. B., Eaton, M. A., et al. (2007). *The predation of wild birds in the UK: A review of its conservation impact and management*. RSPB Research Report No. 23. Sandy: RSPB.

Grant, M. C., Orsman, C., Easton, J., Lodge, C., Smith, M., Thompson, G., et al. (1999). Breeding success and causes of breeding failure of curlew *Numenius arquata* in Northern Ireland. *Journal of Applied Ecology*, *36*, 59–74.

Green, R. E. (1988). Effects of environmental factors on the timing and success of breeding of common Snipe *Gallinago gallinago* (Aves: Scolopacidae). *Journal of Applied Ecology*, *25*, 79–93.

Grimm, M. (2005). Population changes in and threats to Eurasian Curlew *Numenius arquata* in the Belziger Landschaftswiesen (Brandenburg, Germany). *Vogelwelt*, *126*, 333–340.

Henderson, I. G., Wilson, A. M., Steele, D., & Vickery, J. A. (2002). Population estimates, trends and habitat associations of breeding Lapwing *Vanellus vanellus*, Curlew *Numenius arquata* and Snipe *Gallinago gallinago* in Northern Ireland in 1999. *Bird Study*, *49*, 17–25.

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*, 346–363.

Isaksson, D., Wallander, J., & Larsson, M. (2007). Managing predation on ground-nesting birds: The effectiveness of nest exclosures. *Biological Conservation*, *136*, 136–142.

Jackson, D. B. (2001). Experimental removal of introduced hedgehogs improves wader nest success in the Western Isles, Scotland. *Journal of Applied Ecology*, *38*, 802–812.

LaGrange, T. G., Hansen, J. L., Andrews, R. D., Hancock, A. W., & Kienzler, J. M. (1995). Electric fence predator exclosure to enhance duck nesting: A long-term case study in Iowa. *Wildlife Society Bulletin*, *23*, 261–266.

Latham, R. M. (1952). The fox as a factor in the control of weasel populations. *The Journal of Wildlife Management*, *16*, 516–517.

López-Bao, J. V., Palomares, F., Rodríguez, A., & Ferreras, P. (2011). Intraspecific interference influences the use of prey hotspots. *Oikos*, *120*, 1489–1496.

MacDonald, M. A., & Bolton, M. (2008a). Predation of Lapwing *Vanellus vanellus* nests on lowland wet grassland in England and Wales: Effects of nest density, habitat and predator abundance. *Journal of Ornithology*, *149*, 555–563.

MacDonald, M. A., & Bolton, M. (2008b). Predation on wader nests in Europe. *Ibis*, *150*, 54–73.

Manolis, J. C., Andersen, D. E., & Cuthbert, F. J. (2000). Uncertain nest fates in songbird studies and variation in Mayfield estimation. *The Auk*, *117*, 615–626.

Mason, C. F., & Macdonald, S. M. (1976). Aspects of the breeding biology of the Snipe. *Bird Study*, *23*, 33–38.

Mayer, P. M., & Ryan, M. R. (1991). Electric fences reduce mammalian predation on Piping Plover nests and chicks. *Wildlife Society Bulletin*, *19*, 59–63.

Mayfield, H. (1961). Nesting success calculated from exposure. *Wilson Bulletin*, *73*, 255–261.

Mayfield, H. (1975). Suggestions for calculating nest success. *Wilson Bulletin*, *87*, 456–466.

McKillop, I. G., Pepper, H. W., Butt, R., & Poole, D. W. (1999). *Electric fence reference manual*. Research and Development Surveillance Report 607. Department for Environment, Food and Rural Affairs (DEFRA).

Murphy, R. K., Greenwood, R. J., Ivan, J. S., & Smith, K. A. (2003). Predator exclusion methods for managing endangered shorebirds: Are two barriers better than one? *Waterbirds*, *26*, 156–159.

Murphy, R. K., Michaud, I. M. G., Prescott, D. R. C., Ivan, J. S., Anderson, B. J., & French-Pombier, M. L. (2003). Predation on adult Piping Plovers at predator exclosure cages. *Waterbirds*, *26*, 150–155.

Nordström, N., Högmander, J., Laine, J., Nummelin, J., Laanetu, N., & Korpimäki, E. (2003). Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. *Biological Conservation*, *109*, 359–368.

Pauliny, A., Larsson, M., & Blomqvist, D. (2008). Nest predation management: Effects on reproductive success in endangered shorebirds. *The Journal of Wildlife Management*, *72*, 1579–1583.

Peach, W. J., Thompson, P. S., & Coulson, J. C. (1994). Annual and long-term variation in the survival rates of British Lapwings *Vanellus vanellus*. *Journal of Animal Ecology*, *63*, 60–70.

PECBMS. (2012). *Population trends of common European breeding birds 2012*. Prague: CSO/RSPB.

Poole, D. W., & McKillop, I. G. (2002). Effectiveness of two types of electric fence for excluding the Red Fox (*Vulpes vulpes*). *Mammal Review*, *32*, 51–57.

R Development Core Team. (2009). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rickenbach, O., Grüebler, M. U., Schaub, M., Koller, A., Naef-Daenzer, B., & Schifferli, L. (2011). Exclusion of ground predators improves Northern Lapwing *Vanellus vanellus* chick survival. *Ibis*, *153*, 531–542.

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, *12*, 982–998.

Rohner, C., & Krebs, C. J. (1998). Response of great horned owls to experimental “hot spots” of snowshoe hare density. *The Auk*, *115*, 694–705.

Rushton, S. P., Shirley, M. D. F., Macdonald, D. W., & Reynolds, J. C. (2006). Effects of culling fox populations at the landscape scale: A spatially explicit population modelling approach. *The Journal of Wildlife Management*, *70*, 1102–1110.

Šálek, M., & Šmilauer, P. (2002). Predation on Northern Lapwing *Vanellus vanellus* nests: The effect of population density and spatial distribution of nests. *Ardea*, *90*, 51–60.

Schekkerman, H., Teunissen, W., & Oosterveld, E. (2009). Mortality of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* chicks in wet grasslands: Influence of predation and agriculture. *Journal of Ornithology*, *150*, 133–145.

Schifferli, L., Rickenbach, O., Koller, K., & Grüebler, M. (2009). Massnahmen zur Förderung des Kiebitzes *Vanellus vanellus* im Wauwilermoos (Kanton Luzern): Schutz der Nester vor Landwirtschaft und Prädation [In German with an English summary: Nest protection from agriculture and predation to improve nest and chick survival of the Northern Lapwing *Vanellus vanellus* in Swiss farmland]. *Der Ornithologische Beobachter*, *106*, 311–326.

Seymour, A. S., Harries, S., Ralston, C., & White, P. C. L. (2003). Factors influencing the nesting success of Lapwings *Vanellus vanellus* and behaviour of Red Fox *Vulpes vulpes* in Lapwing nesting sites. *Bird Study*, *50*, 39–46.

Smart, J., Gill, J. A., Sutherland, W. J., & Watkinson, A. R. (2006). Grassland-breeding waders: Identifying key habitat requirements for management. *Journal of Applied Ecology*, *43*, 454–463.

Smith, R. K., Pullin, A. S., Stewart, G. B., & Sutherland, W. J. (2010). Effectiveness of predator removal for enhancing bird populations. *Conservation Biology*, *24*, 820–829.

Smith, R. K., Pullin, A. S., Stewart, G. B., & Sutherland, W. J. (2011). Is nest predator exclusion an effective strategy for enhancing bird populations? *Biological Conservation*, *144*, 1–10.

Stephens, D. A., & Krebs, J. R. (1986). *Foraging theory*. Princeton: Princeton University Press.

Taylor, I. R., & Grant, M. C. (2004). Long-term trends in the abundance of breeding Lapwing *Vanellus vanellus* in relation to land-use change on upland farmland in southern Scotland. *Bird Study*, *51*, 133–142.

Teunissen, W., Schekkerman, H., Willems, F., & Majoor, F. (2008). Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis*, *150*, 74–85.

Tharme, A. P., Green, R. E., Baines, D., Bainbridge, I. P., & O'Brien, M. (2001). The effect of management for red grouse shooting on the population density of breeding birds on heather-dominated moorland. *Journal of Applied Ecology*, *38*, 439–457.

Wilson, A. M., Ausden, M., & Milson, T. P. (2004). Changes in breeding wader populations on lowland wet grasslands in England and Wales: Causes and potential solutions. *Ibis*, *146*, 32–40.

Wilson, A. M., Vickery, J. A., Langston, R. H. W., Smallshire, D., Wotton, S., & Vanhinsbergh, D. (2005). Changes in the numbers of breeding waders on lowland wet grasslands in England and Wales between 1982 and 2002. *Bird Study*, *52*, 55–69.

Zanette, L. Y., White, A. F., Allen, M. C., & Clinchy, M. (2011). Perceived predation risk reduces the number of offspring songbirds produce per year. *Science*, *334*, 1398–1401.

