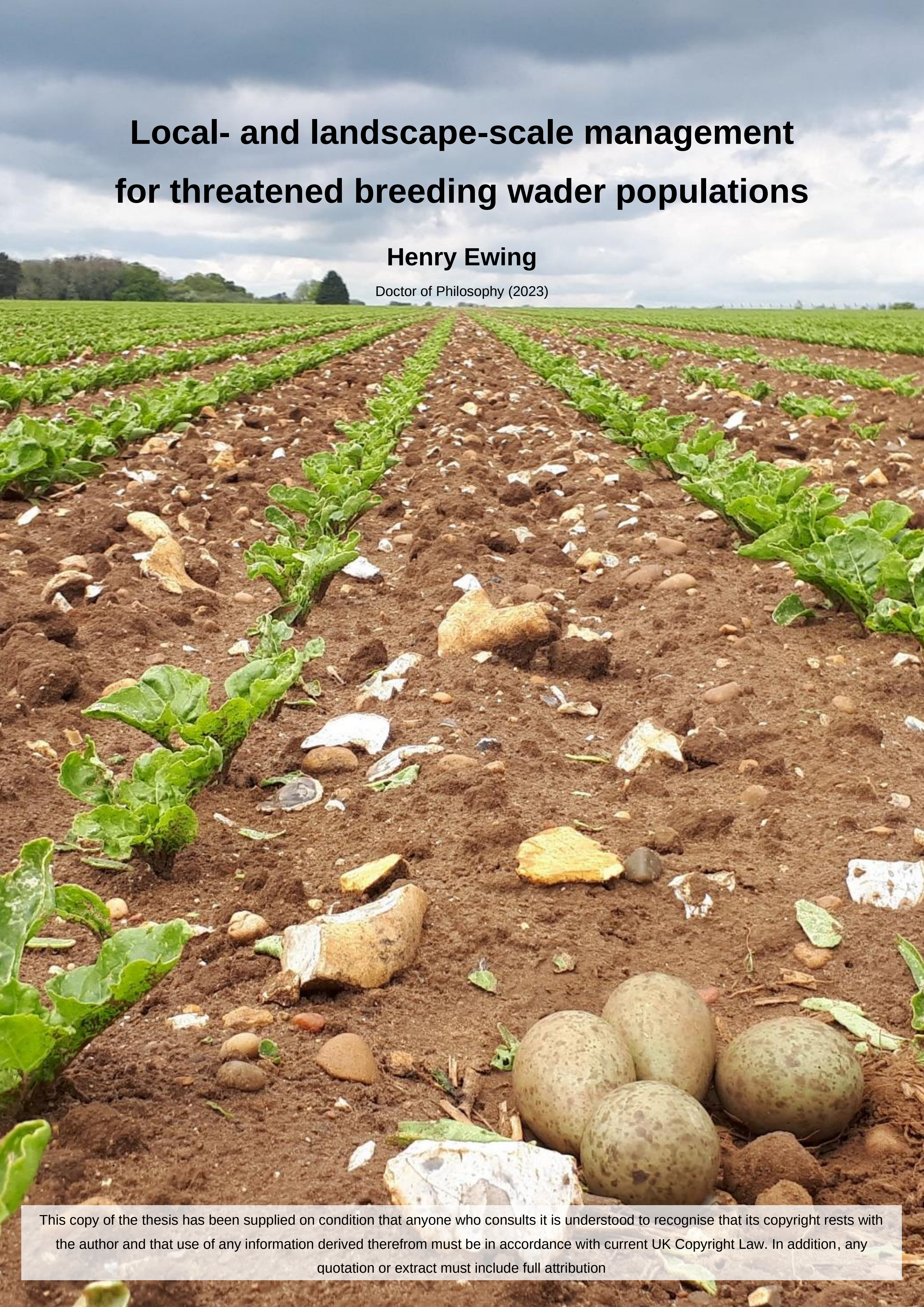


Local- and landscape-scale management for threatened breeding wader populations

Henry Ewing

Doctor of Philosophy (2023)

This thesis is dedicated to my father, Martyn Ewing (27th March 1961 – 19th October 2011), without whom I would have never picked up a pair of binoculars, and discovered my love of bird watching, agriculture and the Norfolk countryside.

Abstract

Persistent declines of widespread, formerly common species are threatening global biodiversity and ecosystem services, but actions to tackle such declines have so far been insufficient. New strategies are required to facilitate species recovery and must include targeted actions capable of boosting low demographic rates (survival and/or productivity). A group of species for which such actions are increasingly required are waders *Charadriiforms spp*., of which the Eurasian curlew *Numenius arquata* is a particularly widespread but vulnerable species, with unsustainably low rates of breeding productivity contributing to ongoing population declines across Europe. In this thesis, intensive, field-based monitoring of demographic variation in a lowland curlew population in Breckland, eastern England, is used to inform the development of conceptual frameworks and simulation models to identify appropriate conservation actions and explore the benefits that such approaches could deliver. Curlew breed at very low densities across a range of habitats in Breckland, but consistently high rates of nest predation across the landscape mean that sustainable levels of breeding productivity were not achieved in any of the four study years. However, access to cover vegetation (> 40 cm height) was associated with an increased probability of chicks fledging, and the use and benefits of cover vegetation increased with chick age. Most curlew in Breckland breed in open, grassland habitats, but breeding successes were more frequent for the few curlew breeding in arable-dominated areas, highlighting the need for habitat-specific conservation actions. Simulation modelling suggested that the most efficient and effective actions to boost curlew breeding productivity would involve a combination of predator-exclusion fencing and maintenance or provision of cover vegetation in the few remaining areas with large numbers of breeding curlew. Such actions are likely to require multi-stakeholder nature recovery programmes to save this iconic but increasingly threatened species.

Access Condition and Agreement

Each deposit in UEA Digital Repository is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of the Data Collections is not permitted, except that material may be duplicated by you for your research use or for educational purposes in electronic or print form. You must obtain permission from the copyright holder, usually the author, for any other use. Exceptions only apply where a deposit may be explicitly provided under a stated licence, such as a Creative Commons licence or Open Government licence.

Electronic or print copies may not be offered, whether for sale or otherwise to anyone, unless explicitly stated under a Creative Commons or Open Government license. Unauthorised reproduction, editing or reformatting for resale purposes is explicitly prohibited (except where approved by the copyright holder themselves) and UEA reserves the right to take immediate ‘take down’ action on behalf of the copyright and/or rights holder if this Access condition of the UEA Digital Repository is breached. Any material in this database has been supplied on the understanding that it is copyright material and that no quotation from the material may be published without proper acknowledgement.

Contents

Acknowledgements

First, I'd like to say a huge thank you to my inspirational team of supervisors; Jenny Gill, Jen Smart, Sam Franks and Niall Burton. You've all made my PhD an incredibly fun and rewarding experience, and I feel privileged to have had such a supportive team pushing me forwards – I'm very much looking forward to working with you all in the future. A special mention goes to Jenny, without whom I would never have got this far. Your infectious enthusiasm for science and waders has kept me motivated throughout and you've made me believe in my ability as a scientist. You're an outstanding supervisor and I appreciate everything you've done for me.

Thank you to the EnvEast DTP and NERC for funding this PhD – keep funding applied ecology research! Also, massive thank you to the British Trust of Ornithology (and their major donors) for supporting me throughout my PhD, but particularly during the last six months – I would have been very poor without you. Thank you as well to the RSPB for letting me borrow Jen and some nest cameras, and to the Defence Infrastructure Organisation for paying for my beautiful fieldwork trucks.

UEA's Centre for Ecology, Evolution and Conservation has been a brilliant place to do a PhD and my second home for the last 11+ years. I've loved every minute of it and will be sad to leave. There are many, many awesome people who have passed through BIO since I've been here but the following deserve a special mention for putting up with me during the last few months of PhD stress; Enya O'Reilly (desk neighbour), Imogen Ryan (daily hugs), Elie Kent (BESt conference pal), Claire Buchan (my fave), Nat Zielonka (OG curlew boss), Jen Livesey (10pm office club), Alex Siddall (second lunches), Stephen Vickers (birding with Colin McRae), Kirsty Franklin (Jenny's fave), Mabel Sydney (BIO drinks CEO), Emily Fowler (post-BIO drinks carer), Dave Collins (OG BIO drinks CEO), Will Nash (legend), Ryan Brock (bikes), Nathan McConnell (pastries), Cat Morrison (best laugh), Iain Barr (OG undergrad supervisor), Simon Butler (Mahindra-ed), Richard Davies (estuaries), and Phil Leftwich, Becky Lewis and Ellen Bell (Ireland). Sorry if I've forgotten anyone but I love you all, even if you aren't on this list – thank you for being the best colleagues, friends and BIO drinks pals. Thanks too to Elizabeth Hare for being a great MSc project student.

A couple more special UEA CEEC people who I wouldn't have reached this stage without; Becky Laidlaw and Phil Saunders. Phil gave me my first few opportunities as a research assistant by recommending me for a position in China and then asking me to work with him in Cyprus. Phil also introduced me to Becky who got me addicted to waders and nest searching (and those Icelandic cinnamon snacks), introduced me to Jenny, and is the loveliest person I’ve ever worked with. Thank you for putting up with me (especially my driving), for supporting me and for being great friends and mentors.

Outside of CEEC, I’d like to thank all the many land owners, managers, farmers, gamekeepers, graziers, conservationists and other members of the Breckland community who enabled fieldwork to run smoothly and were friendly faces throughout my time chasing curlew around the Brecks – looking forward to working with you all as a BTO Research Ecologist. Big thanks also to Nigel and Jacquie Clark, and the Wash Wader Research Group for assisting with curlew catching, ringing and tagging – you’re brilliant. Also to Mary Colwell, curlew PR agent and an all-round great person to be representing the study species that I love so much – thank you.

Finally, thank you to my best mate, Josh Jenkins-Shaw, who’s been with me since day one of undergrad, helped me rediscover my love of ornithology and is always there for chats about birds, beetles, beers, bikes and other stuff beginning with B. Thanks too to Jen Donelan, Jamie Murphy and Olivia Weekes for being such great friends.

The absolute last thank you, goes to my mum, Sarah – I couldn’t have done any of this without you (and the 2 am meals). I’ll move out now, I promise.

Author contributions

The chapters in these thesis are collaborative efforts, although in each case the majority of the work is my own.

Author list: Harry Ewing, Jennifer A. Gill, Samantha E. Franks, Jennifer Smart, Niall Burton, Catriona Morrison and Elizabeth Hare

In Chapters 2 – 5 of this thesis I collected and analysed all data and led the writing, JAG, SEF, JS and NB contributed to study design and production of chapters. EH assisted with data collection for Chapter 3 and CM provided guidance on the construction and application of Chapter 5.

Chapter 1

General Introduction

General Introduction

The global biodiversity crisis

The rapid, large-scale loss and degradation of biodiversity is one of the most critical global environmental problems facing the planet today (Cardinale *et al.* 2012). Over the past 500 years, anthropogenic threats such as habitat destruction, overexploitation, pollution and invasive species, compounded by the effects of human-induced climate change (Urban 2015), have resulted in unprecedented levels of species decline (Young *et al.* 2016). Conservative estimates suggest that at least 42% of the > 3,500 invertebrate species assessed by the IUCN are threatened with extinction (Baillie *et al.* 2012) and that the average rate of vertebrate species loss over the last century is up to 100 times higher than background rates, comparable to rates during the previous five mass extinction events (Ceballos *et al.* 2015).

This widespread loss of species across all taxa has significant consequences for ecosystem services and, unless rates are slowed, will ultimately threaten human wellbeing (Dirzo *et al.* 2014). However, actions to tackle biodiversity loss have been largely insufficient (Tittensor *et al.* 2014), with national conservation strategies consistently failing to meet goals set by the Convention on Biological Diversity (CBD) (most recently the 2020 Aichi Targets) (Xu *et al.* 2021). Various studies have attributed these failures to excessively complex and imprecise goal setting (Butchart *et al.* 2016), weak national biodiversity strategies (Whitehorn *et al.* 2019), failure to mainstream biodiversity policy (Milner-Gulland *et al.* 2021), inadequate financial resources (McCarthy *et al.* 2012, Johnson *et al.* 2017) and lack of political will (Mace *et al.* 2018, Morrison *et al.* 2020).

Without substantial change in approach and ambition across all levels of government, previous failures could be repeated (Mace *et al.* 2018, Watson *et al.* 2021). The development of the post-2020 strategic plan for the Convention on Biological Diversity (CBD) potentially represents the last opportunity for governments to set out measurable and unambiguous targets (Hughes *et al.* 2022), but to deliver for nature, ambitious targets must then be translated into effective, real-world conservation actions (Milner-Gulland *et al.* 2021, Chan *et al.* 2023).

Conservation actions and the need to improve

Conservation actions aim to mitigate the direct and indirect negative effects of human activity on biodiversity and ecosystem services, through protection, creation and restoration of favourable environmental conditions, across a range of spatial scales (Boyd *et al.* 2008). One of the most fundamental components of conservation action is designation of protected area (PAs), which has long been considered a cornerstone of conservation, and hopes of restoring biodiversity and ecosystem services have largely been pinned on expansion of PA networks (Watson *et al.* 2014, UNEP-WCMC 2021, Carroll & Noss 2022).

Currently, ~16% of the earth's terrestrial surface and ~7% of the oceans fall under at least one type of PA designation (UNEP-WCMC 2021), and a major goal of the CBD post-2020 strategic plan is to increase this coverage to 30% of terrestrial and marine area by 2030 (Carroll & Noss 2022). Protected area designations can be prescribed at an international (e.g. Ramsar Sites and World Heritage Sites), regional (e.g. Special Areas of Conservation, Special Protection Areas and Marine Protected Areas in Europe), or national level (e.g. National Nature Reserves, Site of Special Scientific Interest) (UNEP-WCMC 2021), with such designations being in place to enable natural areas to retain habitats and biodiversity without threats of encroaching changes in land-use and overexploitation (Watson *et al.* 2014). However, despite strong evidence for PAs resulting in positive outcomes for some threatened taxa (e.g. Cazalis *et al.* 2020, Barnes *et al.* 2023), on average, their contribution has not been sufficient to resist anthropogenic pressures on ecosystems and biodiversity (Geldmann *et al.* 2019), with a large number of studies attributing ongoing loss and degradation within PAs to under-resourced management (e.g. Le Saout *et al.* 2013, Gill *et al.* 2017, Wauchope *et al.* 2017, 2022, Coad *et al.* 2019, Geldmann *et al.* 2019).

While further expansion of PAs is a positive step towards preserving the > 78% of known threatened species currently persisting without adequate protection (Maxwell *et al.* 2020), protection alone is unlikely to slow or reverse rates of global biodiversity loss without increased effectiveness of conservation actions, both within and outwith PAs (Strassburg *et al.* 2020, Bailey *et al.* 2022, Leadley *et al.* 2022).

One of the major hurdles impeding conservation management are chronic shortfalls in funding (Waldron *et al.* 2017, Watson *et al.* 2021, Xu *et al.* 2021). Conservation is primarily resourced through regional and national-level governments yet, despite the stated commitment of nations to meet biodiversity targets (Pisupati & Prip 2015) and the substantial financial risk that environmental degradation poses to economies (Watson *et al.* 2021, Kedward *et al.* 2022), the financial resources provided so far have been insufficient

(McCarthy *et al.* 2012, Seidl *et al.* 2020). Addressing the current shortfall, estimated at multiple hundreds-of-billions of dollars (Maxwell *et al.* 2020, Xu *et al.* 2021), is likely to involve increasing use of economic instruments such as payments for ecosystem services and carbon taxes (Salzman *et al.* 2018, Barbier *et al.* 2020), as well as inclusion of the private sector to help alleviate financial pressure on governments (Barbier *et al.* 2018, Dinerstein *et al.* 2019).

In key sectors such as fisheries, forestry and agriculture, there are clear and direct parallels between high financial returns and effective conservation management (Sala *et al.* 2016, Barbier *et al.* 2018, Dinerstein *et al.* 2019). Through embedding components of conservation into the strategies and practices of the stakeholders that impact or rely on biodiversity, the disconnect between the organisations damaging nature and actions to restore nature will likely narrow, potentially provoking a collective sense of accountability and empowering proactive and preventative investments in conservation (Redford *et al.* 2015, Whitehorn *et al.* 2019, Milner-Gulland *et al.* 2021). This concept of mainstreaming conservation has great potential for facilitating translation of ambitious biodiversity targets into real-world actions (Milner-Gulland *et al.* 2021) but, for it to work in practice, well-supported conservation actions also have to be capable of delivering meaningful outcomes.

During the last four decades, the majority of conservation success stories have involved single species recovery programmes, typically involving species that are highly localised, isolated and rare, and for which active management is used to create and restore favourable environmental conditions (e.g. Davies *et al.* 2011, Simón *et al.* 2012, Waterhouse *et al.* 2020, Wilson *et al.* 2020). For example, efforts to prevent the extinction of the Mauritius kestrel *Falco punctatus*, an island endemic which had declined to four individuals in 1974, used captive breeding, habitat restoration and supplementary feeding to boost low rates of breeding productivity caused by loss of nesting habitat, use of organochlorine pesticide and invasive mammalian nest predations (Jones *et al.* 1995) and, by the mid-2000s, the population had increased to over 800 individuals (Jones *et al.* 1995, Burgess *et al.* 2009). While such conservation successes make valuable contributions towards slowing the rate of biodiversity loss, their impact is increasingly overshadowed by the continued, widescale population declines of formerly common and widespread species (Díaz *et al.* 2019, Hayhow *et al.* 2019).

Perhaps the most famous example of such a decline is that of the passenger pigeon *Ectopistes migratorius*. This species was once estimated to be 40% of the total bird population in North America, numbering up to two-billion individuals, but mass overhunting drove the species to extinction in 1914 (Schorger 1955). Over a century later and the story risks repeating itself with the once superabundant and widespread yellow-breasted bunting *Emberiza aureola* rapidly heading towards extinction, also as a result of overhunting (Kamp *et al.* 2015a). Numerous other previously common and widespread birds (e.g. Galewski & Devictor 2016, Rosenberg *et al.* 2019, Burns *et al.* 2021), small mammals (e.g. Coomber *et al.* 2021), pollinating insects (e.g. Potts *et al.* 2010, Dicks *et al.* 2021, Wagner *et al.* 2021) and plants (e.g. Sekercioglu 2011, Eichenberg *et al.* 2021) are also in decline globally, with no sign of trends reversing (Young *et al.* 2016).