# Appendix

## Supplementary materials for publication II

**Online Resource 1.** The 145 European bird species for which population trend data was available.

| | | | | **Number of states:** | | |
|---|---|---|---|---|---|---|
| **Species** | **Logged body mass** | **Migratory strategy** | **Habitat** | **Total** | **In which sp. is in CST+ group** | **In which sp. is in CST- group** |
| Accipiter nisus | 5.339 | SD | FO | 14 | 8 | 6 |
| Acrocephalus arundinaceus | 3.303 | LD | IW | 9 | 8 | 1 |
| Acrocephalus palustris | 2.477 | LD | O | 16 | 7 | 9 |
| Acrocephalus schoenobaenus | 2.416 | LD | IW | 13 | 1 | 12 |
| Acrocephalus scirpaceus | 2.510 | LD | IW | 14 | 7 | 7 |
| Actitis hypoleucos | 3.945 | LD | IW | 5 | 1 | 4 |
| Aegithalos caudatus | 2.104 | R | O | 18 | 12 | 6 |
| Alauda arvensis | 3.616 | SD | FA | 20 | 12 | 8 |
| Anas platyrhynchos | 6.968 | SD | IW | 15 | 9 | 6 |
| Anthus campestris | 3.332 | LD | O | 5 | 4 | 1 |
| Anthus pratensis | 2.912 | SD | FA | 15 | | 15 |
| Anthus trivialis | 3.223 | LD | FO | 18 | 5 | 13 |
| Apus apus | 3.627 | LD | O | 17 | 10 | 7 |
| Ardea cinerea | 7.344 | SD | IW | 16 | 10 | 6 |
| Bombycilla garrulus | 4.135 | SD | FO | 2 | | 2 |
| Bonasa bonasia | 6.061 | R | FO | 3 | 1 | 2 |
| Burhinus oedicnemus | 6.205 | SD | FA | 2 | | 2 |
| Buteo buteo | 6.788 | SD | O | 17 | 10 | 7 |
| Calandrella brachydactyla | 3.135 | LD | FA | 2 | 2 | |
| Carduelis cannabina | 2.728 | SD | FA | 18 | 8 | 10 |
| Carduelis carduelis | 2.747 | SD | O | 18 | 15 | 3 |
| Carduelis chloris | 3.325 | SD | O | 20 | 15 | 5 |
| Carduelis flammea | 2.565 | SD | FO | 11 | 1 | 10 |
| Carduelis spinus | 2.674 | SD | FO | 11 | 3 | 8 |
| Carpodacus erythrinus | 3.182 | LD | O | 5 | 2 | 3 |
| Certhia brachydactyla | 2.140 | R | FO | 12 | 10 | 2 |
| Certhia familiaris | 2.197 | R | FO | 14 | 3 | 11 |
| Cettia cetti | 2.534 | R | IW | 3 | 1 | 2 |
| Ciconia ciconia | 8.153 | LD | FA | 5 | 3 | 2 |
| Circus aeruginosus | 6.402 | LD | IW | 11 | 9 | 2 |
| Cisticola juncidis | 2.303 | R | IW | 2 | 1 | 1 |
| Coccothraustes coccothraustes | 3.989 | R | FO | 14 | 9 | 5 |
| Columba oenas | 5.635 | SD | FO | 16 | 7 | 9 |
| Columba palumbus | 6.194 | SD | O | 20 | 13 | 7 |
| Corvus corax | 7.054 | R | O | 16 | 4 | 12 |
| Corvus corone | 6.346 | R | O | 20 | 14 | 6 |
| Corvus frugilegus | 6.190 | R | FA | 11 | 6 | 5 |
| Corvus monedula | 5.505 | R | O | 17 | 13 | 4 |
| Cuculus canorus | 4.727 | LD | O | 20 | 14 | 6 |
| Cyanopica cyanus | 4.290 | R | FO | 1 | | 1 |
| Cygnus olor | 8.959 | SD | IW | 9 | 1 | 8 |
| Delichon urbica | 2.674 | LD | O | 18 | 14 | 4 |
| Dendrocopos major | 4.402 | R | O | 18 | 12 | 6 |
| Dendrocopos medius | 4.174 | R | FO | 8 | 4 | 4 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Dendrocopos minor | 2.986 | R | FO | 12 | 5 | 7 |
| Dendrocopos syriacus | 4.337 | R | O | 1 | 1 | |
| Dryocopus martius | 5.771 | R | FO | 15 | 3 | 12 |
| Emberiza cia | 3.219 | R | O | 3 | 1 | 2 |
| Emberiza cirlus | 3.140 | R | FA | 4 | 3 | 1 |
| Emberiza citrinella | 3.277 | R | FA | 20 | 10 | 10 |
| Emberiza hortulana | 3.170 | LD | FA | 7 | 4 | 3 |
| Emberiza melanocephala | 3.350 | LD | FA | 1 | 1 | |
| Emberiza rustica | 2.970 | LD | FO | 2 | | 2 |
| Emberiza schoeniclus | 2.907 | SD | IW | 16 | 4 | 12 |
| Erithacus rubecula | 2.901 | SD | O | 19 | 13 | 6 |
| Falco tinnunculus | 5.380 | SD | FA | 16 | 14 | 2 |
| Ficedula albicollis | 2.332 | LD | FO | 6 | 4 | 2 |
| Ficedula hypoleuca | 2.451 | LD | FO | 13 | 1 | 12 |
| Fringilla coelebs | 3.040 | SD | O | 19 | 13 | 6 |
| Fringilla montifringilla | 3.178 | SD | O | 3 | | 3 |
| Fulica atra | 6.685 | SD | IW | 11 | 10 | 1 |
| Galerida cristata | 3.735 | R | FA | 7 | 7 | |
| Galerida theklae | 3.597 | R | FA | 1 | | 1 |
| Gallinago gallinago | 4.754 | SD | IW | 12 | | 12 |
| Gallinula chloropus | 7.155 | SD | IW | 11 | 9 | 2 |
| Garrulus glandarius | 5.081 | R | FO | 18 | 11 | 7 |
| Hippolais icterina | 2.681 | LD | O | 14 | 3 | 11 |
| Hippolais polyglotta | 2.398 | LD | O | 3 | 1 | 2 |
| Hirundo rupestris | 3.157 | SD | O | 3 | 1 | 2 |
| Hirundo rustica | 2.760 | LD | FA | 20 | 8 | 12 |
| Jynx torquilla | 3.512 | LD | O | 15 | 6 | 9 |
| Lanius collurio | 3.398 | LD | FA | 17 | 10 | 7 |
| Lanius minor | 3.818 | LD | FA | 2 | 2 | |
| Lanius senator | 3.555 | LD | FA | 2 | 2 | |
| Limosa limosa | 5.728 | SD | FA | 2 | 1 | 1 |
| Locustella fluviatilis | 2.896 | LD | O | 7 | 3 | 4 |
| Locustella naevia | 2.588 | LD | O | 14 | 2 | 12 |
| Lullula arborea | 3.292 | R | FA | 9 | 2 | 7 |
| Luscinia luscinia | 3.170 | LD | O | 8 | 2 | 6 |
| Luscinia megarhynchos | 2.907 | LD | O | 13 | 12 | 1 |
| Melanocorypha calandra | 4.082 | R | FA | 2 | 1 | 1 |
| Merops apiaster | 4.036 | LD | FA | 4 | 3 | 1 |
| Miliaria calandra | 4.047 | R | FA | 12 | 6 | 6 |
| Motacilla alba | 3.045 | SD | O | 20 | 7 | 13 |
| Motacilla cinerea | 2.845 | SD | IW | 11 | 9 | 2 |
| Motacilla flava | 2.632 | LD | FA | 16 | 3 | 13 |
| Muscicapa striata | 2.681 | LD | FO | 19 | 7 | 12 |
| Nucifraga caryocatactes | 5.130 | R | FO | 5 | 2 | 3 |
| Numenius phaeopus | 6.052 | LD | O | 2 | | 2 |
| Oenanthe hispanica | 2.848 | LD | FA | 2 | 1 | 1 |
| Oenanthe oenanthe | 3.105 | LD | O | 14 | 2 | 12 |
| Oriolus oriolus | 4.369 | LD | O | 15 | 12 | 3 |
| Parus ater | 2.208 | R | FO | 18 | 8 | 10 |
| Parus caeruleus | 2.588 | R | O | 19 | 14 | 5 |
| Parus cristatus | 2.322 | R | FO | 16 | 3 | 13 |
| Parus major | 2.944 | R | O | 19 | 13 | 6 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Parus montanus | 2.322 | R | FO | 15 | 1 | 14 |
| Parus palustris | 2.361 | R | FO | 15 | 9 | 6 |
| Passer domesticus | 3.311 | R | O | 19 | 6 | 13 |
| Passer montanus | 3.091 | R | FA | 17 | 11 | 6 |
| Perdix perdix | 5.943 | R | FA | 12 | 8 | 4 |
| Petronia petronia | 3.418 | R | FA | 1 | | 1 |
| Phoenicurus ochruros | 2.803 | SD | O | 12 | 5 | 7 |
| Phoenicurus phoenicurus | 2.674 | LD | FO | 17 | 3 | 14 |
| Phylloscopus bonelli | 2.186 | LD | FO | 4 | 2 | 2 |
| Phylloscopus collybita | 2.015 | SD | FO | 18 | 12 | 6 |
| Phylloscopus sibilatrix | 2.104 | LD | FO | 16 | 3 | 13 |
| Phylloscopus trochilus | 2.163 | LD | FO | 17 | 2 | 15 |
| Pica pica | 5.112 | R | O | 20 | 11 | 9 |
| Picus canus | 4.920 | R | FO | 6 | 4 | 2 |
| Picus viridis | 5.170 | R | FO | 15 | 10 | 5 |
| Pluvialis apricaria | 5.394 | SD | O | 2 | | 2 |
| Prunella modularis | 2.981 | SD | FO | 19 | 7 | 12 |
| Pyrrhocorax pyrrhocorax | 5.720 | R | O | 1 | | 1 |
| Pyrrhula pyrrhula | 3.082 | R | FO | 18 | 5 | 13 |
| Regulus ignicapilla | 1.723 | SD | FO | 11 | 6 | 5 |
| Regulus regulus | 1.740 | SD | FO | 18 | 3 | 15 |
| Saxicola rubetra | 2.809 | LD | FA | 18 | 4 | 14 |
| Saxicola torquata | 2.728 | SD | FA | 12 | 9 | 3 |
| Serinus serinus | 2.416 | SD | O | 12 | 11 | 1 |
| Sitta europaea | 3.091 | R | FO | 17 | 12 | 5 |
| Streptopelia decaocto | 4.984 | R | O | 16 | 12 | 4 |
| Streptopelia turtur | 4.883 | LD | FA | 15 | 12 | 3 |
| Sturnus unicolor | 4.508 | R | FA | 2 | | 2 |
| Sturnus vulgaris | 4.381 | SD | FA | 20 | 9 | 11 |
| Sylvia atricapilla | 2.741 | SD | FO | 20 | 14 | 6 |
| Sylvia borin | 2.632 | LD | O | 19 | 4 | 15 |
| Sylvia cantillans | 2.380 | LD | O | 3 | 1 | 2 |
| Sylvia communis | 2.674 | LD | FA | 20 | 13 | 7 |
| Sylvia curruca | 2.313 | LD | O | 17 | 4 | 13 |
| Sylvia hortensis | 3.020 | LD | O | 2 | 1 | 1 |
| Sylvia melanocephala | 2.425 | R | O | 3 | 3 | |
| Sylvia nisoria | 3.219 | LD | FA | 8 | 4 | 4 |
| Sylvia undata | 2.251 | R | O | 1 | | 1 |
| Tringa glareola | 4.174 | LD | O | 2 | | 2 |
| Tringa ochropus | 4.317 | SD | FO | 3 | | 3 |
| Tringa totanus | 4.756 | SD | IW | 7 | 2 | 5 |
| Troglodytes troglodytes | 2.186 | R | FO | 19 | 15 | 4 |
| Turdus iliacus | 4.114 | SD | O | 4 | | 4 |
| Turdus merula | 4.727 | R | O | 19 | 16 | 3 |
| Turdus philomelos | 4.199 | SD | FO | 19 | 13 | 6 |
| Turdus pilaris | 4.644 | SD | O | 14 | | 14 |
| Turdus viscivorus | 4.745 | SD | FO | 18 | 7 | 11 |
| Upupa epops | 4.117 | LD | O | 7 | 6 | 1 |
| Vanellus vanellus | 5.421 | SD | FA | 17 | 5 | 12 |

**Online Resource 2.** The 20 European countries ("states") from which bird species population trend data was available. East and West Germany were included separately due to historical differences in bird monitoring

| | **First year of** | **Number of species included:** | | |
|---|---|---|---|---|
| **State** | **monitoring data** | **Total** | **in CST+ group** | **in CST- group** |
| Austria | 1998 | 79 | 59 | 20 |
| Belgium | 1990 | 80 | 10 | 70 |
| Czech Republic | 1982 | 100 | 54 | 46 |
| Denmark | 1976 | 80 | 42 | 38 |
| Estonia | 1983 | 74 | 24 | 50 |
| Finland | 1975 | 76 | 56 | 20 |
| France | 1989 | 89 | 16 | 73 |
| Germany (East) | 1991 | 101 | 58 | 43 |
| Germany (West) | 1989 | 100 | 38 | 62 |
| Hungary | 1999 | 87 | 50 | 37 |
| Italy | 2000 | 104 | 10 | 94 |
| Latvia | 1995 | 36 | 15 | 21 |
| Netherlands | 1984 | 96 | 26 | 70 |
| Norway | 1996 | 55 | 48 | 7 |
| Poland | 2000 | 101 | 63 | 38 |
| Republic of Ireland | 1998 | 53 | 23 | 30 |
| Spain | 1998 | 96 | 37 | 59 |
| Sweden | 1975 | 101 | 82 | 19 |
| Switzerland | 1999 | 97 | 80 | 17 |
| United Kingdom | 1966 | 81 | 43 | 38 |