In general, efforts to reverse the decline of common and widespread species have typically relied on generic, large-scale environmental approaches. For example, agri-environment schemes offer financial compensation for taking land out of production, changing farming practices and providing key resources for focal taxa in agricultural landscapes (Batáry *et al.* 2015). Through such actions, some successes have been achieved, however these have tended to be at local levels (e.g. Aebischer *et al.* 2016, McHugh *et al.* 2018) and often relate to single-species (e.g. Davies *et al.* 2011, Perkins *et al.* 2011). Overall, large-scale conservation management has mostly failed to translate local successes into reversal of broader-scale population declines for common and widespread species, and alternative strategies are urgently required to design and deliver more effective conservation management.

Over the last twenty years, substantial efforts have been made to enhance the impact of conservation management. These efforts have largely focused on increasing the availability, quality and use of data to support the design and delivery of more evidence-based conservation actions (Sutherland *et al.* 2004, 2019, 2020, Salafsky *et al.* 2019, Downey *et al.* 2021). This increasingly prominent approach to conservation is being widely adopted across the conservation sector and could have a transformative effect on management outcomes. However, a growing number of studies suggest that better targeting of conservation actions will also be needed to complement this increased use of evidence (Robinson *et al.* 2014, Morrison *et al.* 2021, 2022). Recovering declining populations often requires interventions to boost rates of productivity and/or survival, and identifying actions capable of delivering these goals and the situations in which such actions can be effective will increasingly be needed to restore widespread populations.

Targeted conservation actions to boost persistently low demographic rates (survival and/or productivity) could be a powerful and efficient tool to enhance population growth (Morrison *et al.* 2021, 2022). Such actions could involve protection, creation or restoration of the environmental conditions capable of supporting high levels of demographic success, and could be deployed spatially and/or temporally (Morrison *et al.* 2022). For example, restorative actions might be targeted in areas or periods of time in which productivity or survival are persistently low and could feasibly be boosted through management to provide key resources such as artificial nests in places where natural sites have been lost (Gameiro *et al.* 2020) or food during periods of scarcity (Siriwardena *et al.* 2008), remove cause of mortality (Swan *et al.* 2006) or exclude predators from areas where their impact is unsustainably high (Verhoeven *et al.* 2022). In contrast, areas supporting high rates of demographic success are likely to be good candidates for protection. The design and delivery of such actions requires information on spatial and temporal variation in survival and productivity, the drivers of that variation, and the capacity of different actions to boost the demographic rates being targeted (Johnson *et al.* 2020, Plard *et al.* 2020, Morrison *et al.* 2021).

Global declines in wading birds

A group of species for which targeted management is increasingly required are waders *Charadriiform spp*., a ubiquitous, diverse and charismatic avian group that occurs across many biotopes and nearly every shoreline in the world (Colwell 2010). Waders are generally characterised by their long-legs and thin, pointed bills, adapted for foraging on arthropod prey in aquatic and marine environments (Barbosa & Moreno 1999). Morphology such as body size and bill length varies strongly between species, for example, the least sandpiper is the world’s smallest wader, weighing as little as 17 g (Butler & Kaiser 1995), and the far eastern curlew is the biggest, with females weighing up to 1.3 kg (Minton *et al.* 2011).

Most wader species are migratory, open-habitat specialists, and make use of all of major flyways to move between wintering and breeding sites (Fig. 1). During the non-breeding season, many waders occur at high densities at intertidal, coastal hotspots (e.g. Catry *et al.* 2011, Studds *et al.* 2017) whereas, during the breeding season, they typically occur at lower densities, widespread across a range of habitats including tundra, wetlands, grassland and agricultural land (e.g. Gunnarsson *et al.* 2006, Smart *et al.* 2006, Jóhannesdóttir *et al.* 2018, Smith *et al.* 2020). Migratory distances between non-breeding and breeding grounds vary between species and individuals, with some species undertaking marathon non-stop flights of 11,000 km between arctic breeding grounds and southern hemisphere wintering sites (e.g. Gill *et al.* 2005). Waders breeding in tropical regions are more likely to be resident, or to move with seasonal rainfall patterns (Conklin 2019).

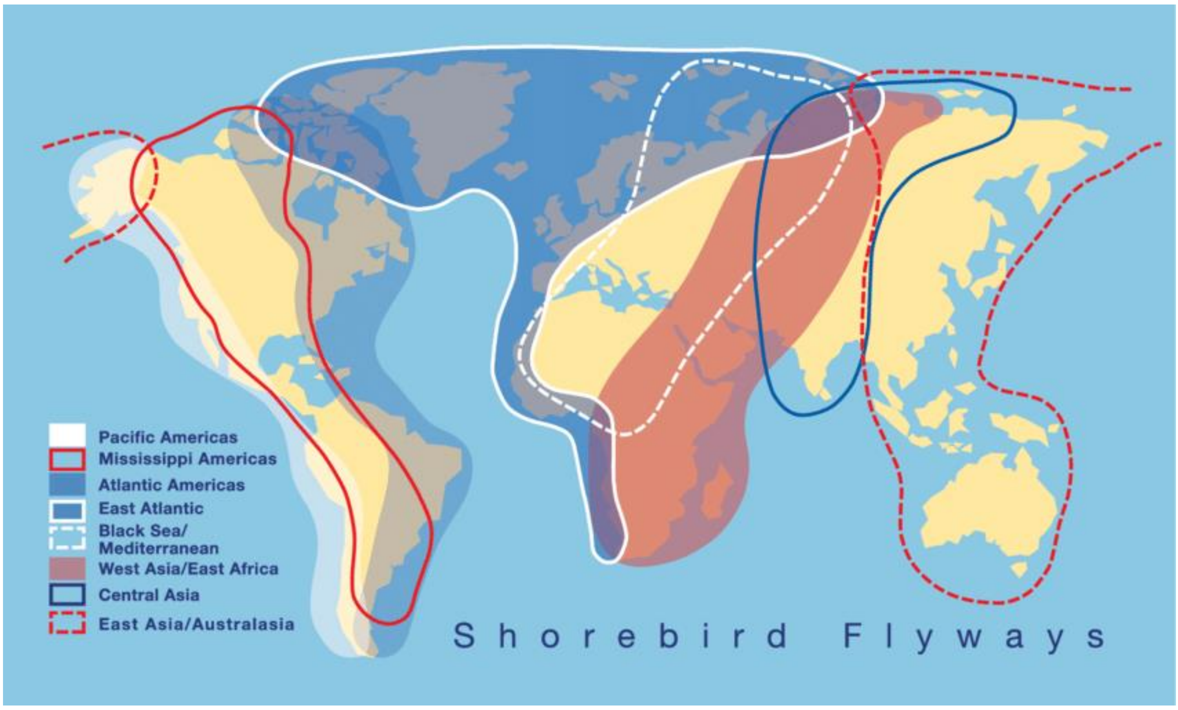


Figure 1: The eight major migratory flyways of waders, taken from Boere & Stroud (2006).

Waders generally nest on the ground (although some *Tringa spp*. can nest in trees; e.g. Maslovsky *et al.* 2023), lay a clutch of three to four eggs and chicks are precocial (Cramp *et al.* 1983). The breeding systems of waders are varied, with different species exhibiting monogamy (e.g. Kwon *et al.* 2022), polygamy (e.g. Kempenaers & Valcu 2017), polyandry (e.g. Owens *et al.* 1994), sex-role reversal (e.g. Schamel *et al.* 2004) and complex lekking behaviour (e.g. Vervoort & Kempenaers 2020).

Owing to their relatively large body size and conspicuous behaviour, many wader populations are well-monitored. For example, in Europe, several established, long-running surveys take place during the non-breeding (e.g. Frost *et al.* 2020, Nagy & Langendoen 2020) and breeding (e.g. Brlík *et al.* 2021, Harris *et al.* 2022) season and, individual-level studies using colour-marking (e.g. Gill *et al.* 2019, Méndez *et al.* 2020, 2022), remote tracking (e.g. Carneiro *et al.* 2019, Verhoeven *et al.* 2020) and monitoring of breeding attempts (e.g. Laidlaw *et al.* 2020, Kaasiku *et al.* 2022) are common. The threats acting on populations are therefore relatively well-understood (Sutherland *et al.* 2012). The availability of long-term survey data for waders has allowed the IUCN to classify the conservation status of > 85% of known wader species, more than one-third of which are classified as Near-Threatened or worse (Table 1).

Table 1: Proportion of species within ten of the largest avian groups exhibiting a negative population trend and that are currently listed as globally Near Threatened, Vulnerable, Endangered or Critically Endangered (IUCN 2022). Species for which trends are unknown are excluded.

Avian group	**No. of species**	**Species declining (%)**	**NT, VU, EN, CR (%)**
Gamebirds	302	75.2	60.6
Waders	153	60.1	35.3
Kingfishers, bee-eaters & rollers	177	59.3	27.7
Parrots	397	58.7	43.6
Raptors and owls	542	58.7	32.7
Woodpeckers	455	55.8	16.9
Pigeons	348	55.5	33.0
Seabirds	307	55.0	46.3
Ducks and Geese	155	54.2	26.5
Passerines	6176	44.8	19.0

The threats that waders face impact different components of their demography, span breeding and non-breeding ranges, and make varying contributions to population decline across flyways and regions (Sutherland *et al.* 2012). During the non-breeding season, at staging and wintering sites, threats generally relate to habitat loss through land-claim of tidal flats and wetlands (e.g. Murray *et al.* 2014), hunting (e.g. Watts & Turrin 2016, Gallo-Cajiao *et al.* 2020, Andres *et al.* 2022), overharvesting of shellfish prey (e.g. Atkinson *et al.* 2003, Verhulst *et al.* 2004) and disturbance (e.g. Navedo *et al.* 2019, van der Kolk *et al.* 2020a, 2020b, Palacios *et al.* 2022). These threats can impact survival rates (e.g. Piersma *et al.* 2016) and potentially also recruitment of juveniles into breeding populations (e.g. Syroechkovski *et al.* 2010). Coastal land-claim has had particularly severe effects on wader populations on the East Asian Australasian Flyway (EAAF), where loss and degradation of major staging sites in the Yellow Sea (Amano *et al.* 2010), in some cases exacerbated by hunting on wintering grounds (Chowdhury *et al.* 2022, Loktionov *et al.* 2023), have resulted in major populations declines, with three species now classified as globally Endangered and one as Critically Endangered (IUCN 2022).

During the breeding season, the threats acting on waders are complex and interconnected, but are often primarily driven by intensification of land management (e.g. Kleijn *et al.* 2010), which has resulted in a suite of environmental changes. These include widespread drainage of wetlands and wet grasslands (e.g. Angelstam *et al.* 2022), homogenisation of vegetation structure (e.g. Kentie *et al.* 2015), changes in grazing and cutting practices (e.g. Verhulst *et* *al.* 2007, Exo *et al.* 2017) and afforestation of open landscapes (e.g. Douglas *et al.* 2014, Kaasiku *et al.* 2022, Pálsdóttir *et al.* 2022). In addition to loss of breeding habitat, these changes have contributed to making nests and chicks more vulnerable to predation by increasingly high abundances of native (e.g. Roos *et al.* 2018) and non-native (e.g. Calladine *et al.* 2017, Niemczynowicz *et al.* 2017) mesopredators. This has had a particularly severe impact on breeding wader populations on the East Atlantic flyway, where widespread land-use change and agricultural intensification has led to landscape composition becoming less suitable for specialists like breeding waders and more suitable for generalist mesopredators like the red fox *Vulpes vulpes* (Amar *et al.* 2011, Roos *et al.* 2018, Laidlaw *et al.* 2021), resulting in unsustainably high rates of nest and chick predation (Macdonald & Bolton 2008, Roodbergen *et al.* 2012).

Changing climatic conditions may also exacerbate threats to wader populations through direct loss of coastal habitats such as saltmarsh as a result of sea level rise (Smart & Gill 2003), and through impacts on breeding phenology which could alter predation dynamics (e.g. Laidlaw *et al.* 2020) and prey availability (e.g. Pearce-Higgins *et al.* 2010, Saalfeld *et al.* 2019, Kwon *et al.* 2022). Over time, the direct and indirect effects of climate change are likely to become increasingly apparent, and the long-term impacts on demography are yet to be fully understood (Kentie *et al.* 2018, Alves *et al.* 2019, Gill *et al.* 2019).

Global decline of Numeniini

Arguably the most globally threatened group of wader species are those belonging to the tribe Numeniini (Pearce-Higgins *et al.* 2017), which is comprised of 13 species, two of which are listed as globally Critically Endangered and are likely extinct (Eskimo Curlew *Numenius borealis* and Slender-billed Curlew *N. tenuirostris*), one as Endangered (Far Eastern Curlew *N. madagascariensis*), one as Vulnerable(Bristle-thighed Curlew *N. tahitiensis*), and three as Near Threatened (Eurasian Curlew *N. arquata*, Bar-tailed Godwit *Limosa lapponica* and Black-tailed Godwit *L. limosa*) (IUCN 2022). Six species in the tribe can be further divided into thirty separate populations or subspecies, with populations within the same species often occurring on different flyways (Pearce-Higgins *et al.* 2017).

Numeniini species are generally large-bodied, exhibit a relatively delayed age of maturity, low fecundity and high survival rates (Piersma *et al.* 2000). In addition, most are specialists of open, semi-natural habitats, ground-nesters and long-distance migrants (e.g. Gerasimov *et al.* 1997, Gunnarsson *et al.* 2006, Smart *et al.* 2006, Battley *et al.* 2012, Alves *et al.* 2016, Franks *et al.* 2017, Galtbalt *et al.* 2021). All of these traits have been linked to increased rates of extinction and negative population trends in bird species (e.g. Gaston & Blackburn

1995, Owens & Bennett 2000, Julliard *et al.* 2004, Thaxter *et al.* 2010, Sullivan *et al.* 2015), and are likely to at least partially explain why so many species within the Numeniini tribe are increasingly of major conservation concern (Pearce-Higgins *et al.* 2017).

Given the delayed maturity, high survival and low fecundity of Numeniini species, population trends are likely to be most sensitive to variation in survival rates (Sæther & Bakke 2000). However, sustained periods of low breeding productivity (e.g. Kentie *et al.* 2015, Cook *et al.* 2021, Viana *et al.* 2023) may also result in declines and can limit the capacity of populations to recover from periods of low survival (e.g. Robinson *et al.* 2014, Morrison *et al.* 2016).

Globally, the threats acting on Numeniini species vary between flyways and reflect those acting on other wader populations (Pearce-Higgins *et al.* 2017). Given the widespread decline in Numeniini populations, restoration efforts will require international collaborations (Pearce-Higgins *et al.* 2017) and a focus on populations, rather than the overall status of the species, as the relevant threats often differ between populations and flyways (Pearce-Higgins *et al.* 2017). For example, eastern populations of Eurasian curlew *Numenius arquata ornientalis* and whimbrel *Numenius phaeopus variegatus* on the EAAF are particularly threatened by coastal development (e.g. Sutherland *et al.* 2012, Murray *et al.* 2014, Hua *et al.* 2015), whilst the nominate populations of Eurasian curlew *N. a arquata* and whimbrel *N. p. phaeopus* are more threatened by changes in land-use on breeding sites constraining productivity and habitat availability (Franks *et al.* 2017, Pálsdóttir *et al.* 2022).

Ecology of the Eurasian curlew

One of the most threatened species in the Numeniini tribe is the Eurasian curlew *Numenius arquata* (hereafter, curlew). Named after their elongated, downcurved bill (*Numenius* translates to ‘new moon’, and *arquata* to ‘archers bow’), the curlew is the largest and one of the most iconic waders in Europe (Fig. 2). A bird of uplands and lowlands, wilderness areas and farmland, curlew are engrained in the natural heritage of many communities (Colwell 2018). Sadly, the curlew is classified as Near Threatened at a global and European level, and the history of extinction of species among the Numeniini tribe makes the curlew’s threatened status of great conservation concern (Pearce-Higgins *et al.* 2017).

Figure 2: Male Eurasian curlew in grass-heath habitat, Breckland, eastern England, 2022.

Curlew comprise three subspecies; *Numenius arquata arquata, N. a. orientalis* and *N. a. suschkini.* All birds breeding to the west of the Urals are considered to be *N. a. arquata,* which has a core breeding range including the UK, Fennoscandia, northern continental Europe and European Russia (Fig. 3; Thorup 2006). Those from the Urals eastwards are thought to be *N. a. orientalis*, with a breeding range stretching across temperate latitudes of Siberia to just west of Lake Baikal, while *N. a. suschkini* breeds on steppe areas to the south of the Urals in Russia and Kazakhstan (Fig. 3; Thorup 2006). Considerable uncertainty remains over the population size of the *orientalis* and *suschkini* subspecies (although likely around 50,000 and 10,000 pairs, respectively; Delany *et al.* 2009, Cao *et al.* 2010), whereas *N. a. arquata* is the most numerous of the three, and is the subspecies on which the remainder of this thesis will be focused. The estimated population of 700,000 – 1,000,000 *N. a. arquata* individuals globally (BirdLife International 2021) is split between Russia (~32% of global pairs), Finland (~30%), the UK (~28%), Scandinavia and northern Europe (~10%).

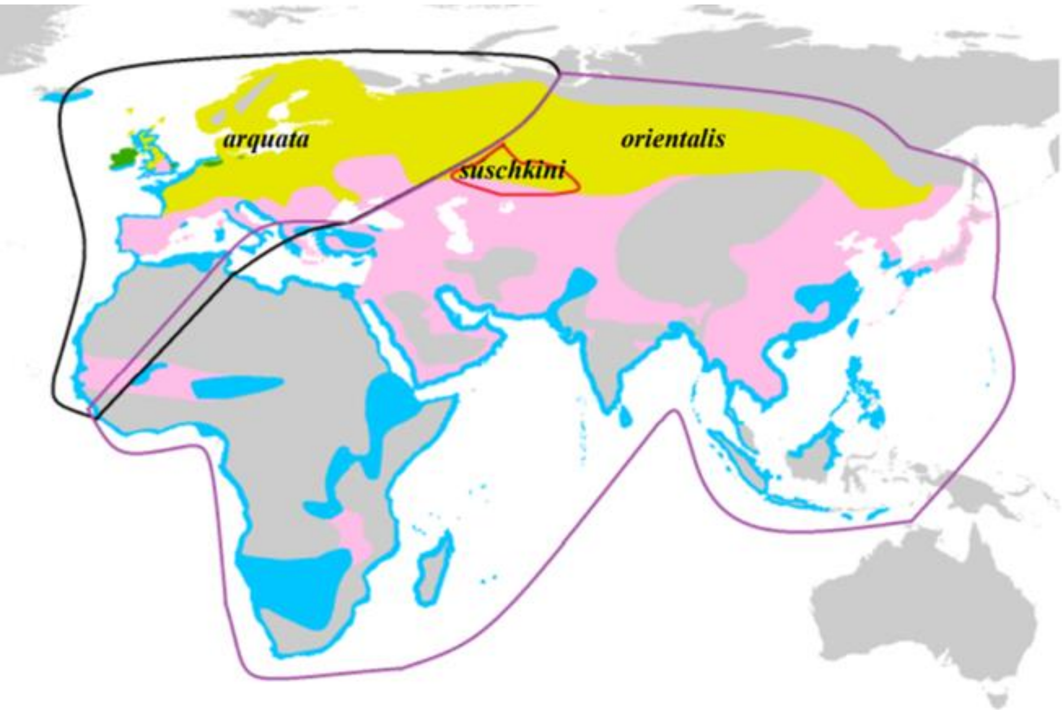


Figure 3: Global range of the Eurasian Curlew including the approximate distribution of the three subspecies, and indicating breeding (yellow), passage (pink) and wintering (blue) ranges, and areas where the species occurs all year round (green). Taken from Brown (2015).

Curlew breeding sites across the European range comprise a variety of coastal, lowland and upland landscapes (Brown 2015), typically in open habitat away from woodland (e.g. Douglas *et al.* 2014). Curlew can breed in wet or dry conditions, in semi-natural habitats including unimproved grasslands, meadows, heathland, moorland, peat-bog and mires, and also in agricultural habitats such as permanent pastures and cropland monocultures (e.g. Berg 1992, Valkama *et al.* 1998, Johnstone 2007, Fletcher *et al.* 2010, Franks *et al.* 2017, Zielonka *et al.* 2020, Baines *et al.* 2022, Ewing *et al.* 2022). Coastal marshes and dune systems are also used for nesting (e.g. Kämpfer & Fartmann 2022). During the breeding season, curlew have a varied diet comprising beetles (order Coleoptera), flies (order Diptera), grasshoppers and crickets (order Orthoptera), earthworms (suborder Lumbricina) and crane flies *Tipulidae*, while they may also forage for bilberry *Vaccinium myrtillus* and crowberry *Empetrum nigrum* in Scandinavia (Cramp *et al.* 1983).

At the end of the breeding season, curlew generally migrate south-west to intertidal systems spanning much of the northwest Europe, north and west African coastlines (Pederson *et al.* 2022), where polychaete worms and a variety of crustaceans make up a large proportion of their diet (Cramp *et al.* 1983). Like most migratory waders, curlew exhibit low migratory connectivity, with the distance over which they migrate varying greatly between and within populations (Pederson *et al.* 2022). For example, curlew breeding in Ireland appear to largely migrate < 100 km to the Irish coast (Bainbridge & Minton 1978), whereas birds breeding in Poland have been shown to overwinter across a range of sites from eastern England to southern Iberia, moving distances of > 3000 km (e.g. Pederson *et al.* 2022). Individual curlews typically use the same non-breeding sites repeatedly within and between years. For example, of 3,000 curlew caught at one site in Wales over 36 years, only one bird had been recovered elsewhere during the winter (Taylor & Dodd 2013) and, of 258 winter recoveries of curlew ringed as fully grown birds in the UK, 81% were recovered within 30 km of the original ringing site in subsequent winters (Bainbridge & Minton 1978).

Like most waders, curlew nest on the ground and lay a clutch of three to four eggs (typically around 68 mm in length, 48 mm in breadth and 76 g in mass; BTO Birdfacts 2023) in a shallow depression lined with grass or straw (Fig. 4). One egg is laid every 1.5 days, resulting in a total laying period (for a clutch of 4 eggs) of six days (Grant 1996). Incubation starts once the final egg is laid and lasts 28 – 29 days, with precocial chicks fledging ~35 – 40 days after hatching (Grant 1996, Currie *et al.* 2001). Nesting usually takes place from mid-April to late-May, although some very early eggs can be laid in late-March (Ewing *et al.* 2022). Curlew are monogamous and contribute equally to incubation, however females typically leave chicks 16 – 25 days after hatching, while males remain until chicks fledge (Currie *et al.* 2001).

Figure 4: Eurasian curlew nest on rough grassland, Breckland, eastern England, 2019.

Curlew that survive to the post-fledging stage live for around 11 years, on average (longevity record: 32.5 years; BTO BirdFacts 2023), and exhibit a high degree of site fidelity to breeding sites, rarely nesting more than 250 m from previous nesting attempts (Berg 1992, Valkama *et al.* 1998). Curlew can also exhibit very high levels of natal philopatry, with average dispersal distance of only ~3.8 km reported from the Netherlands (Gerritsen 2021), although long-distance dispersal events away from well-monitored breeding sites are likely under-detected.

Across Europe, reported rates of adult survival range from between 0.59 and 0.92 (Boyd 1962, Bainbridge & Minton 1978, Evans & Pienkowski 1984, Ylimaunu *et al.* 1987, Berg 1994, Valkama & Currie 1999, Kipp & Kipp 2009, Roodbergen *et al.* 2012, Taylor & Dodd 2013, Robinson *et al.* 2020, Cook *et al.* 2021), and have generally shown a positive trend over the last half century, with no survival rates < 0.75 reported after 1985 (Viana *et al.* 2023). A recent study of curlew demography using ring-recovery data of 1047 curlew ringed as chicks between 1968 and 2016 across Europe estimated the current adult survival rate of the European curlew population to be ~0.9 (Viana *et al.* 2023).

As a long-lived species, curlew populations are likely to be especially sensitive to changes in adult survival (Sæther & Bakke 2000, Pearce-Higgins *et al.* 2017). Curlew are hunted across several parts of the non-breeding range, however, since 1994 only Ireland and France have allowed an open season for the species (Jensen & Lutz 2007). Hunting bans have been implemented in Denmark, the UK (1982 for Scotland, England and Wales, 2011 in Northern Ireland) and Ireland (2012) (Brown 2015), and bag numbers prior to bans are very poorly understood (Jensen & Lutz 2007). Most concerning are the levels of hunting that have recently occurred in France, which supports 25,000 – 80,000 wintering curlew, with many more passing through. Reportedly, 7000 – 8000 birds were shot annually prior to 2008 (Fouquet 2013). In 2008, a hunting moratorium was put in place but this has been periodically lifted a number of times since then (Fouquet 2013). Curlew are also thought to be hunted across the eastern edge of the European distribution in Russia, Belarus, Ukraine and Romania, although they are not thought to be a popular quarry species (Brown 2015). Overall, hunting pressure is likely to have declined considerably across northwest Europe in recent decades, due to national bans, however it still remains a threat that needs to be monitored closely in France (e.g. Jiguet *et al.* 2021).

An additional emerging potential threat to curlew populations in Europe is infrastructure development on key staging and winter sites (Sutherland *et al.* 2012, Pearce-Higgins *et al.* 2017). For example, a proposed airport development threatens the Tagus Estuary in Lisbon, an internationally important staging and wintering site for an estimated 300,000 waders (Alves & Dias 2020, Catry *et al.* 2022), and development of renewable energy infrastructure including tidal barrages could potentially become an increasing issue as governments attempt to mitigate climate change (Clark 2006). However, as yet, development of non-breeding sites in Europe is not thought to have impacted survival rates of curlew or other waders in the region (Brown 2015).

In contrast to the generally stable and high rates of survival, levels of curlew breeding productivity are more worrying. Although breeding productivity appears to vary across Europe, with published estimates ranging from 0.05 to 1.4 fledged chicks per pair per year between 1975 and 2020 (Dornberger 1986, Ylimaunu *et al.* 1987, Berg 1992, Boschert & Rupp 1993, Grant *et al.* 1999, Valkama & Currie 1999, Jensen & Lutz 2007, Hemerik *et al.* 2009, Kipp & Kipp 2009, Roodbergen *et al.* 2012, O'Donoghue 2019, Colwell *et al.* 2020, Zielonka *et al.* 2020), the only studies reporting rates > 0.6 chicks per pair have been from Sweden and Finland (Ylimaunu *et al.* 1987, Berg 1992). Additionally, the most recent estimate, modelled using breeding productivity data from 23 studies, suggests that current rates across Europe are ~0.58 chicks per pair per year, below the rate required for population sustainability (~0.68), estimated by the same study (Viana *et al.* 2023).

In Europe, the low rates of productivity exhibited by many breeding wader populations has been widely attributed to high rates of nest and chick predation, which has increased substantially over the last four decades (Roodbergen *et al.* 2012). During that period, populations of generalist mesopredators have also increased across Europe, including the red fox, European badger *Meles meles* and carrion crow *Corvus corone* (e.g. Deinet *et al.* 2013, Newton 2017). The increased fox numbers are of particular importance as they are regularly identified as the primary predator of wader nests and chicks across Europe (e.g. Macdonald & Bolton 2008, Teunissen *et al.* 2008, Eglington *et al.* 2009, Mason *et al.* 2018, Zielonka *et al.* 2020, Kaasiku *et al.* 2022), although this can vary spatially, for example introduced hedgehogs *Erinaceus europaeus* can be the primary predator on islands (e.g. Jackson & Green 2000, Calladine *et al.* 2017).

The reasons for these increases in generalist predator abundance are not fully understood, but are likely to involve a combination of improved foraging opportunities due to urbanisation (e.g. Marzluff & Neatherlin 2006, Handler *et al.* 2020), mesopredator release as a result of widespread removal of apex predators (Ritchie & Johnson 2009, Ritchie *et al.* 2012) and changes in land-use practices, landscape composition and fragmentation which may have favoured generalist species (e.g. Lees *et al.* 2013, Pringle *et al.* 2019, Kaasiku *et al.* 2022, Pálsdóttir *et al.* 2022). In addition, many predators (particularly raptors) have recovered following decades of persecution and secondary pesticide poisoning (Burfield 2008, Newton 2017), as well as successful reintroductions of species such as the red kite *Milvus milvus* (Seddon *et al.* 2007, Stevens *et al.* 2020) and spread of non-native species, such as the racoon dog *Nyctereutes procyonoides* (e.g. Krüger *et al.* 2018).

For curlew, predation of eggs and chicks is typically identified as the most frequent cause of low breeding productivity (Berg 1992, Grant *et al.* 1999, Valkama & Currie 1999, Johnstone 2007, Zielonka *et al.* 2020). As well as increased abundance of generalist predators, the environmental conditions in the range of habitats and landscapes in which curlew breed have frequently become less favourable, likely increasing the vulnerability of nests and chicks to predation and other forms of failure. For example, in areas where pastoral farming is the dominant land-use, simplification of grassland structure, from heterogeneous semi-natural grassland to improved grassland through soil drainage, fertilisation and re-seeding could limit the ability of wader chicks to evade predation and/or increase the frequency of chick starvation (Kentie *et al.* 2013). Carrion crow abundance is greater in improved grassland, which could potentially result in high predation rates in these habitats (Dallimer *et al.* 2010), although there is little evidence for crows making substantial contributions to low rates of wader productivity. Curlew breeding in areas with adjacent woodland, particularly commercial conifer plantations, have also shown reduced breeding success (Douglas *et al.* 2014, Kaasiku *et al.* 2022), potentially owing to increased predator activity in close proximity to these habitats (Hancock *et al.* 2020). While predation is likely to be the main cause of breeding failure in most habitats, curlew nest in a variety of agricultural grasslands and crops, also making them susceptible to nest destruction through farm operations and potentially trampling by livestock (Berg 1992, Grant *et al.* 1999, Verhulst *et al.* 2007). Sheep have also been recorded as a (likely incidental) predator of curlew nests (Zielonka *et al.* 2020). To compound threats further, human-induced climate change may reduce the available of invertebrate food resources for chicks, especially on peatlands that have already been subject to drainage (Pearce-Higgins *et al.* 2010).

As a consequence of low breeding productivity, the majority of breeding curlew populations in Europe are declining, with 30 – 49% of pairs being lost in the last 35 years (BirdLife International 2015). The steepest national declines have been recorded in Ireland, where the population is on the cusp of extirpation having lost at least 96% of breeding pairs since the 1980s (O’Donoghue 2019), and long-term declines of 30 – 50% have been recorded in the Netherlands and Germany (Hötker *et al.* 2007). The largest population of European-breeding curlew occurs in Russia where 5 – 30% of breeding pairs have been lost since the 1980s however, Finland’s population, which comprises ~30% of the European population, appears to have been stable since 2001 (Brown 2015).

UK breeding curlew population

The country with the third largest population of breeding curlew in Europe is the UK (Brown 2015), which hosts ~58,000 breeding pairs (Woodward *et al.* 2020); roughly equal to 28% of the European and 27% of the global breeding curlew population (Brown 2015, Harris *et al.* 2022). The most recent national trends show that 48% of breeding pairs were lost in the UK between 1995 and 2020, and a range contraction of ~20% has occurred since the 1970s (Balmer *et al.* 2013, Harris *et al.* 2022). Declines have been greatest in Scotland (60%; Harris *et al*. 2022), Wales (73%; Harris *et al*. 2022) and Northern Ireland (82%; Colhoun *et al.* 2022), while a 29% decline has been estimated in England (Harris *et al*. 2022). As a result of these declines, curlew are now on the UK Birds of Conservation Concern Red List (Stanbury *et al.* 2021).

In common with other curlew populations across Europe, declines in the UK have been attributed to unsustainably low rates of breeding productivity, with the current rate estimated to be ~0.25 fledged chicks per nest per year, lower than the estimated rate required for sustainability of ~0.43, while apparent annual survival since 1996 has been estimated to be ~0.92 (Cook *et al.* 2021).

In the UK, curlew breed predominately in uplands areas, including moorland areas of heath, bog and grassland and enclosed grasslands around the moorland edge (Franks *et al.* 2017). These landscapes are characterised by large, open habitats with heterogeneous vegetation structures (Pearce-Higgins & Grant 2006), low levels of human disturbance (Haworth & Thompson 1990) and, at many sites, management for gamebird shooting (Fletcher *et al.* 2010, Baines *et al.* 2022). However, despite these favourable conditions, curlew are still thought to be declining across upland regions, partially owing to increases in afforestation (Douglas *et al.* 2014) and intensification of grassland management on the moorland edge (Franks *et al.* 2017).

Other breeding curlew in the UK occur on the Northern Isles and the Inner and Outer Hebrides, where there are few mammalian predators (although introduced hedgehogs are a predator of wader nests; Calladine *et al.* 2017) and breeding densities can reach 16 – 17 pairs per km^2 (Brown 2015). A smaller, more patchily distributed population of curlew (estimated at 500 pairs; Colwell *et al*. 2020) colonised the southern lowlands of England in the mid-nineteenth century, where they breed on arable land, heath and a variety of grassland habitats (Colwell *et al.* 2020). Open landscapes of the southern lowlands are highly fragmented by woodland patches, arable land and urban areas and curlew breeding here do so at low densities (Brown 2015). Threats to the lowland population are varied

(Colwell *et al.* 2020), mirroring those acting on curlew across Europe, but are generally linked to land-use change and agricultural intensification.

Given that the curlew population is the most westerly in Europe (Keller *et al.* 2020), and comprises a large proportion of the global population, the ongoing, rapid declines in the UK are likely to be adversely affecting the global population size and breeding range of the species (Brown *et al.* 2015). To slow and reverse declines of curlew in the UK, urgent, effective conservation actions are required.

Targeted conservation management for threatened breeding curlew populations

Over the last twenty years, considerable effort has gone into the design, trial and deployment of targeted management actions with the aim of boosting wader breeding productivity at sites across Europe (Franks *et al.* 2018, Jellesmark *et al.* 2021, Laidlaw *et al.* 2021). These actions all target the incubation and chick-rearing stages of the breeding cycle, and fit into three main categories:

1. Habitat management to create and restore favourable environmental conditions can improve the suitability of breeding sites for waders, by altering hydrology (e.g. Eglington *et al.* 2008), vegetation structure (e.g. Buchanan *et al.* 2017, Laidlaw *et al.* 2017, Douglas *et al.* 2023) and timing of grassland management practices (e.g. Verhulst *et al.* 2007) to ensure that suitable areas for nests and chick-rearing are available. Such actions can result in increased local abundances within managed areas (e.g. Eglington *et al.* 2008, Smart *et al.* 2013, Douglas *et al.* 2023) and may have positive effects on hatching rates (e.g. Sheldon *et al.* 2007, Bodey *et al.* 2010, Laidlaw *et al.* 2017) and potentially also chick survival to fledging (e.g. Verhulst *et al.* 2007, Bellebaum & Bock 2008).
2. Predator-exclusion fencing (e.g. Rickenbach *et al.* 2011, Smith *et al.* 2011, Malpas *et al.* 2013, Verhoeven *et al.* 2022) and/or lethal control (e.g. Baines *et al.* 2022) of predators can also reduce predator impacts on breeding waders. Evidence of the positive effects of lethal control on wader breeding productivity is restricted to the UK uplands (e.g. Fletcher *et al.* 2010, Ludwig *et al.* 2019, Baines *et al.* 2022), where benefits to waders are typically a by-product of a highly intensive and often controversial management to maintain high densities of red grouse *Lagopus lagopus scotica* for recreational shooting (Mustin *et al.* 2018, Newton 2021, Baines *et al.* 2022). As yet, no published studies have been able to replicate the magnitude of improvement in wader breeding success achieved on grouse moors in other landscapes, where effects appear to vary depending

on the complex dynamics of local predator communities (Bolton *et al.* 2007, Smith *et al.* 2011, Laidlaw *et al.* 2021, Douglas *et al.* 2023). In contrast, there is strong evidence that fencing to exclude mammalian mesopredators (primarily red fox and European badger) can substantially enhance nest and chick survival of breeding waders (e.g. Rickenbach *et al.* 2011, Smith *et al.* 2011, Malpas *et al.* 2013, Verhoeven *et al.* 2022). Different types predator-exclusion fencing have been developed for use over a range of temporal and spatial scales, depending on land-use requirements, the species' breeding ecology and project budgets (White & Hirons 2019, Laidlaw *et al.* 2021). For example, temporary fencing tends to involve electrified fences that are easy to construct and manipulate spatially, but require management throughout the season, while permanent, site-scale fencing tends to involve barrier fences of sufficient height and buried depth to exclude mammalian mesopredators (White & Hirons 2019, Laidlaw *et al.* 2021). Combination fences provide both a physical and an electric barrier and are commonly used in nature reserves. Both combination and barrier fencing can be used to protect large numbers of nests of colonial or semi-colonial species, and temporary fencing might be used to protect individual nests of species breeding at low densities (White & Hirons 2019). Increases in hatching success within fenced areas often also result in larger numbers of successful early-season nests than are typical outwith fences, which could have positive, secondary effects, as clutch sizes in waders are often higher in clutches laid earlier in the season (Weiser *et al.* 2018), and recruitment rates of chicks hatched from early nests can also be greater (Alves *et al.* 2019).