**Online Resource 3.** The 380 North American bird species for which population trend data was available for the USA.

| | | | | **Number of states:** | | |
|---|---|---|---|---|---|---|
| **Species** | **Logged body mass** | **Migratory strategy** | **Habitat** | **Total** | **In which sp. is in CST+ group** | **In which sp. is in CST- group** |
| Accipiter cooperii | 6.084 | R | FS | 47 | 20 | 27 |
| Accipiter gentilis | 6.850 | R | FS | 18 | 4 | 14 |
| Accipiter striatus | 4.930 | R | FS | 42 | 12 | 30 |
| Actitis macularius | 3.783 | LD | W | 30 | 9 | 21 |
| Aechmophorus clarkii occidentalis | 7.034 | SD | W | 10 | 5 | 5 |
| Aeronautes saxatalis | 3.497 | R | FS | 12 | 12 | |
| Agelaius phoeniceus | 3.959 | R | W | 48 | 10 | 38 |
| Aimophila ruficeps | 2.929 | R | FS | 4 | | 4 |
| Aix sponsa | 6.489 | R | W | 43 | 22 | 21 |
| Ammodramus bairdii | 2.910 | LD | G | 4 | 1 | 3 |
| Ammodramus caudacutus nelsoni | 2.958 | SD | W | 2 | 1 | 1 |
| Ammodramus henslowii | 2.549 | SD | G | 15 | 4 | 11 |
| Ammodramus leconteii | 2.565 | SD | G | 4 | 1 | 3 |
| Ammodramus maritimus | 3.139 | R | O | 3 | 3 | |
| Ammodramus savannarum | 2.879 | R | G | 38 | 8 | 30 |
| Amphispiza belli | 2.896 | R | FS | 10 | 10 | |
| Amphispiza bilineata | 2.603 | R | FS | 8 | 8 | |
| Anas acuta | 6.853 | M | W | 12 | | 12 |
| Anas americana | 6.627 | R | W | 10 | 1 | 9 |
| Anas clypeata | 6.418 | R | W | 16 | 3 | 13 |
| Anas cyanoptera | 5.934 | SD | W | 11 | 10 | 1 |
| Anas discors | 5.886 | LD | W | 23 | 3 | 20 |
| Anas fulvigula | 6.896 | R | W | 3 | 2 | 1 |
| Anas platyrhynchos | 7.065 | SD | W | 47 | 7 | 40 |
| Anas rubripes | 7.131 | R | W | 14 | 6 | 8 |
| Anas strepera | 6.821 | R | W | 14 | 8 | 6 |
| Anhinga anhinga | 7.141 | SD | W | 9 | 8 | 1 |
| Anthus spragueii | 3.239 | M | G | 3 | | 3 |
| Aphelocoma californica | 4.399 | R | FS | 9 | 6 | 3 |
| Aquila chrysaetos | 8.358 | R | G | 15 | 9 | 6 |
| Archilochus alexandri | 1.224 | LD | FS | 10 | 10 | |
| Archilochus colubris | 1.131 | LD | FS | 35 | 23 | 12 |
| Ardea herodias | 7.795 | R | W | 47 | 21 | 26 |
| Arremonops rufivirgatus | 3.111 | R | FS | 1 | 1 | |
| Asio flammeus | 5.846 | R | G | 10 | | 10 |
| Athene cunicularia | 5.017 | R | G | 18 | 13 | 5 |
| Auriparus flaviceps | 1.960 | R | O | 4 | 4 | |
| Aythya affinis | 6.709 | R | W | 11 | 1 | 10 |
| Aythya americana | 6.981 | R | W | 14 | 7 | 7 |
| Aythya collaris | 6.558 | R | W | 15 | 3 | 12 |
| Aythya valisineria | 7.093 | M | W | 8 | | 8 |
| Baeolophus bicolor | 3.082 | R | FS | 35 | 29 | 6 |
| Baeolophus inornatus | 2.775 | R | FS | 2 | 2 | |
| Baeolophus ridgwayi | 2.782 | R | FS | 6 | 6 | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Bartramia longicauda | 5.069 | LD | G | 22 | 5 | 17 |
| Bombycilla cedrorum | 3.453 | R | FS | 33 | 12 | 21 |
| Bonasa umbellus | 6.277 | R | FS | 22 | 6 | 16 |
| Botaurus lentiginosus | 6.225 | R | W | 29 | 3 | 26 |
| Branta canadensis | 8.151 | SD | W | 44 | 4 | 40 |
| Bubo virginianus | 7.099 | R | FS | 45 | 16 | 29 |
| Bubulcus ibis | 5.903 | LD | W | 17 | 4 | 13 |
| Bucephala albeola | 6.000 | R | W | 5 | | 5 |
| Buteo jamaicensis | 7.021 | R | O | 48 | 14 | 34 |
| Buteo lineatus | 6.409 | R | FS | 34 | 32 | 2 |
| Buteo platypterus | 6.120 | LD | FS | 31 | 21 | 10 |
| Buteo regalis | 7.293 | R | G | 15 | 9 | 6 |
| Buteo swainsoni | 6.865 | LD | G | 19 | 10 | 9 |
| Butorides virescens | 5.260 | M | W | 40 | 28 | 12 |
| Calamospiza melanocorys | 3.627 | M | G | 8 | 1 | 7 |
| Calcarius ornatus | 3.011 | M | G | 5 | 2 | 3 |
| Callipepla californica | 5.159 | R | FS | 6 | 5 | 1 |
| Callipepla gambelii | 5.112 | R | O | 7 | 7 | |
| Callipepla squamata | 5.215 | R | G | 5 | 4 | 1 |
| Calypte anna | 1.447 | R | FS | 2 | 2 | |
| Calypte costae | 1.131 | M | O | 2 | 2 | |
| Campylorhynchus brunneicapillus | 3.661 | R | FS | 5 | 4 | 1 |
| Caprimulgus arizonae vociferus | 4.016 | M | FS | 29 | 25 | 4 |
| Caprimulgus carolinensis | 4.751 | LD | FS | 19 | 15 | 4 |
| Caracara cheriway | 6.970 | R | G | 2 | 2 | |
| Cardinalis cardinalis | 3.753 | R | FS | 37 | 18 | 19 |
| Cardinalis sinuatus | 3.561 | R | FS | 3 | 2 | 1 |
| Carduelis lawrencei | 2.393 | SD | FS | 1 | 1 | |
| Carduelis pinus | 2.542 | R | FS | 12 | 4 | 8 |
| Carduelis psaltria | 2.233 | R | FS | 8 | 7 | 1 |
| Carduelis tristis | 2.549 | R | G | 43 | 7 | 36 |
| Carpodacus cassinii | 3.277 | R | FS | 11 | 8 | 3 |
| Carpodacus mexicanus | 3.054 | R | FS | 46 | 43 | 3 |
| Carpodacus purpureus | 3.239 | R | FS | 17 | 2 | 15 |
| Casmerodius albus | 6.773 | M | W | 32 | 26 | 6 |
| Cathartes aura | 7.438 | R | O | 47 | 25 | 22 |
| Catharus fuscescens | 3.555 | LD | FS | 25 | 4 | 21 |
| Catharus guttatus | 3.305 | R | FS | 23 | 8 | 15 |
| Catharus ustulatus | 3.541 | LD | FS | 18 | 1 | 17 |
| Catherpes mexicanus | 2.445 | R | FS | 12 | 12 | |
| Catoptrophorus semipalmatus | 5.525 | R | W | 19 | 7 | 12 |
| Centrocercus minimus urophasianus | 7.409 | R | FS | 8 | 8 | |
| Certhia americana | 2.143 | R | FS | 24 | 12 | 12 |
| Chaetura pelagica | 3.105 | LD | O | 38 | 11 | 27 |
| Chaetura vauxi | 2.865 | LD | FS | 5 | 2 | 3 |
| Chamaea fasciata | 2.691 | R | FS | 2 | 2 | |
| Charadrius montanus | 4.562 | SD | G | 3 | 1 | 2 |
| Charadrius vociferus | 4.570 | R | W | 48 | 14 | 34 |
| Chondestes grammacus | 3.367 | LD | G | 28 | 10 | 18 |
| Chordeiles acutipennis | 3.871 | LD | FS | 4 | 4 | |
| Chordeiles minor | 4.327 | LD | G | 46 | 6 | 40 |
| Cinclus mexicanus | 4.045 | R | W | 9 | 5 | 4 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Circus cyaneus | 6.078 | R | G | 32 | 4 | 28 |
| Cistothorus palustris | 2.369 | R | W | 28 | 11 | 17 |
| Cistothorus platensis | 2.073 | SD | G | 11 | 3 | 8 |
| Coccothraustes vespertinus | 4.066 | R | FS | 14 | 2 | 12 |
| Coccyzus americanus | 4.277 | LD | FS | 37 | 13 | 24 |
| Coccyzus erythropthalmus | 3.902 | LD | FS | 31 | 9 | 22 |
| Colaptes chrysoides | 4.705 | R | O | 1 | 1 | |
| Colinus virginianus | 5.112 | R | G | 37 | 18 | 19 |
| Columbina inca | 3.823 | R | O | 3 | 2 | 1 |
| Columbina passerina | 3.442 | R | FS | 7 | 7 | |
| Contopus cooperi | 3.571 | LD | FS | 20 | 13 | 7 |
| Contopus sordidulus | 2.561 | LD | FS | 15 | 8 | 7 |
| Contopus virens | 2.625 | LD | FS | 37 | 21 | 16 |
| Coragyps atratus | 7.414 | R | G | 23 | 21 | 2 |
| Corvus brachyrhynchos | 6.207 | R | O | 48 | 3 | 45 |
| Corvus corax | 7.149 | R | O | 26 | 20 | 6 |
| Corvus cryptoleucus | 6.280 | R | G | 5 | 4 | 1 |
| Corvus ossifragus | 5.652 | R | W | 22 | 21 | 1 |
| Crotophaga sulcirostris | 4.409 | SD | O | 1 | 1 | |
| Cyanocitta cristata | 4.329 | R | FS | 39 | 7 | 32 |
| Cyanocitta stelleri | 4.783 | R | FS | 10 | 4 | 6 |
| Cyanocorax yncas | 4.280 | R | FS | 1 | 1 | |
| Cypseloides niger | 3.693 | LD | FS | 2 | 1 | 1 |
| Dendragapus obscurus | 6.965 | R | FS | 6 | 3 | 3 |
| Dendrocygna autumnalis | 6.624 | LD | W | 3 | 3 | |
| Dendrocygna bicolor | 6.629 | LD | W | 2 | 2 | |
| Dendroica caerulescens | 2.317 | LD | FS | 14 | 10 | 4 |
| Dendroica castanea | 2.423 | LD | FS | 5 | 1 | 4 |
| Dendroica cerulea | 2.203 | LD | FS | 16 | 8 | 8 |
| Dendroica coronata | 2.474 | R | FS | 21 | 6 | 15 |
| Dendroica discolor | 2.035 | LD | FS | 28 | 26 | 2 |
| Dendroica dominica | 2.272 | LD | FS | 21 | 19 | 2 |
| Dendroica fusca | 2.277 | LD | FS | 14 | 4 | 10 |
| Dendroica graciae | 2.054 | LD | FS | 4 | 2 | 2 |
| Dendroica magnolia | 2.098 | LD | FS | 12 | 1 | 11 |
| Dendroica nigrescens | 2.073 | LD | FS | 9 | 9 | |
| Dendroica occidentalis | 2.246 | LD | FS | 3 | 1 | 2 |
| Dendroica palmarum | 2.158 | LD | W | 4 | 1 | 3 |
| Dendroica pensylvanica | 2.230 | LD | FS | 19 | 4 | 15 |
| Dendroica petechia | 2.249 | LD | FS | 44 | 6 | 38 |
| Dendroica pinus | 2.366 | R | FS | 32 | 29 | 3 |
| Dendroica striata | 2.472 | LD | FS | 3 | | 3 |
| Dendroica tigrina | 2.308 | LD | FS | 7 | 1 | 6 |
| Dendroica townsendi | 2.180 | LD | FS | 4 | 2 | 2 |
| Dendroica virens | 2.163 | LD | FS | 19 | 8 | 11 |
| Dolichonyx oryzivorus | 3.452 | LD | G | 27 | 5 | 22 |
| Dryocopus pileatus | 5.660 | R | FS | 39 | 24 | 15 |
| Dumetella carolinensis | 3.861 | LD | FS | 45 | 8 | 37 |
| Egretta caerulea | 5.827 | LD | W | 16 | 15 | 1 |
| Egretta thula | 5.920 | M | W | 22 | 10 | 12 |
| Egretta tricolor | 5.926 | R | O | 9 | 8 | 1 |
| Elanoides forficatus | 6.110 | LD | FS | 6 | 5 | 1 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Elanus leucurus | 5.670 | R | G | 2 | 1 | 1 |
| Empidonax alnorum traillii | 2.595 | LD | FS | 38 | 11 | 27 |
| Empidonax difficilis occidentalis | 2.327 | LD | FS | 12 | 6 | 6 |
| Empidonax flaviventris | 2.485 | LD | FS | 7 | | 7 |
| Empidonax hammondii | 2.347 | LD | FS | 8 | 5 | 3 |
| Empidonax minimus | 2.442 | LD | FS | 26 | 4 | 22 |
| Empidonax oberholseri | 2.339 | LD | FS | 10 | 9 | 1 |
| Empidonax virescens | 2.569 | LD | FS | 28 | 25 | 3 |
| Empidonax wrightii | 2.510 | LD | FS | 9 | 9 | |
| Eremophila alpestris | 3.553 | R | G | 42 | 15 | 27 |
| Eudocimus albus | 6.802 | R | W | 7 | 6 | 1 |
| Euphagus carolinus | 4.090 | SD | W | 4 | | 4 |
| Euphagus cyanocephalus | 4.138 | R | G | 16 | 8 | 8 |
| Falco columbarius | 5.250 | R | O | 7 | | 7 |
| Falco mexicanus | 6.599 | R | G | 15 | 13 | 2 |
| Falco peregrinus | 6.811 | R | O | 7 | 4 | 3 |
| Falco sparverius | 4.718 | R | G | 48 | 12 | 36 |
| Fulica americana | 6.465 | SD | W | 21 | 8 | 13 |
| Gallinago gallinago | 4.722 | R | W | 21 | 1 | 20 |
| Gallinula chloropus | 5.789 | SD | W | 10 | 7 | 3 |
| Geococcyx californianus | 5.788 | R | FS | 9 | 6 | 3 |
| Geothlypis trichas | 2.246 | M | W | 48 | 8 | 40 |
| Glaucidium gnoma | 4.175 | R | FS | 9 | 2 | 7 |
| Grus canadensis | 8.406 | SD | W | 13 | 3 | 10 |
| Gymnorhinus cyanocephalus | 4.654 | R | FS | 9 | 9 | |
| Haliaeetus leucocephalus | 8.464 | R | W | 21 | 7 | 14 |
| Helmitheros vermivorum | 2.653 | LD | FS | 21 | 16 | 5 |
| Himantopus mexicanus | 5.222 | R | W | 11 | 11 | |
| Hirundo rustica | 2.789 | LD | G | 48 | 9 | 39 |
| Hylocichla mustelina | 3.915 | LD | FS | 34 | 27 | 7 |
| Icteria virens | 3.215 | LD | FS | 41 | 22 | 19 |
| Icterus bullockii | 3.611 | LD | FS | 17 | 14 | 3 |
| Icterus cucullatus | 3.190 | LD | FS | 4 | 4 | |
| Icterus galbula | 3.492 | LD | FS | 36 | 9 | 27 |
| Icterus parisorum | 3.589 | LD | O | 6 | 5 | 1 |
| Icterus spurius | 3.091 | LD | FS | 36 | 8 | 28 |
| Ictinia mississippiensis | 5.628 | R | FS | 13 | 2 | 11 |
| Ixobrychus exilis | 4.417 | LD | W | 9 | 6 | 3 |