3. Headstarting is a relatively new technique in avian conservation which involves transferring eggs laid in the wild with a high chance of failure to avicultural facilities, where the eggs are incubated and chicks reared until fledging, before being released into areas of suitable breeding habitat. This removes the threat of egg and chick predation and can result in rapid, high-magnitude effects on breeding productivity (e.g. Pain *et al.* 2018, Loktionov *et al.* 2023). The high-level of expertise, resources and funding that this requires means that this technique is typically used for highly threatened populations for which other types of management are unlikely to be sufficiently effective at preventing extirpation or extinction.

All three of these targeted management actions have contributed to the conservation of threatened wader populations however, they have taken place on nature reserves, into which the breeding range of many wader species in UK has contracted (Smart *et al.* 2014, Jellesmark *et al.* 2021). Given the widespread distribution of curlew in the UK and Europe, and the low densities at which they breed in many areas, deploying management actions capable of boosting nest and chick survival in the wild at the scales required to achieve meaningful increases in breeding productivity will be challenging, particularly as the interventions outlined above have not yet been demonstrated to work effectively and sustainably outwith protected areas.

To date, conservation actions to boost lowland curlew populations have been limited. Management of lowland habitats for curlew is constrained by a limited knowledge of breeding requirements, particularly for chicks (Franks *et al.* 2018), predator control is mostly incidental and rarely conducted at the intensity required to produce meaningful, consistent outcomes (Douglas *et al.* 2023), predator-exclusion fencing is only deployed to protect a very small number of (usually single) nests (Colwell *et al.* 2020), and the contribution that headstarting can make to boosting curlew populations is currently unclear, although trials are ongoing using eggs from airfields that would otherwise be destroyed for air safety reasons (Natural England 2022).

There has also been little research on lowland-breeding curlew, with studies from the UK predominately focused on upland populations, of which only two have directly assessed the potential impacts of conservation management on curlew breeding productivity (Baines *et al.* 2022, Douglas *et al.* 2023). Consequently, there is limited understanding of the ecology and demography of curlew populations breeding in the UK lowlands, which is constraining delivery of effective conservation actions. Without such actions, there is a real danger that this vulnerable, highly fragmented population could be lost (Schnell *et al.* 2013), which would lead to the species' breeding range in the UK population contracting by around third. In addition, curlew populations in Europe primarily breed in lowland areas (Brown *et al.* 2015), so studies of populations breeding in similar conditions will contribute towards a broader understanding of how best to conserve curlew in landscapes across Europe. Such studies should aim to identify how rates of nest and chick survival vary spatially and temporally, the drivers of that variation, and the actions capable of enhancing low rates of breeding productivity.

Study system – breeding curlew in Breckland

One of the largest curlew populations in the southern lowlands of England occurs in Breckland, a 1019 km^2 bio-geographical region of East Anglia. The diversity of land uses and land management in Breckland, and the region's relatively large population of curlew (now estimated to be ~150 pairs), provides an excellent opportunity to examine the breeding ecology of lowland curlew and identify potential relevant conservation tools.

Breckland is characterised by sandy, low-nutrient soils and a semi-continental microclimate, and is differentiated from the rest of the East Anglian region by greater extremes of temperature and lower annual rainfall (Watt 1936). Traditionally, Breckland has been regarded as a landscape comprised of semi-natural, fallow land, disturbed and maintained over time by fluctuating patterns of livestock and rabbit grazing and low intensity, rotational farming methods (Dolman *et al.* 2010). This, and the region's unusually warm and dry climate, means the Brecks hosts a suite of nationally scarce and range-restricted flora and fauna, more commonly associated with steppe or Mediterranean regions, and which require low nutrient soils and ground disturbance (Dolman *et al.* 2010). However, during the 19th and early-20th centuries, sheep grazing and traditional farming methods declined in Breckland due to agricultural recession, later taken over by more profitable afforestation and intensive farming in the mid-20th century (Dolman *et al.* 2010). These changes led to conversion of formally extensive fen, wetland and heathland areas to productive arable cropping and the largest area of lowland coniferous forest in the UK (Eycott *et al.* 2006).

Currently, the Breckland landscape is a mosaic of habitats dominated mainly by forestry and private estates, managed for agriculture, livestock farming, shooting, and equine breeding. Only 70 km^2 of patchily distributed heathland remains in Breckland, with even smaller areas of semi-natural grassland and wetland (Dolman *et al.* 2010), a large proportion of which is owned and managed by the Ministry of Defence as airfield bases and areas for training of troops. Due to the rapid expansion of intensive agriculture in Breckland, fallow land has been almost entirely absent for the last sixty years and grazing is greatly reduced (Dolman *et al.* 2010). Nevertheless, despite this extreme change in land-use and management, the region still holds nationally and internationally important biodiversity, recognised by designations of four National Nature Reserves (NNR) and 55 Sites of Special Scientific Interest (SSSI), which cover 40% of the Breckland land area (Dolman *et al.* 2010).

The largest known population of breeding curlew in Breckland occur on Stanford Training Area (Stanta), an extensive area of SSSI-designated grass heathland, used as a military training area since World War Two. Here, figures from Norfolk Bird and Mammal Reports 1961-2016 suggest that the curlew population has increased from a regular count of 12 pairs in the late twentieth century, to fluctuating annual counts of between 15 and 34 breeding pairs, over the last twenty years. Similarly, curlew breeding at Brettenham Heath, a much smaller area of grass heathland, have also increased in abundance, with the number of pairs increasing from two or three in the 1980s and early 1990s, to seven in 2018 (unpublished data, Natural England; Zielonka *et al.* 2020). Despite the mostly anecdotal nature of these data, population trends at both Stanta and Brettenham Heath reflect those published in Bird Atlas 07-11, which suggests that curlew populations in Breckland have been largely stable over the last fifty years, with some increases in range and abundance during the last twenty years (Balmer *et al.* 2013). However, the longevity of curlew means that populations can persist for many years despite low productivity, and so a stable population trend is not necessarily an indicator that this population is sustainable in the long term.

Currently, very little is known about the breeding productivity of curlew in Breckland. The only intensive monitoring of the breeding curlew population was conducted during 2017 and 2018 on Stanta and Brettenham Heath, when monitoring of fifty nests revealed that mean productivity (number of fledged chicks per breeding pair ± se) was substantially higher at Brettenham Heath (0.685 ± 0.12, n=13) than at Stanta (0.032 ± 0.03, n=37) (Zielonka *et al.* 2020). Of these fifty nests, 72% failed at the egg stage, mainly owing to egg predation by red foxes, while chick mortality was also high, at 81% (Zielonka *et al.* 2020). The spatial variation in productivity revealed in this Breckland study suggests a potential opportunity to identify the causes of this variation, which can help to inform targeted conservation actions.

Thesis aims and outline

The aim of this thesis is to assess how key components of curlew breeding productivity vary spatially and temporally, identify the environmental conditions influencing such variation, and explore where and how conservation actions could be targeted to restore threatened lowland populations. Whilst this thesis is focused on a lowland curlew population breeding in Breckland, eastern England, the results presented extend beyond this study system to contribute towards a broader understanding of the strategies required to target conservation actions aimed at slowing and reversing declines of other widespread but threatened populations in Europe.

Each chapter has been written as a stand-alone paper for submission to peer-reviewed journals and, at the time of writing, Chapter 2 is published in *IBIS* and Appendix 1 is published in *Wader Study*. Only minor alterations have been made to published chapters to improve the cohesiveness and formatting of this thesis.

Chapter 2 takes advantage of the diverse range of sites and environmental conditions in which curlew breed in Breckland, and three years of monitoring curlew nests, to quantify spatial (across eight sites) and temporal (annual and seasonal) variation in curlew nest survival rates, assess potential drivers of this variation, identify likely nest predators and other causes of failure, and explore the conservation actions that might be capable of exploiting this variation. This work revealed widespread, consistent low levels of nest survival, with most nests failing as a result of nocturnal (and therefore likely mammalian predation).

In **Chapter 3**, we use daily tracking of curlew broods over three years, in combination with vegetation surveys of the areas used by broods, to explore how chick survival and habitat use vary in relation to vegetation structure across the mosaic of grassland and arable habitats in Breckland. We found chick survival to be consistently low across years and between sites, but was significantly higher with tall vegetation in the surrounding landscape. In addition, chick habitat use and survival in relation to available vegetation structures varied through the pre-fledging period, with use and benefits of tall vegetation being more apparent in older chicks.

Identifying environmental conditions associated with consistently high or low demographic rates can be a key step in developing actions to boost those rates. However, the types of actions that will be appropriate can also depend on the extent and spatial structure of those conditions across a population. In **Chapter 4**, we develop a conceptual framework to explore how integrating demographic success and occurrence of focal species in different environmental settings can be used to do identify appropriate actions. Applying this framework to Breckland-breeding curlew suggests potential benefits of actions to (a) preserve habitats and improve curlew productivity in areas of open grassland and (b) create suitable grassland patches within arable-dominated areas to encourage breeding attempts in areas where successes are more common.

In **Chapter 5** we then develop a simulation model, parameterised for the Breckland-breeding curlew population, to explore the consequences of deploying actions to boost hatching fledging success in isolation or in combination, using the results from **Chapter 2** and **Chapter 3**. This model suggests substantial benefits to targeting the deployment of permanent predator-proof fencing in areas where favourable vegetation structures exist or could be created, and that field trials of these actions would be worthwhile, while numbers and breeding densities remain sufficiently high to make such trials feasible.

Finally, in **Chapter 6**, the key findings are summarised and discussed in the broader context of targeting conservation actions, and suggest how species recovery might be achieved for curlew in the UK lowlands and beyond.

Chapter 2

Nest survival of threatened Eurasian curlew (Numenius arquata) breeding at low densities across a human-modified landscape

Nest survival of threatened Eurasian curlew (Numenius arquata) breeding at low densities across a human-modified landscape

Harry Ewing*,[1] Samantha Franks,[2] Jennifer Smart,[1,3] Niall Burton[2] & Jennifer A. Gill[1]

[1] School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich, NR4 7TJ, UK

[2] British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK

[3] RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK

Published in *IBIS*, Dec 2022: doi.org/10.1111/ibi.13180

Abstract

Targeted management actions to boost key demographic rates can help to restore rare and localised populations but are increasingly required to stabilise or reverse declines of formerly common and widespread species. Many breeding wader populations across Europe are declining because of unsustainably low rates of productivity, and the conservation tools designed to boost wader breeding productivity have been most effectively used for semi-colonial species within protected areas. Targeted management for wader species that breed at low densities across human-modified landscapes, such as the rapidly declining Eurasian curlew *Numenius arquata*, is likely to be more challenging. Here, we quantify variation in curlew nest survival in order to explore how management could be targeted to boost this key component of breeding productivity. Up to 80 pairs of curlew were monitored annually between 2019 and 2021 in eight locations across Breckland, eastern England, where nesting densities range from < 1 to ~7 pairs km^{-2}. For 136 nests across grassland- and arable-dominated sites, the majority of failure (86%) was caused by (primarily nocturnal) predation and the mean probability of surviving incubation (PSI) for all hatched or predated nests (127) was ~0.25. Nest survival showed little annual or seasonal variation but did vary slightly between sites, however, this spatial variation was not clearly related to management conditions or nest concealment at these sites. Fencing to exclude mammalian nest predators can be effective for waders, but too few curlews currently nest within fenced areas in Breckland to produce observable effects. Fencing the few sites with high nesting densities could potentially double the number of chicks hatched each year within the study area, but landscape-scale actions to reduce predator impacts on nests and chicks are likely to be needed to maintain breeding numbers in the wider countryside.

Introduction

Human-driven biodiversity loss is one of the most critical global environmental problems for which mitigation actions are not currently sufficient (Cardinale *et al.* 2012, Tittensor *et al.* 2014, Mace *et al.* 2018). Conservative estimates suggest that the average rate of vertebrate species loss over the last century is up to 100 times higher than background rates (Ceballos *et al.* 2015). Unless slowed, this is likely to threaten ecosystem services and, ultimately, human wellbeing (Dirzo *et al.* 2014). To meet post-2020 targets set by the Convention on Biological Diversity, substantial changes to environmental policy across all levels of government are required (Mace *et al.* 2018, Lim 2021), as well as evidence-based, targeted management to restore and maintain biodiversity (Sutherland *et al.* 2004, Mazor *et al.* 2018).

Targeted management can potentially help to restore threatened populations by implementing specific actions capable of boosting a given demographic rate (usually productivity or survival) in locations and/or at times when those rates are low and could potentially be improved (Morrison *et al.* 2022). To inform this type of management, research is required to identify; 1) the demographic rates influencing population growth, 2) spatial and temporal variation in these demographic rates, 3) the drivers of that variation and, 4) the actions required to boost demographic rates (Johnson *et al.* 2020, Plard *et al.* 2020, Morrison *et al.* 2022).

This evidence-based approach to conservation has been used effectively to conserve several rare and localised species of birds and mammals (e.g. Stanbury *et al.* 2010, Simón *et al.* 2012, Nicoll *et al.* 2021), and is now increasingly required to reverse or stabilise population declines of once abundant and widespread species (McRae *et al.* 2017), including bees *Anthophila spp.* (Drossart & Gérard 2020), butterflies *Rhopalocera spp.* (Van Dyck *et al.* 2009), small mammals (e.g. Pettett *et al.* 2018, Coomber *et al.* 2021) and numerous species of ground-nesting birds (e.g. Silva *et al.* 2018, Assandri *et al.* 2019). However, successful attempts to restore populations occurring sparsely and at low densities have so far been limited (Vickery *et al.* 2004, Butler & Norris 2013, Pe'er *et al.* 2014), particularly in human-modified landscapes where space to restore habitats is constrained by other land-uses (e.g. Xun *et al.* 2017).

A group of species for which targeted management is increasingly required are waders *Charadriiform spp.*, one of the world's most threatened but also most comprehensively monitored avian groups (Harrington *et al.* 2002, Amano *et al.* 2010). The relatively large body size and conspicuous behaviour of waders means that their populations are often well-monitored, in both breeding (e.g. Brlík *et al.* 2021, Harris *et al.* 2021) and non-breeding seasons (e.g. Frost *et al.* 2019, Nagy & Langendoen 2020), and individual-level studies of distribution and demography are common (e.g. Gill *et al.* 2019, Méndez *et al.* 2020, Verhoeven *et al.* 2020). Consequently, the multitude of complex, interrelated threats that act on waders (Sutherland *et al.* 2012), and the demographic rates influencing population growth, are often quite well understood (e.g. Macdonald & Bolton 2008, Roos *et al.* 2018, Cook *et al.* 2021).

In Europe, studies have linked wader population declines to changes in landscape composition (e.g. Wilson *et al.* 2014, Jóhannesdóttir *et al.* 2019), breeding habitat quality (e.g. Wilson *et al.* 2004, Smart *et al.* 2006), vegetation structure (e.g. Kentie *et al.* 2015) and land management practices (e.g. Verhulst *et al.* 2007, Exo *et al.* 2017), caused mainly by agricultural intensification (e.g. Kleijn *et al.* 2010) and afforestation (e.g. Douglas *et al.* 2014, Kaasiku *et al.* 2022, Pálsdóttir *et al.* 2022). These environmental changes have resulted in nests and chicks becoming more vulnerable to predation, which is thought to be the main driver of ongoing wader population declines across the region (Macdonald & Bolton 2008, Roodbergen *et al.* 2012, Roos *et al.* 2018). To compound threats further, human-induced climate change is rapidly altering environmental conditions, reducing habitat suitability (e.g. Smart *et al.* 2006) and the availability of invertebrate prey (e.g. Pearce-Higgins *et al.* 2010), as well as driving changes in wader breeding phenology for which the long-term impacts on demography are yet to be fully understood (Kentie *et al.* 2018, Alves *et al.* 2019, Gill *et al.* 2019). Warmer, drier springs are also advancing mowing and grazing dates such that they can now coincide with incubation and chick-rearing in agricultural landscapes (Schroeder *et al.* 2012), and effective management of grassland breeding habitat is predicted to become more challenging in the face of increasingly severe drought and flood events (Joyce *et al.* 2016).

In response to wader declines across Europe, considerable effort has been made to design, trial and deploy targeted management actions with the aim of boosting wader breeding productivity (Franks *et al.* 2018, Jellesmark *et al.* 2021, Laidlaw *et al.* 2021). These actions include habitat management to increase the suitability of breeding sites by altering conditions such as hydrology (e.g. Eglington *et al.* 2008), vegetation structure (e.g. Laidlaw *et al.* 2017) and timing of grassland management practices (e.g. Verhulst *et al.* 2007), controlling predator activity through targeted culling (e.g. Bolton *et al.* 2007, Smith *et al.* 2010) and/or exclusion fencing (e.g. Smith *et al.* 2011, Malpas *et al.* 2013), and headstarting (raising eggs and chicks in captivity through the early weeks of life) (e.g. Pain *et al.* 2018, Laidlaw *et al*. 2021).

These tools target the nesting, incubation and chick-rearing stages of the breeding cycle and have helped to increase breeding productivity in some threatened wader populations, particularly those restricted to nature reserves or other protected areas (Smart *et al.* 2014, Jellesmark *et al.* 2021). In these areas, land-use and management are usually aimed at biodiversity and conservation goals and, as breeding wader densities tend to be higher in nature reserves (Silva-Monteiro *et al.* 2021), targeted management in these areas can impact relatively large numbers of birds in a relatively small area. However, not all threatened wader species breed in large numbers within nature reserves or protected areas, and some breed at much lower densities across human-modified landscapes (Silva-Monteiro *et al.* 2021). Targeted management for such species is likely to be challenging, particularly as the interventions outlined above have not yet been demonstrated to work effectively and sustainably outwith protected areas.

The globally Near-Threatened Eurasian curlew *Numenius arquata* (hereafter, curlew) (IUCN 2022) was once an abundant and widespread species across much of western, northern and eastern Europe. However, in recent decades the number of breeding pairs has declined steeply in these regions (Keller *et al.* 2020) with some populations already on the verge of extirpation (e.g. O'Donoghue 2019). These declines have been attributed to low rates of breeding productivity (Berg 1992, Valkama & Currie 1999, Johnstone 2007, Zielonka *et al.* 2020), likely driven by the same mechanisms influencing productivity in other breeding wader populations across western Europe (Fletcher *et al.* 2010, Douglas *et al.* 2014, Franks *et al.* 2017). These population declines, alongside the recent history of extinction among related species in the Numeniini tribe (Pearce-Higgins *et al.* 2017), mean that conservation interventions are urgently needed to prevent the further extirpation of breeding populations. A greater understanding of how key components of curlew breeding productivity vary in space and time is required to enable these interventions to be targeted effectively.

Here, we quantify spatial and temporal variation in nest survival, assess potential drivers of this variation, and identify likely nest predators and other causes of nest failure for curlew breeding at low densities across a human-modified landscape. We use these findings to explore opportunities for targeting management to boost nest survival in such species and landscapes, and the types of actions likely to be required.

Methods

Study area

The study took place in Breckland, a 1019 km^2 region of eastern England, where breeding curlew are thought to be stable or possibly increasing in abundance and range (Balmer *et al.* 2013). Traditionally, the region comprised large areas of semi-natural fallow land, disturbed and maintained over time by fluctuating patterns of livestock and rabbit grazing and low intensity, rotational farming methods (Dolman *et al.* 2010). However, wide-scale land-use change has transformed the Breckland landscape into a mosaic of habitats dominated mainly by commercial forestry and arable fields, interspersed with remaining patches of semi-natural grassland (Dolman *et al.* 2010). Landowners and stakeholders in the region include private estates managed for agriculture, livestock farming, shooting and equine breeding, Forestry England, the Ministry of Defence and conservation NGOs.

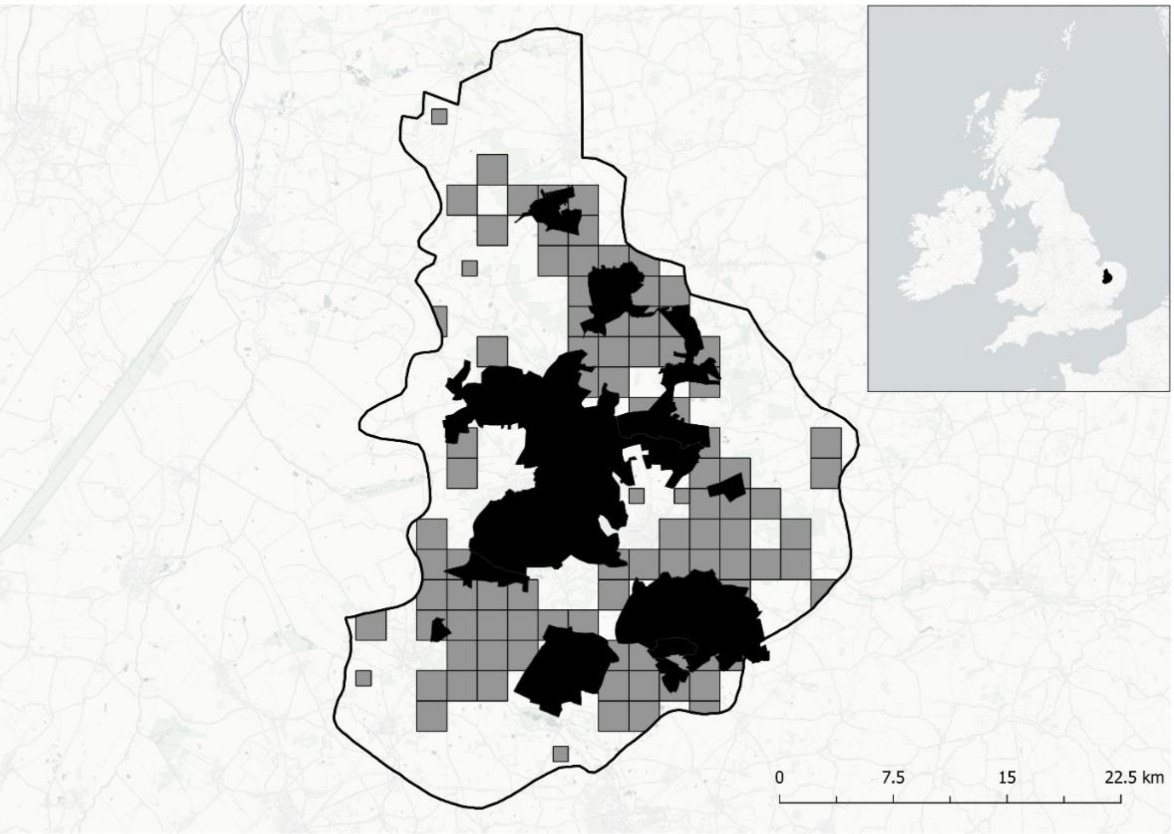


Figure 1: Areas within Breckland (outlined in grey) in which curlew have been reported as possible, probable or confirmed breeding (grey blocks) in national bird monitoring schemes (Balmer *et al.* 2013, Harris *et al.* 2021) over the last decade, and the study area (black polygons) within which breeding curlew were monitored between 2019 and 2021. Inset indicates the location of Breckland within the UK.

Permission to monitor breeding curlew was granted at eight sites across Breckland; the entirety of two private estates, two grassland sites within two other private estates, an arable farm, a military training area, an RAF base and the entire area managed by Forestry England (Fig. 1). All eight sites were monitored during 2019 and 2021, but only four sites were monitored during 2020, when access restrictions were tightened due to the Covid-19 pandemic.

The eight study sites were dominated by arable fields or semi-natural grassland, which were maintained by mowing or livestock grazing. Five sites contained ground-disturbance plots; ca.4 ha areas of semi-natural grassland, recently rotovated to create bare ground to encourage breeding stone curlew *Burhinus oedicnemus* (Hawkes *et al.* 2019, 2021). Public access was restricted at all sites and some areas within grassland sites were enclosed by fencing. Fences were in place to prevent wild mammalian herbivores (e.g. deer spp. *Cervidae* or European brown hare *Lepus europaeus*) from penetrating boundaries or to restrict human access to hazardous areas on military sites, and were also likely to act as barriers to mammalian predators (e.g. red fox *Vulpes vulpes* and European badger *Meles meles*). Most grassland sites were either unfenced or partially or fully enclosed by livestock fences (large-mesh or non-electrified stranded fence, mostly less than 2 m high), which were unlikely to act as a barrier to mammalian predators (White & Hirons 2019). Nests were therefore classified as fenced if they were within areas that were fully enclosed by fencing with mesh sufficiently small to prevent access by foxes and badgers, at least 2 m in height, with no obvious access points in or under the fence line.

Nest finding and monitoring

In 2019 and 2021, curlew pairs were located between late-March and mid-April by approaching all open areas within each site to at least 100 m on foot or by vehicle. All areas in which a curlew pair was located were revisited throughout the season to classify pairs as possible, probable or confirmed breeders, using breeding evidence codes (see Supporting Information Table S1). Nests, including re-lays, were found between mid-April and mid-June by searching study areas for incubating birds and observing incubating birds returning to nests. In 2020, surveys and nest monitoring did not commence until late-May due to the Covid-19 pandemic.

The location of each nest was recorded with a GPS device, and an iButton temperature logger was deployed in the nest lining (Maxim Integrated Products Ltd, San Jose, CA, USA), set to record every 10 minutes and covered with tape to prevent the metallic surface from reflecting. Predicted hatch dates of nests found on a clutch of one or two eggs, and thus likely during laying, were estimated by back-calculating the lay date of first egg (assuming that one egg was laid every 1.5 days (Grant 1996) and adding 34 days (average laying period plus average incubation period (Grant 1996)). All eggs in clutches of three to five were weighed and measured to enable laying and hatching dates to be predicted, following Grant (1996).

Nests were visited a minimum of every ten days, and daily from three days prior to the predicted hatch date, to determine their status and outcome. Where possible, nest status was checked remotely to reduce disturbance. Nests were recorded as successful if at least one egg hatched. Hatched eggs were confirmed by the presence of empty eggshells, or at least one newly hatched chick, in or around the nest scrape. Chicks were observed in all successful nests, so hatch date was recorded as the first date on which at least one newly hatched chick was found in the nest. Nests were recorded as failed if there were obvious signs of predation, mowing, trampling or abandonment or, if they were found empty before the estimated hatch date with no eggshell fragments in the nest that would have indicated successful hatching (Green *et al.* 1987). Nests were not visited in cold or wet weather conditions and no obvious tracks were left around the nest during nest visits.

For nests that did not hatch, time and date of nest failure was determined by a sudden and sustained drop in temperature recorded on the iButton temperature logger (44 out of 84 predated nests). For nests that failed prior to full incubation, temperatures in the nest were not stable enough for the loggers to detect a sudden drop at the point of failure and, in some cases, a build-up of nest lining resulted in the logger being too deep in the nest scrape to detect a stable incubation temperature, which also meant that time of failure could not be detected. In these cases, when iButton temperature loggers failed to give reliable results (40 out of 84 predated nests), date of nest failure was calculated as the mid-point between the date that the nest was last observed intact and the date on which the nest was recorded as failed (mean ± sd gap = 5.8 ± 2.3 days).

Nesting conditions

Management conditions for each nest were categorised as arable crop, fenced grassland, unfenced grassland or ground-disturbance plot, as defined above. Nest concealment was recorded on the day on which each nest was located, by measuring the height of the tallest sward at four opposite points directly around the edge of the nest scrape and calculating the mean.

Statistical analyses

Variation in daily nest survival rates (DSR) were explored in Mayfield’s logistic exposure models with a binomial error term, in which success (hatched and failed) was modelled with exposure days (number of days from find date to date of hatch or known (from temperature loggers) or estimated (from check midpoints) failure) as the binomial numerator (Shaffer 2004). Nine nests that failed for reasons other than predation were excluded from the analysis so we could focus on predation, the main driver of wader population declines across Europe (Macdonald & Bolton 2008, Roodbergen *et al*. 2012). Removing these nests made very little difference to our models results (Table S2).

To avoid model overfitting, a two-step approach was taken. The initial model assessed spatial and temporal variation in DSR of all nests monitored during the study period by including site, year and their interaction, lay date, year and their interaction and nest age, as fixed factors in a GLM (Table 1, model i). The subsequent model assessed potential drivers of any spatial variation by including management conditions that varied across these sites (arable, fenced grassland, unfenced grassland or ground-disturbance plot), nest concealment and their interaction and nest age as fixed effects, and site as a random intercept (to account for non-independence of nests from the same site) in a GLMM (Table 1, model ii). Most nests were found soon after laying (mean ± sd nest age on day of finding = 9.9 ± 7.8 days; equivalent to 6 days of egg laying plus 3-4 days of incubation for a clutch of four) (Fig. S1-S3). We ran models excluding older nests (found at 14 days from onset of laying) to explore their influence on model findings, but results did not differ from models including nests of all ages (Table S3).

Continuous variables used in model i and ii (lay date, nest concealment and nest age) were scaled and centred to have a mean of zero and a standard deviation of 1. Non-significant ($P > 0.05$) interaction terms were sequentially removed from models, and inference was made from the maximum model retaining all main effects. All models were run in R (v 4.2.1) using the lme4 package (Bates *et al.* 2015).

Predicted DSRs were extracted from models and transformed to probability of nest survival over the incubation period (PSI) by raising DSR to the power of 34 (the average curlew incubation period (days) from the first egg laid). 95% confidence intervals were calculated using the Delta method (Ver Hoef 2012).

As the proportion of monitored nests within fenced areas was low, a power analysis, using data from Malpas *et al.* (2013) on the difference in wader nest survival in fenced and unfenced areas, was also conducted to assess how many nests would need to be enclosed with predator exclusion fencing to detect a statistically significant effect of fencing and to estimate the effect size required to detect an observable effect of fencing with the number of fenced nests monitored during our study (Table S4; Fig. S4).

To assess whether predation events were more likely during night or day, the frequency of observed night/day predation events was compared to the number of night/day hours summed across all monitored nest-days, to account for variation in day length through the season, using a 2 x 2 Fisher's Exact test.

Table 1: Description of the model variables used to explain variation in daily nest survival rate (DSR) of curlew nests found across Breckland between 2019 and 2021. All variables included in interaction terms are also included as main effects in both models.

Type	**Variable**	**Distribution (link)/variable range of values**	**Explanation**
Response	Daily nest survival rate (DSR)	Binomial (logit)	Nest outcome (hatched/failed) accounting for exposure days.
Explanatory	Site	8 sites	Nest site identity
	Year	2019, 2020, 2021	Years in which nests were monitored
	Lay Date (scaled and centred)	Day 1 – 101	Lay date in March days (no. of days from 1st March)
	Management condition	4 management conditions	Arable, fenced grassland, unfenced grassland or ground-disturbance plot
	Nest concealment (scaled and centred)	0 – 57 cm	Mean of four sward height measurements (in cm) taken around the nest scrape.
	Nest age (scaled and centred)	1 – 33 days	Day of the incubation period on which a nest was found.

Model	**Response**		
i	DSR		Site*Year + Lay Date*Year + Nest Age
ii	DSR		Sward Height*Management condition + Nest Age + (1|Site)

Results

In 2019 and 2021, 67 and 80 pairs of curlew, respectively, were found and monitored across the Breckland study area. The density of pairs classified as probable or confirmed breeders within six of the eight study sites (which comprised 95% of the surveyed area) ranged between 0.17 and 0.72 pairs per km^2, while two other sites which comprised only 5% of the surveyed area hosted densities of between 3.3 and 7.4 pairs per km^2 (at least 47% of the probable or confirmed breeding pairs monitored annually; Fig. 2). Only 21 pairs of curlew were classified as probable or confirmed breeders in 2020 as fieldwork was limited to late in the breeding season, due to restrictions imposed as a result of the Covid-19 pandemic.

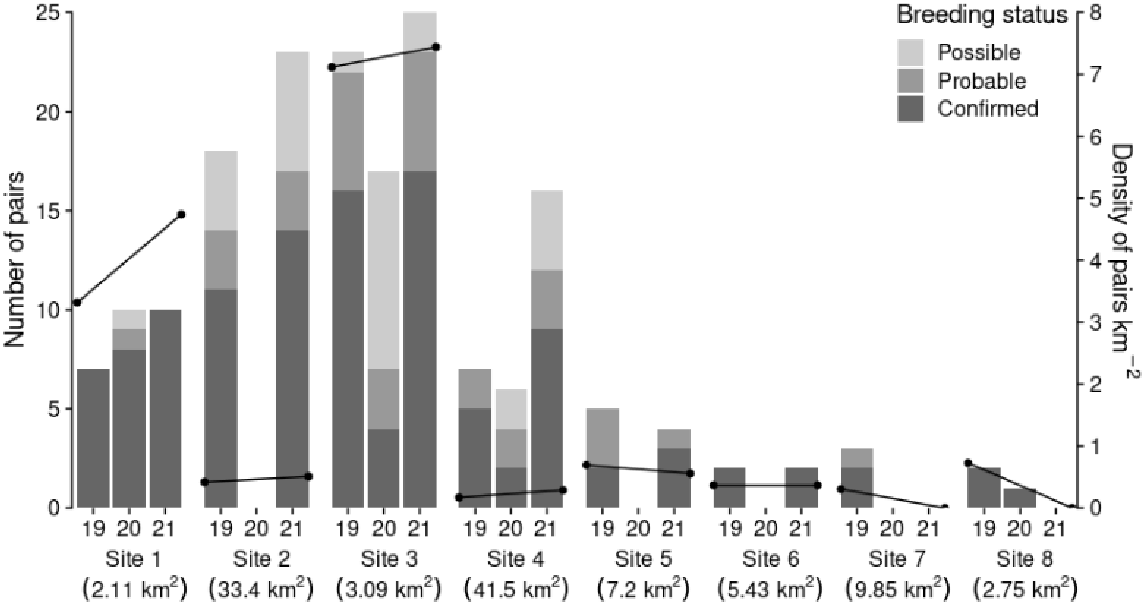


Figure 2: The abundance (bars) and density (points) of possible, probable and confirmed breeding pairs of curlew recorded annually across surveyed areas within eight Breckland study sites, between 2019 and 2021. Density figures for 2020 are excluded due to reduced survey effort. Breeding status categories defined using BTO breeding codes (Table S1)).

A total of 136 curlew nests, comprising 471 eggs, were monitored across Breckland during the study period, with the majority being found in unfenced grassland areas. From these 136 nests, 185 chicks hatched from 52 nests and 84 nests failed (Fig. S5). Only one site out of eight failed to hatch any chicks during the study period (Fig. S5a) and chicks hatched in all four management conditions (Fig. S5b). Predation accounted for 86% of nest failures and other nests failed due to abandonment during laying (*n* = 3), trampling by cattle (*n* = 1) and destruction through mowing or other mechanised farming activities (*n* = 5).