| Junco hyemalis | 2.924 | R | FS | 26 | 12 | 14 |
| Lanius ludovicianus | 3.864 | R | FS | 37 | 14 | 23 |
| Limnothlypis swainsonii | 2.809 | LD | FS | 12 | 10 | 2 |
| Limosa fedoa | 5.882 | M | G | 4 | | 4 |
| Lophodytes cucullatus | 6.425 | R | W | 16 | 10 | 6 |
| Loxia curvirostra | 3.839 | R | FS | 14 | 6 | 8 |
| Loxia leucoptera | 3.245 | R | FS | 3 | | 3 |
| Megaceryle alcyon | 5.168 | R | W | 47 | 4 | 43 |
| Megascops asio | 5.196 | R | FS | 30 | 4 | 26 |
| Megascops kennicottii | 5.170 | R | FS | 5 | 4 | 1 |
| Melanerpes aurifrons | 4.393 | R | FS | 1 | 1 | |
| Melanerpes carolinus | 4.243 | R | FS | 31 | 27 | 4 |
| Melanerpes erythrocephalus | 4.316 | R | FS | 35 | 6 | 29 |
| Melanerpes formicivorus | 4.378 | R | FS | 4 | 1 | 3 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Melanerpes lewis | 4.663 | R | O | 9 | 7 | 2 |
| Melanerpes uropygialis | 4.172 | R | FS | 1 | 1 | |
| Meleagris gallopavo | 8.708 | R | FS | 46 | 12 | 34 |
| Melospiza georgiana | 2.833 | R | W | 19 | 4 | 15 |
| Melospiza lincolnii | 2.809 | M | FS | 15 | 1 | 14 |
| Melospiza melodia | 2.996 | R | O | 42 | 14 | 28 |
| Melozone aberti | 3.828 | R | FS | 2 | 2 | |
| Melozone crissalis | 3.967 | R | FS | 2 | 2 | |
| Melozone fuscus | 3.793 | R | FS | 4 | 3 | 1 |
| Mimus polyglottos | 3.882 | R | FS | 40 | 14 | 26 |
| Mniotilta varia | 2.351 | LD | FS | 32 | 17 | 15 |
| Molothrus aeneus | 4.142 | SD | G | 4 | 2 | 2 |
| Molothrus ater | 3.741 | R | G | 48 | 18 | 30 |
| Myadestes townsendi | 3.481 | R | FS | 12 | 8 | 4 |
| Mycteria americana | 7.847 | R | W | 4 | 3 | 1 |
| Myiarchus cinerascens | 3.309 | LD | FS | 10 | 10 | |
| Myiarchus crinitus | 3.605 | LD | FS | 37 | 14 | 23 |
| Myiarchus tyrannulus | 3.609 | LD | FS | 2 | 1 | 1 |
| Nucifraga columbiana | 4.868 | R | FS | 11 | 6 | 5 |
| Numenius americanus | 6.374 | M | G | 13 | 10 | 3 |
| Nyctanassa violacea | 6.526 | M | W | 14 | 4 | 10 |
| Nycticorax nycticorax | 6.679 | M | W | 37 | 14 | 23 |
| Oporornis agilis | 2.643 | LD | FS | 3 | 1 | 2 |
| Oporornis formosus | 2.650 | LD | FS | 23 | 17 | 6 |
| Oporornis philadelphia | 2.464 | LD | FS | 10 | 1 | 9 |
| Oporornis tolmiei | 2.442 | LD | FS | 11 | 5 | 6 |
| Oreortyx pictus | 5.507 | R | FS | 2 | 1 | 1 |
| Oreoscoptes montanus | 3.766 | SD | FS | 11 | 11 | |
| Oxyura jamaicensis | 6.415 | R | W | 12 | 8 | 4 |
| Pandion haliaetus | 7.304 | R | W | 27 | 11 | 16 |
| Parabuteo unicinctus | 6.743 | R | FS | 2 | 1 | 1 |
| Parkesia motacilla | 3.114 | LD | W | 30 | 22 | 8 |
| Parkesia noveboracensis | 2.815 | LD | W | 14 | | 14 |
| Parula americana | 2.015 | LD | FS | 31 | 27 | 4 |
| Parus atricapillus | 2.451 | R | FS | 32 | 2 | 30 |
| Parus carolinensis | 2.303 | R | FS | 23 | 15 | 8 |
| Parus gambeli | 2.434 | R | FS | 11 | 9 | 2 |
| Parus hudsonicus | 2.282 | R | FS | 6 | 1 | 5 |
| Parus rufescens | 2.241 | R | FS | 5 | 2 | 3 |
| Passerculus sandwichensis | 2.890 | R | O | 31 | 7 | 24 |
| Passerella iliaca | 3.508 | R | FS | 9 | 5 | 4 |
| Passerina amoena | 2.741 | LD | FS | 13 | 12 | 1 |
| Passerina caerulea | 3.311 | LD | FS | 31 | 16 | 15 |
| Passerina ciris | 2.744 | LD | O | 9 | | 9 |
| Passerina cyanea | 2.688 | LD | FS | 43 | 20 | 23 |
| Patagioenas fasciata | 5.864 | R | FS | 7 | 3 | 4 |
| Pelecanus erythrorhynchos | 8.639 | M | W | 15 | 3 | 12 |
| Perisoreus canadensis | 4.272 | R | FS | 12 | | 12 |
| Petrochelidon fulva | 2.952 | LD | O | 1 | 1 | |
| Petrochelidon pyrrhonota | 3.157 | LD | O | 42 | 8 | 34 |
| Peucaea aestivalis | 2.953 | R | FS | 10 | 7 | 3 |
| Peucaea cassinii | 2.939 | SD | G | 4 | 2 | 2 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Phainopepla nitens | 3.096 | R | O | 5 | 5 | |
| Phalaenoptilus nuttallii | 3.878 | R | FS | 13 | 11 | 2 |
| Pheucticus ludovicianus | 3.813 | LD | FS | 25 | 10 | 15 |
| Pheucticus melanocephalus | 3.853 | LD | FS | 16 | 9 | 7 |
| Pica nuttalli | 5.069 | R | O | 1 | 1 | |
| Picoides albolarvatus | 4.113 | R | FS | 3 | 2 | 1 |
| Picoides arcticus | 4.238 | R | FS | 11 | | 11 |
| Picoides borealis | 3.871 | R | FS | 6 | 4 | 2 |
| Picoides dorsalis | 4.010 | R | FS | 4 | | 4 |
| Picoides nuttallii | 3.622 | R | FS | 1 | 1 | |
| Picoides pubescens | 3.285 | R | FS | 48 | 6 | 42 |
| Picoides scalaris | 3.475 | R | FS | 5 | 4 | 1 |
| Picoides villosus | 4.168 | R | FS | 48 | 6 | 42 |
| Pinicola enucleator | 4.032 | R | FS | 6 | | 6 |
| Pipilo chlorurus | 3.381 | M | FS | 10 | 8 | 2 |
| Pipilo erythrophthalmus | 3.690 | R | FS | 33 | 23 | 10 |
| Pipilo maculatus | 3.668 | R | FS | 14 | 8 | 6 |
| Piranga flava | 3.544 | LD | FS | 3 | | 3 |
| Piranga ludoviciana | 3.373 | LD | FS | 12 | 6 | 6 |
| Piranga olivacea | 3.454 | LD | FS | 32 | 25 | 7 |
| Piranga rubra | 3.364 | LD | FS | 25 | 23 | 2 |
| Platalea ajaja | 7.279 | R | W | 3 | 2 | 1 |
| Plegadis chihi | 6.432 | M | W | 7 | 6 | 1 |
| Plegadis falcinellus | 6.452 | M | W | 5 | 4 | 1 |
| Podilymbus podiceps | 6.031 | R | W | 31 | 19 | 12 |
| Polioptila caerulea | 1.792 | LD | FS | 41 | 39 | 2 |
| Polioptila melanura | 1.668 | R | FS | 5 | 5 | |
| Pooecetes gramineus | 3.246 | M | G | 34 | 11 | 23 |
| Porphyrio martinicus | 5.464 | LD | W | 4 | 4 | |
| Porzana carolina | 4.401 | M | W | 18 | 7 | 11 |
| Progne subis | 3.985 | LD | FS | 43 | 14 | 29 |
| Protonotaria citrea | 2.812 | LD | FS | 23 | 5 | 18 |
| Psaltriparus minimus | 1.639 | R | FS | 8 | 3 | 5 |
| Pyrocephalus rubinus | 2.573 | R | O | 2 | 2 | |
| Quiscalus major | 5.066 | R | W | 9 | 8 | 1 |
| Quiscalus mexicanus | 5.130 | R | W | 11 | 6 | 5 |
| Quiscalus quiscula | 4.664 | R | O | 41 | 6 | 35 |
| Rallus elegans | 5.819 | SD | W | 7 | 3 | 4 |
| Rallus limicola | 4.428 | R | W | 16 | 11 | 5 |
| Rallus longirostris | 5.605 | R | O | 8 | 7 | 1 |
| Recurvirostra americana | 5.719 | R | W | 16 | 4 | 12 |
| Regulus calendula | 1.825 | R | FS | 18 | 4 | 14 |
| Regulus satrapa | 1.825 | R | FS | 22 | 10 | 12 |
| Rhynchophanes mccownii | 3.246 | SD | G | 3 | 2 | 1 |
| Riparia riparia | 2.599 | LD | W | 34 | 3 | 31 |
| Rynchops niger | 5.709 | R | O | 7 | 6 | 1 |
| Salpinctes obsoletus | 2.781 | R | O | 16 | 11 | 5 |
| Sayornis nigricans | 2.926 | R | W | 6 | 3 | 3 |
| Sayornis phoebe | 2.907 | R | FS | 37 | 10 | 27 |
| Sayornis saya | 3.040 | R | G | 16 | 12 | 4 |
| Scolopax minor | 5.286 | R | FS | 24 | 20 | 4 |
| Seiurus aurocapilla | 2.955 | LD | FS | 33 | 11 | 22 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Selasphorus platycercus | 1.267 | LD | FS | 8 | 4 | 4 |
| Selasphorus rufus | 1.238 | LD | FS | 6 | 3 | 3 |
| Selasphorus sasin | 1.213 | LD | FS | 1 | 1 | |
| Setophaga ruticilla | 2.110 | LD | FS | 37 | 7 | 30 |
| Sialia currucoides | 3.388 | R | O | 13 | 8 | 5 |
| Sialia mexicana | 3.275 | R | FS | 9 | 4 | 5 |
| Sialia sialis | 3.314 | R | FS | 39 | 20 | 19 |
| Sitta canadensis | 2.349 | R | FS | 22 | 8 | 14 |
| Sitta carolinensis | 3.056 | R | FS | 47 | 12 | 35 |
| Sitta pusilla | 2.322 | R | FS | 12 | 11 | 1 |
| Sitta pygmaea | 2.337 | R | FS | 5 | 3 | 2 |
| Sphyrapicus nuchalis | 3.909 | M | FS | 9 | 9 | |
| Sphyrapicus ruber | 4.060 | R | FS | 3 | 2 | 1 |
| Sphyrapicus thyroideus | 4.088 | R | FS | 9 | 7 | 2 |
| Sphyrapicus varius | 3.942 | R | FS | 11 | 1 | 10 |
| Spiza americana | 3.247 | LD | G | 23 | 3 | 20 |
| Spizella atrogularis | 2.425 | SD | FS | 4 | 2 | 2 |
| Spizella breweri | 2.389 | SD | FS | 12 | 10 | 2 |
| Spizella pallida | 2.416 | LD | G | 7 | 1 | 6 |
| Spizella passerina | 2.510 | R | FS | 47 | 21 | 26 |
| Spizella pusilla | 2.526 | R | G | 40 | 11 | 29 |
| Steganopus tricolor | 4.094 | LD | W | 14 | 1 | 13 |
| Stelgidopteryx serripennis | 2.842 | LD | W | 47 | 19 | 28 |
| Stellula calliope | 0.975 | LD | FS | 6 | 5 | 1 |
| Strix varia | 6.574 | R | FS | 34 | 15 | 19 |
| Sturnella magna | 4.483 | R | G | 37 | 33 | 4 |
| Sturnella neglecta | 4.612 | R | G | 25 | 10 | 15 |
| Tachycineta bicolor | 3.039 | M | W | 39 | 3 | 36 |
| Tachycineta thalassina | 2.650 | LD | FS | 12 | 10 | 2 |
| Thryomanes bewickii | 2.293 | SD | FS | 21 | 8 | 13 |
| Thryothorus ludovicianus | 2.993 | R | FS | 28 | 27 | 1 |
| Toxostoma bendirei | 4.130 | SD | O | 3 | 3 | |
| Toxostoma crissale | 4.138 | R | FS | 4 | 4 | |
| Toxostoma curvirostre | 4.361 | R | FS | 4 | 3 | 1 |
| Toxostoma lecontei | 4.126 | R | FS | 3 | 3 | |
| Toxostoma longirostre | 4.214 | R | FS | 1 | 1 | |
| Toxostoma redivivum | 4.436 | R | FS | 1 | 1 | |
| Toxostoma rufum | 4.231 | R | FS | 40 | 9 | 31 |
| Troglodytes aedon | 2.393 | M | FS | 45 | 15 | 30 |
| Troglodytes troglodytes | 2.225 | R | O | 11 | 4 | 7 |
| Turdus migratorius | 4.379 | R | FS | 47 | 11 | 36 |
| Tympanuchus cupido | 6.763 | R | G | 6 | | 6 |
| Tympanuchus phasianellus | 6.786 | R | FS | 6 | | 6 |
| Tyrannus couchii | 3.750 | SD | FS | 1 | 1 | |
| Tyrannus forficatus | 3.696 | LD | O | 7 | | 7 |
| Tyrannus tyrannus | 3.655 | LD | O | 45 | 4 | 41 |
| Tyrannus verticalis | 3.652 | LD | G | 20 | 10 | 10 |
| Tyrannus vociferans | 3.766 | LD | O | 7 | 5 | 2 |
| Tyto alba | 5.967 | R | G | 8 | 4 | 4 |
| Vermivora celata | 2.098 | M | FS | 9 | 5 | 4 |
| Vermivora chrysoptera | 2.169 | LD | FS | 14 | 7 | 7 |
| Vermivora cyanoptera | 2.134 | LD | G | 22 | 16 | 6 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Vermivora luciae | 1.766 | SD | FS | 3 | 3 | |
| Vermivora peregrina | 2.262 | LD | FS | 7 | 1 | 6 |
| Vermivora ruficapilla | 2.092 | LD | FS | 15 | 1 | 14 |
| Vermivora virginiae | 2.001 | LD | FS | 4 | 3 | 1 |
| Vireo bellii | 2.140 | LD | FS | 14 | 4 | 10 |
| Vireo cassinii | 2.688 | LD | FS | 5 | 2 | 3 |
| Vireo flavifrons | 2.862 | LD | FS | 36 | 30 | 6 |
| Vireo gilvus | 2.595 | LD | FS | 40 | 13 | 27 |
| Vireo griseus | 2.460 | LD | FS | 24 | 22 | 2 |
| Vireo huttoni | 2.425 | R | FS | 4 | 2 | 2 |
| Vireo olivaceus | 2.818 | LD | FS | 41 | 5 | 36 |
| Vireo philadelphicus | 2.472 | LD | FS | 7 | 1 | 6 |
| Vireo plumbeus | 2.797 | LD | FS | 8 | 7 | 1 |
| Vireo solitarius | 2.728 | M | FS | 20 | 6 | 14 |
| Vireo vicinior | 2.549 | SD | FS | 5 | 4 | 1 |
| Wilsonia canadensis | 2.308 | LD | FS | 14 | 1 | 13 |
| Wilsonia citrina | 2.356 | LD | FS | 24 | 22 | 2 |
| Wilsonia pusilla | 1.924 | LD | FS | 13 | 2 | 11 |
| Xanthocephalus xanthocephalus | 4.167 | SD | W | 20 | 7 | 13 |
| Zenaida asiatica | 4.934 | LD | FS | 5 | 5 | |
| Zenaida macroura | 4.779 | R | O | 48 | 19 | 29 |
| Zonotrichia albicollis | 3.195 | R | FS | 10 | | 10 |
| Zonotrichia leucophrys | 3.350 | R | O | 9 | 7 | 2 |
| Zoothera naevia | 4.365 | R | FS | 5 | 2 | 3 |