The mean ± 95% CI probability of surviving incubation (PSI) of the 127 hatched or predated curlew nests monitored across Breckland was 0.2488 (± 0.1786 – 0.3372). There was evidence of variation among sites (Table 2), with PSI being greater at site 1 (15/30 nests predated) than site 2 (24/30 nests predated) (Fig. 3) and being particularly low at site 5, where none of the six nests monitored during the study period hatched successfully (Fig. 3). Mean PSI did not vary significantly through the season, between years or with nest age (Table 2).

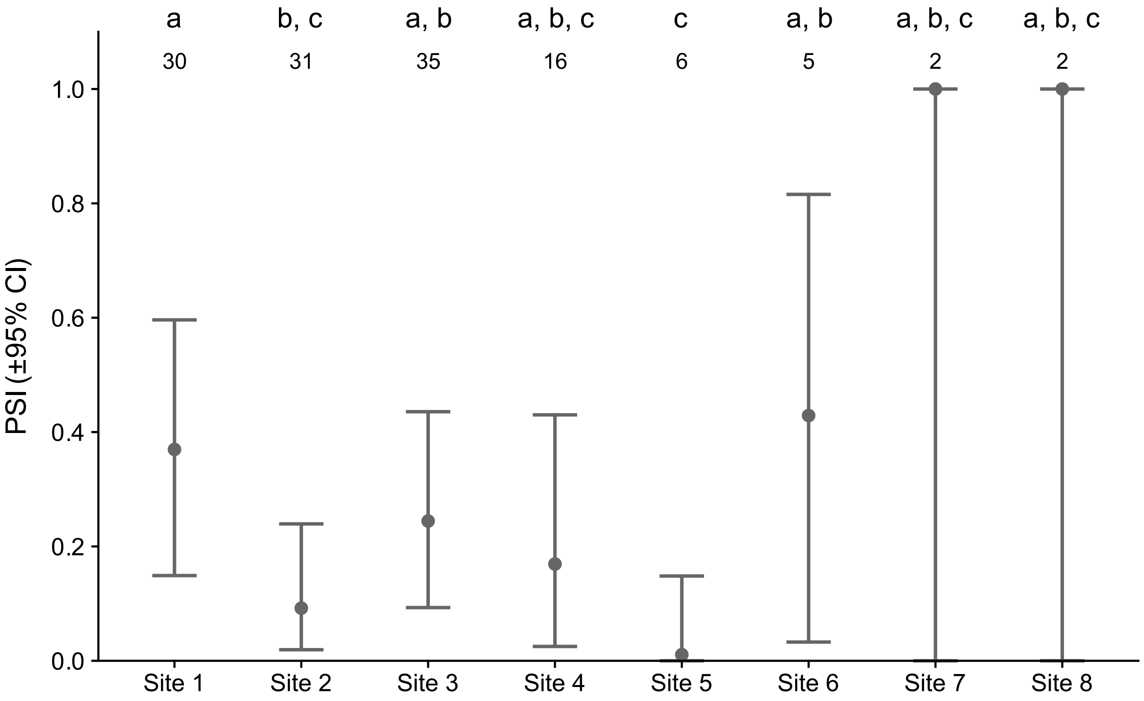


Figure 3: Mean predicted probability of a curlew nest surviving incubation (PSI), and the number of nests monitored (numbers above bars), at eight Breckland study sites, between 2019 and 2021. Sites that do not share a common letter differed significantly (Table 2).

Nest survival was similar in unfenced grassland, fenced grassland, arable fields or ground-disturbance plots, and across levels of nest concealment (Table 2), so the spatial variation in nest survival was not the result of variation in management conditions or nest concealment between sites. Power analysis suggest that 25 nests of the 102 nests found within grassland (fenced and unfenced) would need to have been enclosed by fencing to detect an effect of fencing on nest survival comparable to Malpas *et al*. (2013) (Table S4; Fig. S4). With our sample of nine fenced nests, an effect of fencing would have only been observed had the effect size been > 0.9 (Fig. S4).

Table 2: Results of Mayfield's logistic exposure models of spatial and temporal variation in daily nest survival rates (DSR) (model i) and potential drivers of variation in DSR (model ii) of curlew nests monitored in Breckland between 2019 and 2021 (see Table 1 for model details). Significant predictors of DSR (*P* < 0.05) are highlighted in bold.

Model	Fixed effect	Chi sq.	Df	*p*
i (Spatial and temporal)	Year	4.037	2	0.132
	Lay date	0.039	1	0.842
	Nest age	0.644	1	0.422
	Site	**17.665**	**7**	**0.014**
	Pseudo R^2 = 0.17			
ii (Drivers)	Nest concealment	0.141	1	0.707
	Management condition	5.597	3	0.133
	Nest age	0.569	1	0.450
	Pseudo R^2 = 0.09			

Time of nest failure was extracted from temperature loggers for 44 of the 84 predated nests; 36 nests were predated during the night and eight during the day (Fig. 4). Relative to the ratio of night/day hours monitored (summed across each nest-day monitored; ratio 0.50) predation occurred significantly more often at night than expected by chance (Fisher's Exact test, *P* < 0.01).

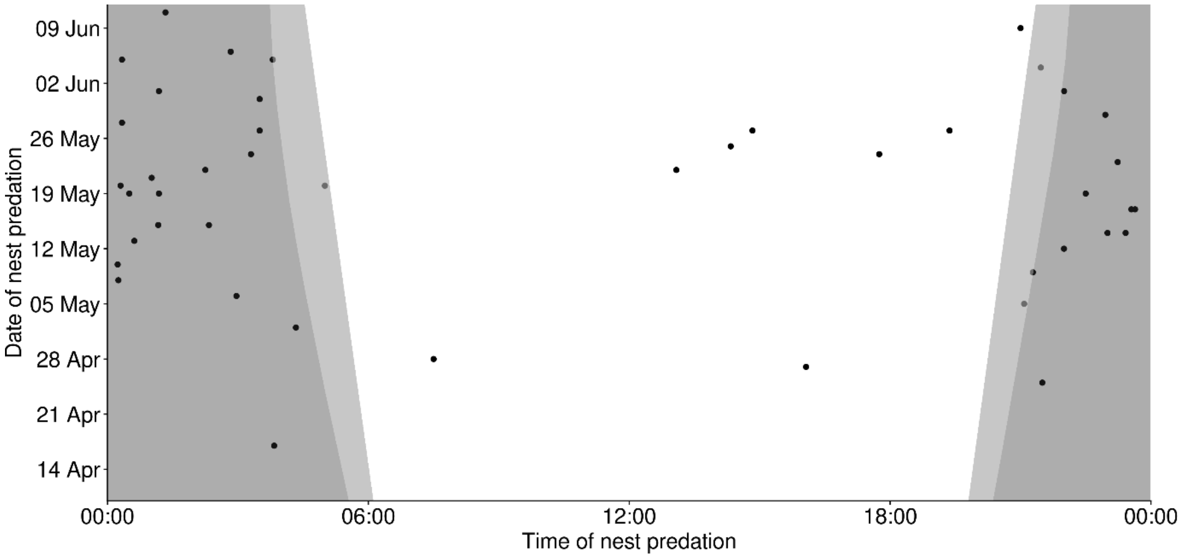


Figure 4: Date and time of 44 curlew nest predation events between 2019 and 2021 in Breckland, eastern England. Shaded area indicates nocturnal (dark grey) and crepuscular (light grey) periods.

Discussion

Breeding curlew were sparsely distributed across the majority of the Breckland study area, with densities at over 95% of the study area being below one pair per km^2. Nests were found in conditions ranging from bare ground on arable fields to tall (~50 cm) grass in silage fields, but the probability of a curlew nest surviving to hatch was consistently low (~0.25). A small amount of variation in nest survival was observed between sites (Fig. 3), but this could not be explained by management conditions or levels of nest concealment. As the great majority (86%) of nests failed because of predation, which primarily occurred at night (indicative of mammalian predation), boosting hatching rates of curlew nests is likely to require actions to reduce mammalian predator impact across the Breckland landscape.

A conservation tool that is commonly deployed to reduce predation on ground-nesting birds' nests is predator-exclusion fencing (Smith *et al.* 2011). Fences have the potential to result in ~two-fold increases in wader hatching rates (Malpas *et al.* 2013) and, as they have already been used to boost hatching rates of some threatened wader populations in western Europe, including black-tailed godwit *Limosa limosa* (Verhoeven *et al.* 2022) and northern lapwing *Vanellus vanellus* (hereafter lapwing) (Malpas *et al.* 2013, Verhoeven *et al.* 2022), it seems likely that they could also be effective at boosting curlew nest survival.

In Breckland, fences were not deployed to protect curlew nests, but a small number of pairs nested within fenced areas (too few to detect an observable effect of fencing on nest survival). Increasing the number of nests enclosed by predator fencing in Breckland could potentially be achieved by deploying temporary electric fencing to protect individual nests, but the substantial efforts required to locate nests and erect and maintain fencing (throughout the season and across years due to the lack of temporal variation in nest survival), means that this is unlikely to be a feasible approach, especially in areas where curlews breed at very low densities.

One way in which targeted deployment of fencing could potentially be effective might be to enclose ground-disturbance plots. These areas are often used by nesting curlew (Zielonka *et al.* 2020) and, although we found curlew nest survival to be just as low under these management conditions as elsewhere, they are generally located in areas in which land-use is sympathetic to ground-nesting birds (e.g., areas under higher tier agri-environment schemes; Evans & Green 2007, Chamberlain *et al.* 2009), potentially making fencing more feasible. Plot-level fencing could also be deployed at the start of the season, without the need to locate nests, and may benefit other ground-nesting species such as stone curlew (Hawkes *et al.* 2021) and lapwing (Chamberlain *et al.* 2009, Rickenbach *et al.* 2011).

However, these plots currently only support ca.4 – 7 breeding pairs of curlew in our study area, and thus the impact of such measures for curlew is likely to be quite modest.

Alternatively, permanent barrier fences could be deployed along the boundary of sites supporting high densities of nesting curlew. Fencing the combined boundary length of the eight Breckland study sites that support ~80 curlew pairs annually would require ca.185 km of fencing, but we found ~45% of those curlew to breed in just two of those sites, with a combined boundary length of only 14 km. Assuming such fences would be as effective as described elsewhere (Malpas *et al.* 2013), enclosing these two high-density sites with permanent barrier fencing could potentially boost the total number of chicks hatched in our Breckland study area by ~44 – 67% (~88 – 94 additional chicks hatched) per year.

Targeting actions to reduce predator impacts, such as fencing high density breeding sites and ground-disturbance plots has the potential to provide a relatively efficient solution to boosting curlew nest survival. However, high-density curlew breeding sites are becoming very rare, particularly in the English southern lowlands (Colwell *et al.* 2020), and so opportunities to target sites with potential to contribute substantial improvements in nest survival are increasingly limited. Failure to identify and protect remaining curlew populations effectively will likely increase the need for intensive and expensive actions such as headstarting (raising eggs and chicks in captivity through the pre-fledging period), which is already being deployed to boost curlew productivity in southern England (Colwell *et al.* 2020).

To sustainably maintain and recover curlew populations in the wider landscape, in Breckland and elsewhere across the breeding range, actions outwith fenced areas are also likely to be required. Lethal control of foxes, the main mammalian nest predator in the region (Zielonka *et al.* 2020), occurs across much of the Breckland study area, and it is possible that variation in the intensity of lethal control between study sites could contribute to the (small amount of) spatial variation in curlew nest survival. The impact of lethal control on breeding success of ground-nesting birds can vary substantially between sites (Bolton *et al.* 2007, Porteus *et al.* 2019), and may be influenced by the predator communities present at those locations and times (Bolton *et al.* 2007, Mason *et al.* 2018). Consequently, the contribution of lethal control to maintaining and recovering breeding curlew populations is currently unknown, and the need for improved understanding of predator behaviour and population dynamics remains urgent (Laidlaw *et al.* 2021).

A greater understanding of the factors influencing nest survival and the causes of nest failure elsewhere across the species' range will also be important so that actions can be targeted across broader spatial scales. For example, nest concealment is a poor predictor of curlew nest survival in Breckland but vegetation in this region is generally short due to the relatively dry conditions (Dolman *et al.* 2010). Elsewhere, vegetation may be considerably taller due to higher spring rainfall and more intensively managed grasslands, potentially resulting in increased nest concealment and a subsequent boost to nest survival. Landscapes are also likely to differ between (and within) regions in which curlew breed, so exploring how factors such as landscape composition and configuration (e.g. Jóhannesdóttir *et al.* 2019) influence curlew distribution and success is likely to help inform effective targeting of actions to boost hatching success in the wider landscape.

Finally, establishment of collaborative stakeholder networks, and integration of evidence-based, curlew-friendly policies into agri-environment schemes are likely to be of particular importance in maintaining breeding populations, given their generally sparse, low-density distribution. Working with stakeholders to trial management actions for curlew (e.g., fencing, headstarting, lethal control) will clearly be important part of this, but any actions to boost nest survival should be targeted in areas likely to support chick growth and survival, and further research is required to understand the land management actions that can create and maintain such conditions at different scales.

Supplementary material to Chapter 2: Nest survival of threatened Eurasian curlew (Numenius arquata) breeding at low densities across a human-modified landscape

Supplementary material

Table S1: Breeding evidence categories used to classify curlews detected on surveys as non-breeding, or possible, probably or confirmed breeding.

Non-breeding

- Single, pair or number of birds flying over suspected to be still on migration
- Observed but suspected to be summering non-breeder(s)

Possible breeding

- Pair observed in suitable nesting habitat in breeding season on just one occasion
- Male present (or bubbling calls heard) in breeding season in suitable breeding habitat

Probable breeding

- Pair observed in suitable nesting habitat in same location on more than one occasion
- Permanent territory presumed through territorial behaviour on at least two different occasions
- Courtship and display judged to be in or near potential breeding habitat
- Pair visiting probable nest site
- Agitated behaviour or anxiety calls from adults, suggesting probable presence of nest or young nearby, observed on just one occasion.
- Pair nest scraping

Confirmed breeding

- Used nest or eggshells found
- Downy young seen
- Adults entering or leaving nest-site in circumstances indicating occupied nest or adults seen incubating – sitting is often followed by lowering of the head (disappearing in tall vegetation) followed by periodic raising and looking around
- Nest containing eggs
- Nest with young seen or heard
- Incubation change-over seen - when approaching the nest curlews appear to ‘move with purpose’ without actively feeding, although not necessarily faster or slower than normal
- Agitated behaviour or anxiety calls from adults, indicating presence of nest or young nearby, observed on three or more occasions

Table S2: Results of Mayfield's logistic exposure models of spatial and temporal variation in daily nest survival rates (DSR) (model i) and potential drivers of variation in DSR (model ii) of all curlew nests (including those mown, trampled and abandoned) monitored in Breckland between 2019 and 2021 (see Table 1 for model details). Significant predictors of DSR ($p < 0.05$) are highlighted in bold.

Model	Fixed effect	Chi sq.	Df	*p*
i (Spatial and temporal)	Year	4.888	2	0.087
	Lay date	0.111	1	0.738
	Nest age	2.073	1	0.483
	Site	**15.084**	**6**	**0.035**
	Pseudo R^2 = 0.14			
ii (Drivers)	Nest concealment	0.027	1	0.868
	Management condition	3.745	3	0.290
	Nest age	2.299	1	0.129
	Pseudo R^2 = 0.07			

Table S3: Results of Mayfield's logistic exposure models of spatial and temporal variation in daily nest survival rates (DSR) (model i) and potential drivers of variation in DSR (model ii) of curlew nests (< 14 days old) monitored in Breckland between 2019 and 2021 (see Table 1 for model details). Significant predictors of DSR ($p < 0.05$) are highlighted in bold.

Model	Fixed effect	Chi sq.	Df	*p*
i (Spatial and temporal)	Year	3.414	2	0.181
	Lay date	0.013	1	0.909
	Nest age	0.490	1	0.483
	Site	**13.862**	**6**	**0.031**
	Pseudo R^2 = 0.24			
ii (Drivers)	Nest concealment	0.096	1	0.756
	Management condition	0.729	3	0.867
	Nest age	0.538	1	0.463
	Pseudo R^2 = 0.10			

Table S4: Sample sizes and standard deviations extracted from Malpas *et al.* (2013), used to calculate the effect size between the nest survival rates inside and outside of predator exclusion fencing.

	Inside fence	**Outside fence**
Number of nests	68	104
Nest survival rate (%)	84	34
Standard Deviation	176.7	88.4
Effect size	0.6	

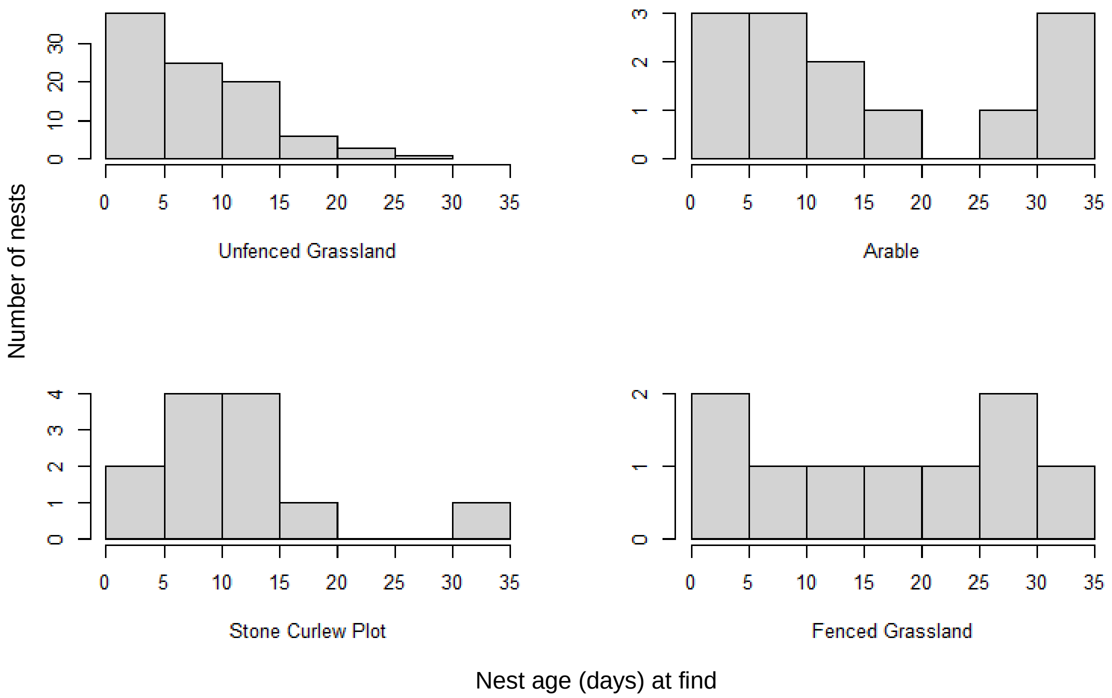


Figure S1: Age structure of curlew nests found in each of the four management conditions in Breckland.