**Online Resource 4.** The 48 USA states from which bird species population trend data was available.

| State | First year of monitoring data | Number of species included: | | |
|---|---|---|---|---|
| | | Total | in CST+ group | in CST- group |
| Alabama | 1968 | 129 | 37 | 92 |
| Arizona | 1968 | 160 | 83 | 77 |
| Arkansas | 1968 | 117 | 45 | 72 |
| California | 1968 | 215 | 106 | 109 |
| Colorado | 1968 | 188 | 127 | 61 |
| Connecticut | 1968 | 124 | 23 | 101 |
| Delaware | 1968 | 114 | 48 | 66 |
| Florida | 1968 | 117 | 17 | 100 |
| Georgia | 1968 | 124 | 45 | 79 |
| Idaho | 1968 | 172 | 86 | 86 |
| Illinois | 1968 | 129 | 49 | 80 |
| Indiana | 1968 | 122 | 44 | 78 |
| Iowa | 1968 | 105 | 40 | 65 |
| Kansas | 1968 | 125 | 43 | 82 |
| Kentucky | 1968 | 115 | 36 | 79 |
| Louisiana | 1968 | 126 | 55 | 71 |
| Maine | 1968 | 143 | 67 | 76 |
| Maryland | 1968 | 146 | 62 | 84 |
| Massachusetts | 1968 | 128 | 43 | 85 |
| Michigan | 1968 | 166 | 60 | 106 |
| Minnesota | 1968 | 179 | 119 | 60 |
| Mississippi | 1968 | 108 | 30 | 78 |
| Missouri | 1968 | 125 | 55 | 70 |
| Montana | 1968 | 177 | 118 | 59 |
| Nebraska | 1968 | 121 | 25 | 96 |
| Nevada | 1968 | 123 | 59 | 64 |
| New Hampshire | 1968 | 136 | 66 | 70 |
| New Jersey | 1968 | 125 | 44 | 81 |
| New Mexico | 1968 | 169 | 88 | 81 |
| New York | 1968 | 160 | 50 | 110 |
| North Carolina | 1968 | 137 | 52 | 85 |
| North Dakota | 1968 | 135 | 101 | 34 |
| Ohio | 1968 | 125 | 50 | 75 |
| Oklahoma | 1968 | 124 | 39 | 85 |
| Oregon | 1968 | 186 | 90 | 96 |
| Pennsylvania | 1968 | 148 | 62 | 86 |
| Rhode Island | 1968 | 66 | 15 | 51 |
| South Carolina | 1968 | 110 | 38 | 72 |
| South Dakota | 1968 | 152 | 95 | 57 |
| Tennessee | 1968 | 117 | 40 | 77 |
| Texas | 1968 | 202 | 89 | 113 |
| Utah | 1968 | 166 | 97 | 69 |
| Vermont | 1968 | 125 | 44 | 81 |
| Virginia | 1968 | 123 | 52 | 71 |
| Washington | 1968 | 174 | 112 | 62 |
| West Virginia | 1968 | 132 | 40 | 92 |

| | | | | |
|---|---|---|---|---|
| Wisconsin | 1968 | 173 | 79 | 94 |
| Wyoming | 1968 | 177 | 107 | 70 |