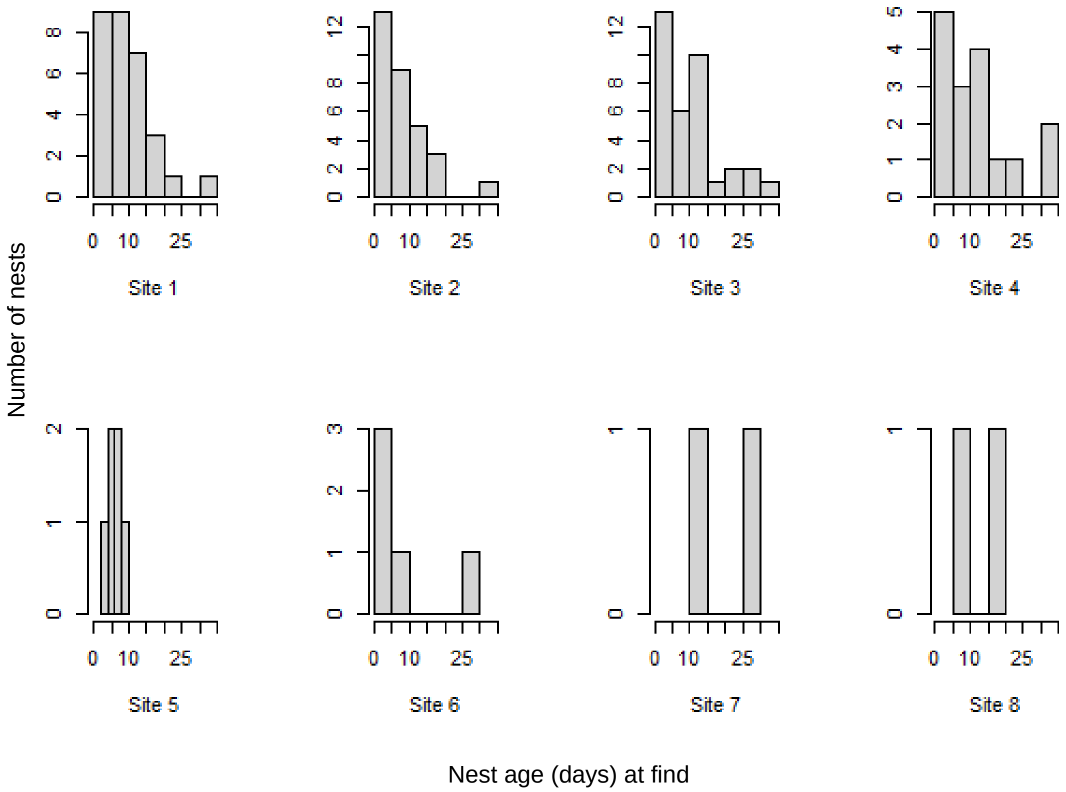


Figure S2: Age structure of curlew nests found in each of the eight sites in Breckland.

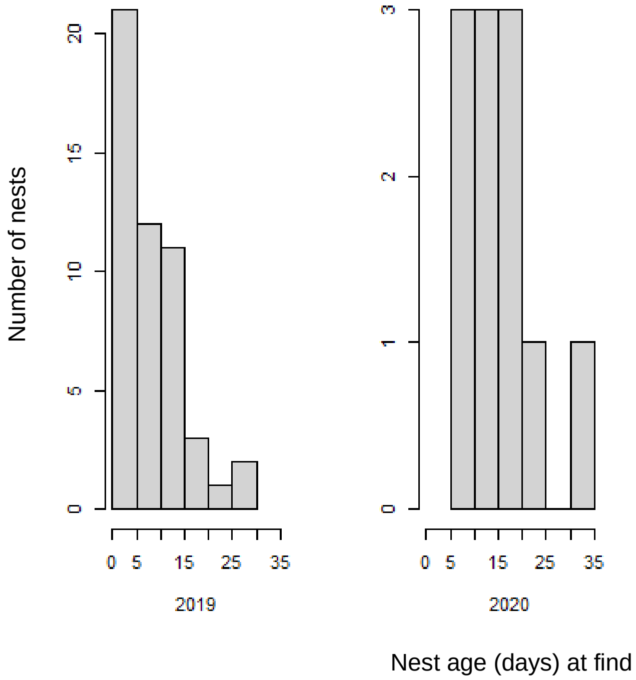


Figure S3: Age structure of curlew nests found in each of the three study years.

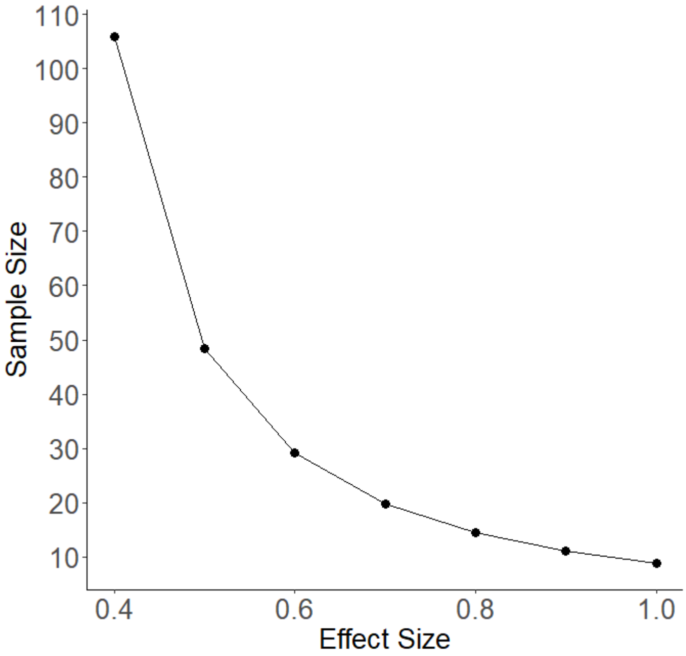


Figure S4: The number of nests required (sample size) to be enclosed by predator exclusion fencing to detect different effect sizes of fencing on nest survival. Based on 93 nests outside of fencing, power = 0.8 and significance level = 0.05.

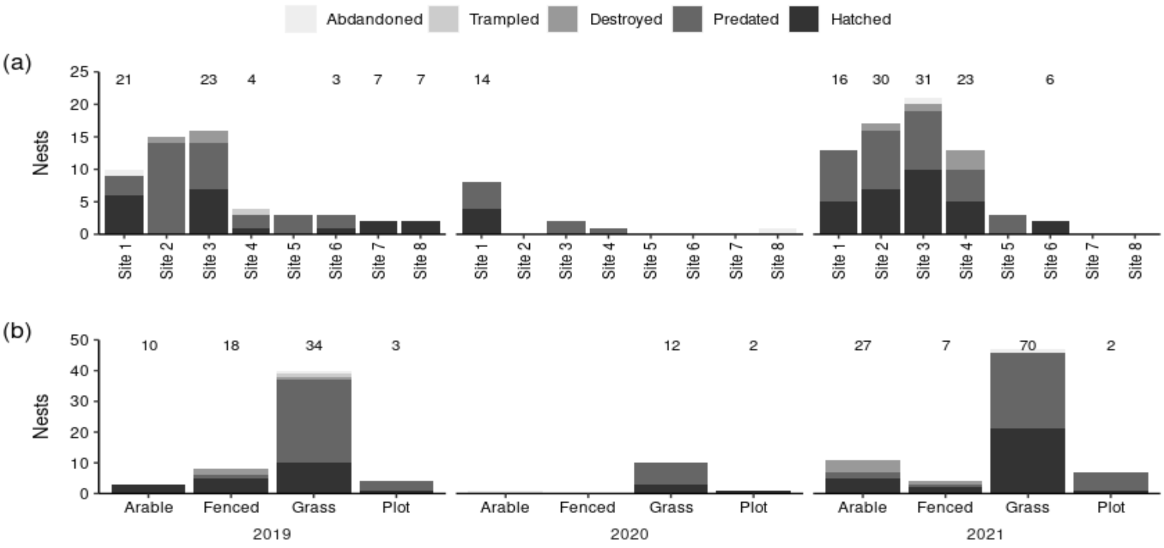


Figure S5: The number of curlew nests that were hatched, predated, destroyed, trampled or abandoned (bars) and the number of hatched chicks (numbers above bars) at each site (a) and in different management conditions (b) in Breckland, between 2019 and 2021.

Chapter 3

Survival of Eurasian curlew chicks varies with vegetation structure in a diverse lowland landscape

Abstract

Loss and degradation of open, semi-natural habitats and associated changes in vegetation structure are major threats to the biodiversity they support. Consequently, incorporation of vegetation management into targeted conservation plans is of great importance, and this requires an understanding of how vegetation structure influences the demography of threatened species. Ground-nesting waders are declining across Europe because of unsustainably low breeding productivity, and targeted conservation actions are needed to prevent further losses. Such actions could include vegetation management if vegetation structures that enhance demographic rates can be identified. Here, we use intensive field-based observations, alongside weekly vegetation surveys, to quantify the habitat use and survival of Eurasian curlew chicks in relation to variation in vegetation structure in Breckland, eastern England. Between 2019 and 2022, a total of 68 curlew broods were monitored, from which > 72% of chicks died before reaching two weeks old and 40 chicks fledged. Chick survival did not vary significantly between years, across seasons or between sites, but increased as the height of the tallest vegetation block in the 78.5 ha landscape surrounding hatched nests increased. However, in their first week of life, chicks were more likely to use areas of shorter vegetation and slightly more likely to survive when using these areas, while older chicks were more likely to use, and much more likely to survive when using taller vegetation. These findings highlight the importance of access to a mix of vegetation heights for curlew chicks, particularly during the first weeks of life, and the need for management actions capable of delivering these heterogeneous conditions at appropriate scales.

Introduction

Open semi-natural habitats, such as grasslands, heathlands and wetlands, provide crucial ecosystem services (e.g. Mitsch *et al.* 2013, Bengtsson *et al.* 2019, Walmsley *et al.* 2021) and support a broad spectrum of specialised flora and fauna (e.g. Petermann & Buzhdygan 2021), making them of great importance to human well-being and biodiversity. Yet many of these landscapes and the species that occur within them are threatened, with land-use and climate change driving widespread loss and degradation of open habitat across the globe (Bardgett *et al.* 2021, Douglas *et al.* 2023, Fluet-Chouinard *et al.* 2023), including large-scale changes in vegetation structure and composition (Foley *et al.* 2005, Zhao *et al.* 2012, Franklin *et al.* 2016).

Vegetation structure plays a major role in the functioning of ecosystems (e.g. Isbell *et al.* 2011, Gaitán *et al.* 2014) and maintenance of biodiversity (e.g. Haddad *et al.* 2009, Hovick *et al.* 2014). Changes in the structure of vegetation (height, cover, density and/or composition) can alter the availability of resources such as food (e.g. Vickery *et al.* 2001), breeding sites (e.g. Carrié *et al.* 2018) and refuge from unfavourable environmental conditions (e.g. Robertson *et al.* 2022) or predation (e.g. Norbury & van Overmeire 2019), and can ultimately drive changes in species abundance (e.g. Wong *et al.* 2021), diversity (e.g. Thomas *et al.* 2022) and demography (e.g. Sandercock *et al.* 2015, Laidlaw *et al.* 2020, Mérő *et al.* 2023).

In western Europe, conversion of open semi-natural habitats to cropland monocultures or improved pasture, and the associated changes in vegetation structure, have contributed to the widespread population declines and range contractions of many, once common, open-habitat specialists (e.g. Reif & Hanzelka 2020, Warren *et al.* 2021). In response to these declines, attempts to maintain and restore favourable vegetation structures in remaining fragments of open semi-natural habitat, as well as in surrounding human-modified landscapes, are often a major focus of conservation efforts across western Europe (Verhoeven 2014, Török *et al.* 2021). Actions to achieve these goals typically include reducing nutrient inputs (e.g. Török *et al.* 2021), altering the timing and intensity of grazing, mowing and/or harvesting regimes (e.g. Verhulst *et al.* 2007, Ravetto Enri *et al.* 2017), reintroduction of traditional management practices (e.g. Fuller *et al.* 2017), and occasional use of prescribed burning (e.g. Valkó *et al.* 2014). All of these approaches aim to increase structural heterogeneity over a range of spatial and temporal scales (Benton *et al.* 2003, Fuller *et al.* 2017).

Manipulation of vegetation structure has the potential to positively influence the abundance (e.g. Sanz-Pérez *et al.* 2019), diversity (e.g. Hawkes *et al.* 2019) and demography (e.g. Bretagnolle *et al.* 2011) of focal taxa, but the likelihood and magnitude of positive outcomes can vary substantially between treatments, landscapes, spatial scales and taxa (Staggenborg & Anthes 2022, Roilo *et al.* 2023). To improve the consistency of management outcomes, a greater understanding of the conditions influencing occurrence and demographic success of focal taxa is required, particularly for widespread but declining populations, for which restorative conservation actions have so far failed to deliver meaningful results (Vickery *et al.* 2004, Pe'er *et al.* 2014, Burns *et al.* 2021).

A group of widespread but declining species in urgent need of effective conservation actions are waders *Charadriiformes spp*. (Sutherland *et al.* 2012), most of which are ground-nesting, open-habitat specialists. These species typically breed in areas comprising vegetation structures that can provide suitable nesting locations, cover from predators and foraging opportunities for adults and precocial chicks (Smart *et al.* 2006, 2008, Kentie *et al.* 2015, Laidlaw *et al.* 2015, 2020). In many parts of the world, these conditions now primarily occur in landscapes managed for agriculture (Franks *et al.* 2018, Silva-Monteiro *et al.* 2021). In western Europe, agricultural intensification has frequently led to changes in vegetation structure and grassland management, which can increase vulnerability of nests and chicks to predation (e.g. Kentie *et al.* 2015) and destruction through mechanised practices (e.g. Verhulst *et al.* 2007, Exo *et al.* 2017). Attempts to restore favourable conditions through vegetation management have had some positive effects on local abundance (e.g. Pearce-Higgins & Grant 2006, Smart *et al.* 2013, Douglas & Pearce-Higgins 2014, Buchanan *et al.* 2017) and nest survival (e.g. Sheldon *et al.* 2007, Bodey *et al.* 2010, Laidlaw *et al.* 2017) of wader populations, but the influence of such actions on chick survival rates is poorly understood (Franks *et al.* 2018).

Here, we explore the potential of vegetation management to boost fledging rates of the globally Near Threatened Eurasian curlew *Numenius arquata* (hereafter, curlew) (IUCN 2022); a widespread, large-bodied wader species that breeds across a range of open semi-natural habitats (Franks *et al.* 2017, Baines *et al.* 2022, Ewing *et al.* 2022) and that has declined across Europe as a result of low breeding productivity (Cook *et al.* 2021, Viana *et al.* 2023). We used weekly vegetation surveys and daily monitoring of curlew broods across Breckland, eastern England, to quantify (1) annual, seasonal and spatial variation in curlew chick survival, and (2) the effects of chick use of differing vegetation structures on survival through the pre-fledging period. We use these results to evaluate how management can be targeted to deliver vegetation structures that enhance chick survival rates in lowland-breeding curlew.

Methods

Study area

Breckland is a 1019 km^2 region of eastern England, dominated by intensively managed arable land and commercial forestry plantations, with remnant semi-natural grassland patches interspersed across the landscape. Breeding curlew are widespread across the region and currently nest at densities of 0.17 – 7.4 pairs per km^2, primarily in grassland habitats with smaller numbers nesting in arable fields and open, clear-felled areas within forests (Ewing *et al.* 2022). Permission to monitor breeding curlew was granted at nine sites across the region, including two arable-dominated estates, a farm, a paddock complex, two grass-heaths, a Royal Air Force base, a Ministry of Defence training area and the entire area managed by Forestry England.

Eight of the nine study sites comprised areas of (predominately calcareous) grassland, the large majority of which consisted of long-established, semi-natural, unimproved grass-heathland or dry grassland, managed extensively by light to medium sheep grazing or one-cut mowing, resulting in closed, tussocky and generally short swards (Table S1). One grass-heath site was dominated by short-turf as a result of heavy livestock grazing, while five sites contained a number of ground-disturbance plots (4 ha areas of semi-natural grassland, recently rotovated to create bare ground to encourage breeding stone curlew *Burhinus oedicnemus* (Hawkes *et al.* 2021)). One of the nine sites also comprised small patches of improved agricultural grassland, harvested for silage production twice per summer season. All other open habitat comprised cropland monoculture at various stages of growth, from bare ground to tall cereal crops.

Brood monitoring

Curlew pairs were located between late-March and mid-April 2019-2022 and classified as possible, probable or confirmed breeders, using breeding evidence codes (Table S2). The GPS location and outcome of nests was recorded between late-March and mid-June in the same years, all following Ewing *et al.* (2022). Curlew broods from hatched nests were visited every one to five days in 2019 and daily in 2020-2022, from day of hatching until all chicks in a brood died (all chicks found dead or neither chicks nor chick-guarding adults located for three consecutive days) or any surviving chicks fledged (became capable of flight). Broods were located by revisiting their last known location and, if necessary, expanding the search outwards (up to a radius of 1500 m), until they were relocated (usually by finding chick-guarding adults). Between 2020 and 2022, broods were observed for one hour per visit from a vehicle positioned at least 100 m away. Date, time of day (any time between dawn and dusk) and vegetation blocks (see below) used were recorded, and the number of chicks was counted whenever possible. In situations where chicks were not visible (generally due to being concealed in long grass), their presence could be confirmed by chick-guarding adults and soft contact calls made to parents. The number of dead and surviving chicks in a brood was confirmed when chicks were 7, 14, 21 and 28 days old by waiting until chicks were observed or by searching for chicks on foot. Individual broods were all identifiable due to a combination of 1) the low densities at which curlew breed in Breckland (Ewing *et al.* 2022), 2) variation in chick age and, 3) colour-marked, chick-guarding adults.