**Online Resource 5.** State-level climate suitability trends (CST), population trends and the period over which these were calculated for European and North American bird species.

| Region | Species | State | Climate suitability trend | Population trend | Period over which trends are measured | |
|---|---|---|---|---|---|---|
| | | | | | Start year | End year |
| Europe | Acrocephalus palustris | Austria | 0.006 | -0.041 | 1998 | 2009 |
| Europe | Aegithalos caudatus | Austria | 0.011 | -0.008 | 1998 | 2009 |
| Europe | Alauda arvensis | Austria | 0.014 | -0.029 | 1998 | 2009 |
| Europe | Anas platyrhynchos | Austria | 0.003 | -0.009 | 1998 | 2009 |
| Europe | Anthus trivialis | Austria | -0.010 | -0.065 | 1998 | 2009 |
| Europe | Apus apus | Austria | 0.002 | -0.015 | 1998 | 2009 |
| Europe | Ardea cinerea | Austria | 0.009 | -0.035 | 1998 | 2009 |
| Europe | Buteo buteo | Austria | 0.009 | 0.000 | 1998 | 2009 |
| Europe | Carduelis cannabina | Austria | 0.004 | -0.040 | 1998 | 2009 |
| Europe | Carduelis carduelis | Austria | 0.013 | -0.017 | 1998 | 2009 |
| Europe | Carduelis chloris | Austria | 0.014 | 0.005 | 1998 | 2009 |
| Europe | Certhia brachydactyla | Austria | 0.025 | -0.007 | 1998 | 2009 |
| Europe | Certhia familiaris | Austria | -0.008 | -0.014 | 1998 | 2009 |
| Europe | Circus aeruginosus | Austria | 0.005 | -0.023 | 1998 | 2009 |
| Europe | Coccothraustes coccothraustes | Austria | 0.011 | -0.012 | 1998 | 2009 |
| Europe | Columba oenas | Austria | 0.003 | 0.014 | 1998 | 2009 |
| Europe | Columba palumbus | Austria | 0.009 | 0.017 | 1998 | 2009 |
| Europe | Corvus corax | Austria | -0.015 | -0.035 | 1998 | 2009 |
| Europe | Corvus corone | Austria | 0.012 | 0.021 | 1998 | 2009 |
| Europe | Corvus monedula | Austria | 0.010 | 0.070 | 1998 | 2009 |
| Europe | Cuculus canorus | Austria | 0.011 | -0.014 | 1998 | 2009 |
| Europe | Delichon urbica | Austria | 0.004 | -0.044 | 1998 | 2009 |
| Europe | Dendrocopos major | Austria | 0.006 | 0.012 | 1998 | 2009 |
| Europe | Dendrocopos medius | Austria | 0.010 | 0.078 | 1998 | 2008 |
| Europe | Dryocopus martius | Austria | -0.001 | 0.027 | 1998 | 2009 |
| Europe | Emberiza citrinella | Austria | 0.009 | -0.016 | 1998 | 2009 |
| Europe | Erithacus rubecula | Austria | 0.005 | -0.005 | 1998 | 2009 |
| Europe | Falco tinnunculus | Austria | 0.011 | 0.011 | 1998 | 2009 |
| Europe | Ficedula albicollis | Austria | 0.013 | 0.089 | 1998 | 2009 |
| Europe | Fringilla coelebs | Austria | 0.009 | -0.001 | 1998 | 2009 |
| Europe | Garrulus glandarius | Austria | 0.005 | -0.013 | 1998 | 2009 |
| Europe | Hippolais icterina | Austria | -0.012 | -0.007 | 1998 | 2009 |
| Europe | Hirundo rustica | Austria | 0.002 | -0.008 | 1998 | 2009 |
| Europe | Jynx torquilla | Austria | -0.001 | -0.011 | 1998 | 2009 |
| Europe | Lanius collurio | Austria | 0.005 | -0.027 | 1998 | 2009 |
| Europe | Luscinia megarhynchos | Austria | 0.027 | 0.020 | 1998 | 2009 |
| Europe | Miliaria calandra | Austria | 0.017 | -0.076 | 1998 | 2009 |
| Europe | Motacilla alba | Austria | 0.003 | -0.013 | 1998 | 2009 |
| Europe | Muscicapa striata | Austria | -0.001 | -0.009 | 1998 | 2009 |
| Europe | Oriolus oriolus | Austria | 0.012 | 0.023 | 1998 | 2009 |
| Europe | Parus ater | Austria | 0.001 | -0.025 | 1998 | 2009 |
| Europe | Parus caeruleus | Austria | 0.010 | 0.002 | 1998 | 2009 |
| Europe | Parus cristatus | Austria | -0.009 | -0.023 | 1998 | 2009 |
| Europe | Parus major | Austria | 0.009 | -0.008 | 1998 | 2009 |
| Europe | Parus montanus | Austria | -0.022 | -0.027 | 1998 | 2009 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Europe | Parus palustris | Austria | 0.013 | -0.012 | 1998 | 2009 |
| Europe | Passer domesticus | Austria | 0.006 | 0.045 | 1998 | 2009 |
| Europe | Passer montanus | Austria | 0.013 | 0.015 | 1998 | 2009 |
| Europe | Perdix perdix | Austria | 0.014 | -0.030 | 1998 | 2009 |
| Europe | Phoenicurus ochruros | Austria | 0.012 | 0.004 | 1998 | 2009 |

…first 50 species-state combinations shown only (8446 in total).

**Online Resource 6**. Full model selection table for the 27 models fitted to test for variation in avian responses to climate change in relation to ecological traits in Europe. Models within 6 ΔAICc units of that with the lowest AICc are emboldened and models within this 6 ΔAICc set which are not more complex versions of a simpler nested model of lower AICc value are grey highlighted. These grey highlighted models are the "best" AICc models reported in the main text. For each model, shown is the log likelihood (logLik), number of estimable parameters (df), AICc value, difference in AICc between a model and that with the lowest AICc (Δ AICc) and the AICc model weight. X indicates inclusion of covariates and two-way interactions.

| Covariates and two-way interactions | | | | | | | Model fit and selection criteria | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| CST | Lmass | HAB | MIG | CST:Lmass | CST:HAB | CST:MIG | logLik | df | AICc | ΔAICc | Model weight |
| **X** | **X** | **X** | | **X** | **X** | | **3039.7** | **13** | **-6053.1** | **0.0** | **0.67** |
| **X** | **X** | **X** | **X** | **X** | **X** | | **3040.7** | **15** | **-6051.1** | **2.0** | **0.25** |
| **X** | **X** | **X** | **X** | **X** | **X** | **X** | **3041.4** | **17** | **-6048.5** | **4.6** | **0.07** |
| X | X | X | | X | | | 3031.8 | 10 | -6043.4 | 9.7 | 0.01 |
| X | X | | | X | | | 3028.1 | 7 | -6042.2 | 10.9 | 0.00 |
| X | X | X | X | X | | | 3032.6 | 12 | -6041.1 | 12.0 | 0.00 |
| X | X | | X | X | | | 3029.6 | 9 | -6041.1 | 12.0 | 0.00 |
| X | X | X | X | X | | X | 3034.3 | 14 | -6040.4 | 12.7 | 0.00 |
| X | X | | X | X | | X | 3031.3 | 11 | -6040.4 | 12.7 | 0.00 |
| X | X | X | | | X | | 3031.6 | 12 | -6039.1 | 14.0 | 0.00 |
| X | X | X | | | | | 3028.0 | 9 | -6037.8 | 15.3 | 0.00 |
| X | X | X | X | | X | | 3032.9 | 14 | -6037.5 | 15.6 | 0.00 |
| X | X | | | | | | 3024.8 | 6 | -6037.6 | 15.5 | 0.00 |
| X | X | X | X | | X | X | 3034.8 | 16 | -6037.2 | 15.9 | 0.00 |
| X | X | | X | | | | 3026.5 | 8 | -6036.9 | 16.2 | 0.00 |
| X | X | | X | | | X | 3028.3 | 10 | -6036.5 | 16.6 | 0.00 |
| X | X | X | X | | | | 3029.0 | 11 | -6035.9 | 17.2 | 0.00 |
| X | X | X | X | | | X | 3030.8 | 13 | -6035.5 | 17.6 | 0.00 |
| X | | X | X | | X | | 3030.5 | 13 | -6034.9 | 18.2 | 0.00 |
| X | | X | X | | X | X | 3032.5 | 15 | -6034.8 | 18.3 | 0.00 |
| X | | | X | | | | 3024.5 | 7 | -6035.0 | 18.1 | 0.00 |
| X | | | X | | | X | 3026.4 | 9 | -6034.7 | 18.4 | 0.00 |
| X | | X | | | X | | 3028.0 | 11 | -6033.8 | 19.3 | 0.00 |
| X | | | | | | | 3021.7 | 5 | -6033.4 | 19.7 | 0.00 |
| X | | X | X | | | | 3026.3 | 10 | -6032.5 | 20.6 | 0.00 |
| X | | X | X | | | X | 3028.2 | 12 | -6032.2 | 20.9 | 0.00 |
| X | | X | | | | | 3024.0 | 8 | -6031.9 | 21.2 | 0.00 |

**Online Resource 7**. Full model selection table for the 27 models fitted to test for variation in avian responses to climate change in relation to ecological traits in the USA. Models within 6 ΔAICc units of that with the lowest AICc are emboldened and models within this 6 ΔAICc set which are not more complex versions of a simpler nested model of lower AICc value are grey highlighted. These grey highlighted models are the "best" AICc models reported in the main text. For each model, shown is the log likelihood (logLik), number of estimable parameters (df), AICc value, difference in AICc between a model and that with the lowest AICc (Δ AICc) and the AICc model weight. X indicates inclusion of covariates and two-way interactions.

| Covariates and two-way interactions | | | | | | | Model fit and selection criteria | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| CST | Lmass | HAB | MIG | CST:Lmass | CST:HAB | CST:MIG | logLik | df | AICc | ΔAICc | Model weight |
| **X** | **X** | **X** | | **X** | **X** | | **10855.6** | **13** | **-21685.2** | **0.0** | **0.23** |
| **X** | **X** | **X** | | **X** | | | **10852.3** | **10** | **-21684.6** | **0.6** | **0.16** |
| **X** | **X** | **X** | | | **X** | | **10854.1** | **12** | **-21684.2** | **1.0** | **0.14** |
| **X** | **X** | | | **X** | | | **10849.0** | **7** | **-21684.0** | **1.3** | **0.12** |
| **X** | **X** | **X** | | | | | **10850.3** | **9** | **-21682.5** | **2.7** | **0.06** |
| **X** | **X** | | | | | | **10847.1** | **6** | **-21682.2** | **3.0** | **0.05** |
| **X** | **X** | **X** | **X** | **X** | **X** | | **10857.2** | **16** | **-21682.2** | **3.0** | **0.05** |
| **X** | **X** | **X** | **X** | **X** | | | **10853.9** | **13** | **-21681.7** | **3.5** | **0.04** |
| **X** | **X** | | **X** | **X** | | | **10850.8** | **10** | **-21681.5** | **3.7** | **0.03** |
| **X** | **X** | **X** | **X** | | **X** | | **10855.5** | **15** | **-21681.0** | **4.2** | **0.03** |
| **X** | **X** | **X** | **X** | | **X** | **X** | **10858.1** | **18** | **-21680.0** | **5.2** | **0.02** |
| **X** | **X** | | **X** | | | | **10848.8** | **9** | **-21679.6** | **5.7** | **0.01** |
| **X** | **X** | **X** | **X** | **X** | **X** | **X** | **10858.8** | **19** | **-21679.5** | **5.7** | **0.01** |
| **X** | **X** | **X** | **X** | | | | **10851.8** | **12** | **-21679.5** | **5.8** | **0.01** |
| X | X | | X | | | X | 10851.6 | 12 | -21679.1 | 6.2 | 0.01 |
| X | X | X | X | | | X | 10854.5 | 15 | -21678.8 | 6.4 | 0.01 |
| X | X | | X | X | | X | 10852.4 | 13 | -21678.8 | 6.4 | 0.01 |
| X | X | X | X | X | | X | 10855.4 | 16 | -21678.8 | 6.4 | 0.01 |
| X | | X | | | X | | 10846.0 | 11 | -21669.9 | 15.3 | 0.00 |
| X | | X | X | | X | | 10848.1 | 14 | -21668.2 | 17.0 | 0.00 |
| X | | X | | | | | 10842.1 | 8 | -21668.1 | 17.1 | 0.00 |
| X | | | | | | | 10838.9 | 5 | -21667.8 | 17.5 | 0.00 |
| X | | X | X | | X | X | 10850.6 | 17 | -21667.0 | 18.2 | 0.00 |
| X | | X | X | | | | 10844.3 | 11 | -21666.6 | 18.6 | 0.00 |
| X | | | X | | | | 10841.0 | 8 | -21666.0 | 19.2 | 0.00 |
| X | | X | X | | | X | 10847.0 | 14 | -21665.9 | 19.3 | 0.00 |
| X | | | X | | | X | 10843.6 | 11 | -21665.3 | 20.0 | 0.00 |

**Online Resource 8**. Regression coefficients b, their standard errors SE and the variance explained by random effects from the top selected linear mixed model of population trend in relation to climate suitability trend (CST) and ecological traits of species for Europe and the USA. See Table 2 in main text for variable codes. Coefficients for models involving the factor HAB represent differences in coefficient between the factor level shown and the reference level (Farmland).

| | Europe | | USA | |
|---|---|---|---|---|
| Independent variable | *b* | SE | *b* | SE |
| HAB | | | | |
| *Intercept (Farmland)* | -0.0168 | 0.0057 | -0.0252 | 0.0075 |
| *Forest* | 0.0093 | 0.0041 | 0.0146 | 0.0056 |
| *Inland Wetland* | 0.0044 | 0.006 | 0.0106 | 0.0065 |
| *Other* | 0.0025 | 0.0034 | 0.0143 | 0.0077 |
| Lmass | 0.0032 | 0.0012 | 0.005 | 0.0012 |
| CST | 0.918 | 0.2033 | -0.0327 | 0.1365 |
| CST:Lmass interaction | -0.1815 | 0.0455 | 0.045 | 0.0258 |
| CST:HAB interaction | | | | |
| *Forest* | -0.2342 | 0.1555 | 0.0912 | 0.0999 |
| *Inland Wetland* | 0.764 | 0.2691 | 0.1891 | 0.1197 |
| *Other* | -0.2365 | 0.1426 | -0.2024 | 0.1625 |

Random effects:
Europe: Species = 0.00025; Country = 0.00005, Residual = 0.00144
US: Species = 0.00096; Country = 0.00007, Residual = 0.00209

**Online Resource 9.** Analysis results (Tables A1 and A2) of the effects of ecological trait variables on the *r* vs. CST relationship for species with comparable mass ranges (10g ≤ mass ≤ 100g) on each continent. Analysis methods were the same as those described for the full species suite in the main text, with model structures as presented in Online Resources 6 and 7.

**TABLE A1** Top sets of linear mixed models of population trend (*r*) in relation to climate suitability trend (CST) and ecological traits of species with mass 10g – 100g for Europe and the USA. Both top sets include only those models simpler than the top model with ΔAICc <6. Models are shown in order of increasing AICc from the top model (shown in bold). Variables included in each model are denoted by codes: HAB = broad habitat association, Lmass = natural logarithm of body mass in grams. The log likelihood (logLik), number of fitted parameters (df) and Akaike weight (*w*) are shown for each model. Two-way interaction terms are coded by placing ":" between two variable codes.

| Continent | Variables retained | logLik | df | AICc | ΔAICc | *w* |
|---|---|---|---|---|---|---|
| Europe | **CST + Lmass + HAB + CST:Lmass** | **1892.8** | **10** | **-3765.4** | **0.0** | **0.22** |
| | CST + HAB | 1890.4 | 8 | -3764.7 | 0.6 | 0.16 |
| | CST + Lmass | 1888.8 | 7 | -3763.6 | 1.8 | 0.09 |
| | CST | 1886.5 | 5 | -3763.0 | 2.3 | 0.07 |
| USA | **CST + Lmass + HAB + CST:HAB** | **7056.9** | **12** | **-14089.9** | **0.0** | **0.53** |
| | CST + HAB | 7053.3 | 11 | -14084.5 | 5.3 | 0.04 |

**TABLE A2** Regression coefficients *b*, their standard errors SE and the variance explained by random effects from the top selected linear mixed model of population trend (*r*) in relation to climate suitability trend (CST) and ecological traits of species with mass 10g – 100g for Europe and the USA. Coefficients are only show for variables contained within the top models (Table A1). Coefficients for models involving the factor HAB represent differences in coefficient between the factor level shown and the reference level (*farmland*).

| | Europe | | USA | |
|---|---|---|---|---|
| Independent variable | *b* | SE | *b* | SE |
| HAB | | | | |
| *Intercept (Farmland)* | -0.0068 | 0.0135 | 0.0138 | 0.0104 |
| *Forest* | 0.0070 | 0.0053 | 0.0141 | 0.0054 |
| *Inland Wetland* | 0.0103 | 0.0090 | 0.0081 | 0.0076 |
| *Other* | -0.0037 | 0.0041 | 0.0178 | 0.0080 |
| Lmass | 0.0009 | 0.0040 | -0.0073 | 0.0027 |
| CST | 1.0188 | 0.3806 | -0.0010 | 0.0930 |
| CST:Lmass interaction | -0.2564 | 0.1224 | | |
| CST:HAB interaction | | | | |
| *Forest* | | | 0.1965 | 0.1039 |
| *Inland Wetland* | | | -0.2185 | 0.1982 |
| *Other* | | | 0.3977 | 0.1460 |

Random effects:

Europe: Species = 0.00032; Country = 0.00007, Residual = 0.00144

US: Species = 0.00049; Country = 0.00007, Residual = 0.00153