Vegetation surveys

Between 2020 and 2022, all vegetation accessible to broods in open habitats (grassland, heathland or arable), within a 500 m radius (78.5 ha; termed ‘brood landscape’) of a hatched curlew nest (500 m = the maximum distance moved by monitored broods in 2019), was surveyed once a week for four weeks or until all chicks in a brood died. If a brood moved outside of the original 78.5 ha, a second survey was conducted in the 78.5 ha surrounding the point at which the brood was first observed outside of the original brood landscape, on the day that the brood was relocated. Surveys of the original and secondary brood landscapes were continued for the rest of the survey period. Only five of the 50 broods monitored between 2020 and 2022 moved outside of the original brood landscape, and none moved further than 1000 m from the nest.

Brood landscapes surrounding each hatched curlew nest were divided into blocks of vegetation or habitat that were homogenous in structure (height and density) and type, with no separating features (fences, roads, tracks or field boundaries). Blocks were a minimum of 0.25 ha (mean = 5.72 ± 7.5 sd). The vegetation within each block was surveyed each week by measuring the height of the tallest sward (to nearest 1 cm) using a tape measure and estimating the percentage cover of short (< 20 cm) vegetation (to nearest 5%), within a 50x50 cm quadrat, located randomly within blocks (5-45 quadrats per block; more quadrats in larger blocks). Vegetation in brood landscapes throughout Breckland predominantly consisted of short swards, with the mean height of the majority of blocks in the first weekly vegetation surveys being < 40 cm (Fig. 1).

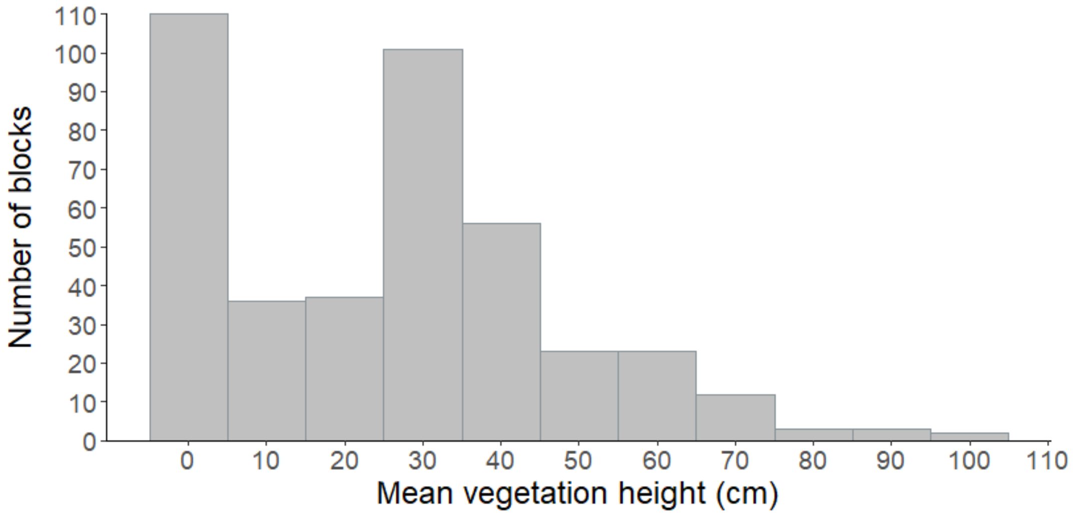


Figure 1: The distribution of mean heights of vegetation blocks measured in the first weekly surveys of each brood landscape.

Statistical analysis

Annual, seasonal and spatial variation in chick survival of all broods monitored between 2019 and 2022 were explored in a General Linear Model with a quasibinomial error term (to adjust for overdispersion > 1.5), in which the number of chicks fledged was modelled with number of chicks that died as the binomial numerator. Site, year and their interaction, and lay date, year and their interaction were included as fixed factors (Table 1, model i). A separate GLM with the same structure was used to assess variation in the survival of chicks monitored in 2020-2022 (the years in which vegetation data were collected) in relation to mean height of the tallest vegetation block present in a brood landscape during the first week after hatching (Table 1, model ii).

Age-specific survival to fledging of curlew chicks was also assessed in relation to the vegetation structure of the blocks used by broods during the preceding week in two GLMMs with binomial error terms. In these models, the weekly status of chicks (alive or dead) was modelled in relation to vegetation height in used blocks, week and their interaction as fixed factors in the first model (Table 1; model iii) and percent cover of vegetation < 20 cm in used blocks, week and their interaction in the second (Table 1; model iv). Vegetation height and percent cover of vegetation < 20 cm could not be included in the same models due to collinearity (r > 0.7). Both models included vegetation block nested within brood as a random factor, to account for the non-independence of chicks within the same brood and of vegetation measurements taken within the same block.

We also assessed variation in weekly habitat use of broods (vegetation block used or not used) in two GLMMs with a binomial error term, with vegetation height, week and their interaction included as fixed factors in the first model (Table 1, model v) and percent cover of vegetation < 20 cm, week and their interaction included as fixed factors in the second (Table 1, model vi). Vegetation block was include as a random factor to account for non-independence of vegetation measurements taken within the same block.

In models iii – vi (Table 1), vegetation height was scaled and centered to have a mean of zero and a standard deviation of 1. Non-significant ($P > 0.05$) interaction terms were sequentially removed from models, and inference was made from the maximum model retaining all main effects. All models were run in R (v 4.2.1, R Core Team (2023)) using the lme4 package (Bates *et al.* 2015).

Table 1: Description of the model variables used to explain variation in survival and habitat use of curlew chicks monitored between 2019 and 2022 in Breckland, eastern England.

Type	**Variable**	**Distribution (link)/variable range of values**	**Explanation**
Response	No. chicks fledged and no. chicks dead	Quasibinomial (logit)	Number of chicks fledged and number of chicks dead per brood
	Alive and dead	Binomial (logit)	Weekly status of each chick in a brood; alive (1) or dead (0)
	Used or not used		Habitat block used (1) or not used (0) by a brood during that week
Explanatory	Site	Nine sites	Site in which each brood occurred
	Year	2019, 2020, 2021, 2022	Years in which brood were monitored
	Hatch Date	Day 121 – 176	Brood hatch date in days from Jan 1st
	Height	0 – 125 cm	Height of tallest sward in each quadrat
	Cover < 20 cm	0 – 100%	Percent cover of vegetation < 20 cm in each quadrat
	Height of tallest block	17 – 104 cm	Mean height of vegetation in tallest block in a brood landscape
	Week	1 – 4	Week after hatching
	Block	Block 1 – 20	Habitat block identity
	Brood	50 broods (2020 – 2022)	Brood identity

Model	**Response**	**Model structure**
i	Chicks fledged and chicks died	Site*Year + Year*Hatch Date
ii	Chicks fledged and chicks died	Height of tallest block
iii	Alive and dead	Height*Week + (1|Brood/Block)
iv	Alive and dead	Cover*Week + (1|Brood/Block)
v	Used and not used	Height*Week + (1| Block)
vi	Used and not used	Cover*Week + (1| Block)

Results

Between 2019 and 2022, a total of 68 broods (235 chicks) hatched successfully in our Breckland study area, but only 40 chicks fledged (Fig. 2). Breeding productivity was highest in 2021, reaching 0.37 fledged chicks per pair, and lowest in 2022 when only three chicks fledged, equating to 0.04 per pair (Fig. 2). The mean probability of at least one chick from a brood fledging successfully was 26.5% (± 5.4 se). Over half of the hatched curlew chicks died before reaching one week old, and > 72% died before reaching two weeks old (Fig. 3). Eight chicks died between three and four weeks old (Fig. 3). All chicks that reached four weeks old fledged, with 2.22 (± 0.22 se) chicks fledging per successful brood.

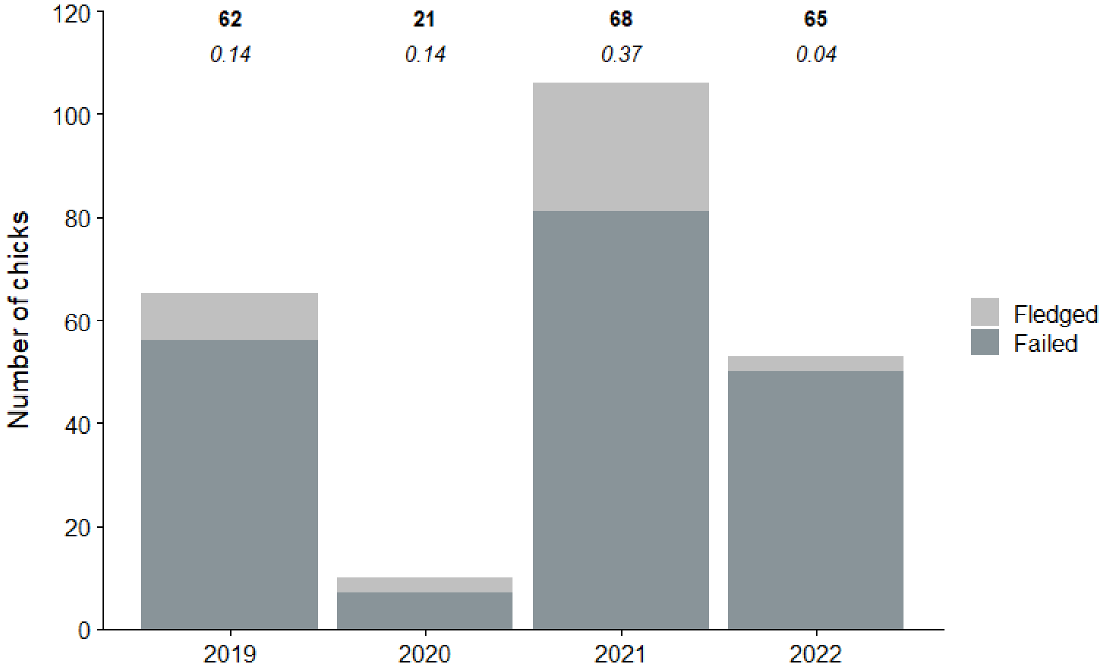


Figure 2: Number of fledged and dead curlew chicks (bars), with the total number of probable and confirmed curlew pairs monitored (above bars in bold) and the annual fledging rates (fledged chicks per pair; above bars in italics) between 2019 and 2022 in Breckland, eastern England.

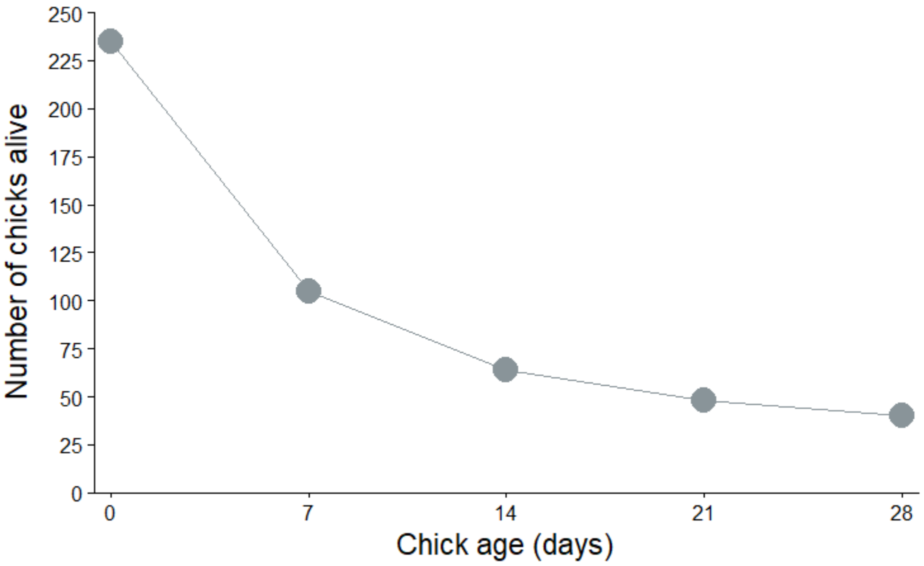


Figure 3: Number of monitored curlew chicks alive at 7, 14, 21 and 28 days old between 2019 and 2022 in Breckland, eastern England. All chicks that reached 28 days old fledged successfully.

No predation events were observed during brood surveys, although two chicks were found having been killed or scavenged by corvids Corvidae spp. (most likely carrion crow *Corvus corone*) and all but one chick from three broods were found killed by mustelids *Mustelidae spp.* (most likely stoat *Mustela erminea*) within two days of hatching. All broods that hatched in grassland remained in grassland, whereas nine of the 11 broods that hatched in arable fields moved to a nearby patch of grassland (always within 500 m of the nest; minimum grassland patch area = 1.1 ha) within one week of hatching. The two broods that remained in arable fields died, one brood within two days of hatching and the other before the chicks reached two weeks old.

The probability of fledging successfully did not differ significantly between sites or years, or with hatch date (Table 2). However, for chicks monitored between 2020 and 2022 (50 broods), the probability of fledging increased as the height of the tallest block in a brood landscape increased (Table 2; Fig. 4).

Table 2: Results of GLMs exploring curlew chick survival in Breckland, eastern England, in relation to (i) spatial and temporal variables and (ii) the mean height of the tallest block in brood landscapes (see Table 1 for description of all model variables and structures). Significant predictors ($p < 0.05$) are highlighted in bold.

Model	**Fixed effect**	**Chi sq.**	**Df**		***p***
i Chick survival	Site	9.135	8		0.331
	Year	6.375	3		0.095
	Hatch Date	0.224	1		0.636
		Estimate	**se**	**t**	***p***
ii	Height of tallest block	0.038	0.014	2.688	**0.01**

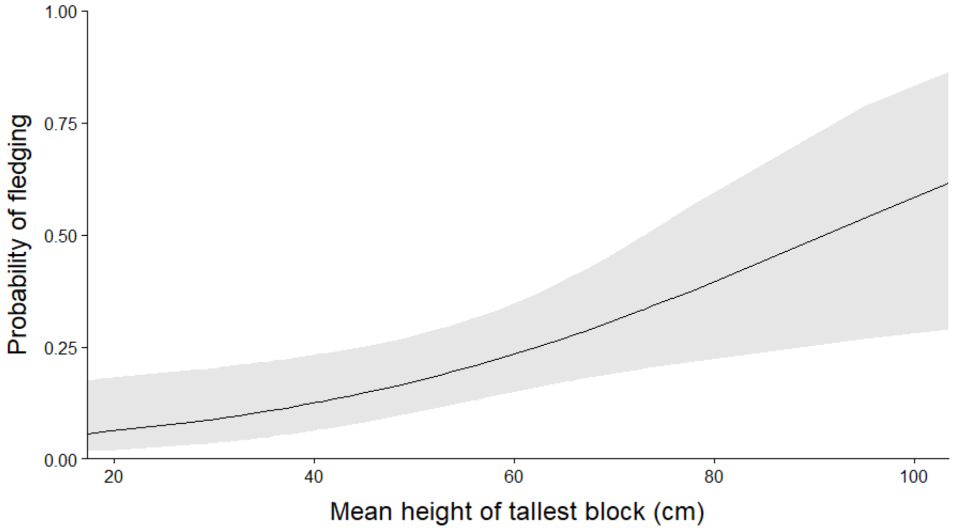


Figure 4: Mean (95% CI) predicted probability of curlew chicks fledging in relation to the mean height of the tallest vegetation block present in a brood landscape during the first week after hatching, in Breckland, eastern England between 2020 and 2022.

Broods monitored between 2020 and 2022 had access to a mean of 8.7 (± 0.5 se) vegetation blocks and 31/50 of brood landscapes had at least one block of tall vegetation (> 40 cm) during the first week after hatching (Fig. S1). Seasonal vegetation growth contributed little to the variation in vegetation structure between brood landscapes and the mean coefficient of variation of mean vegetation block height across brood landscapes was 0.83 (± 0.06 se) and 1.23 (± 0.1 se) for percent cover of vegetation < 20 cm.

Chick survival in relation to both height and percent cover of short (< 20 cm) vegetation in blocks used in the preceding week varied with chick age (Table 3; Fig. 5). Chicks using blocks with shorter vegetation heights (Fig. 5a) and a greater cover of short vegetation (Fig. 5b) were slightly more likely to survive their first week of life but, in week two, survival increased strongly for chicks using blocks of taller vegetation (Fig. 5a) and slightly for chicks using blocks with a lower cover of short vegetation (< 20 cm) (Fig. 5b). In weeks 3 and 4 relatively few chicks died and the beneficial effect of taller vegetation was no longer apparent (Table 3; Fig 5). Blocks with taller vegetation were more likely to be used by broods in all but the first week of life (Table 3; Fig. 6a), while blocks with greater cover of short vegetation were more likely to be used during the first and third week of life (Table 3; Fig. 6b).

Table 3: Results of GLMs exploring variation in curlew chick survival (iii – iv) and habitat use (v – vi) in Breckland eastern England, in relation to vegetation structure and chick age (see Table 2 for description of all model variables and structures). Significant predictors (p < 0.05) are highlighted in bold.

Model	**Fixed effect**	**Chi sq.**	**Df**	***p***
iii Chick survival	Height	0.067	1	0.796
	Week	136.982	3	**< 0.001**
	Height*Week	400.291	3	**< 0.001**
iv	Cover	3.122	1	0.073
	Week	163.001	3	**< 0.001**
	Cover*Week	101.649	3	**< 0.001**
vii Habitat use	Height	1.479	1	0.224
	Week	145.665	3	**< 0.001**
	Height*Week	50.482	3	**< 0.001**
viii	Cover	3.498	1	0.061
	Week	149.481	3	**< 0.001**
	Cover*Week	32.803	3	**< 0.001**

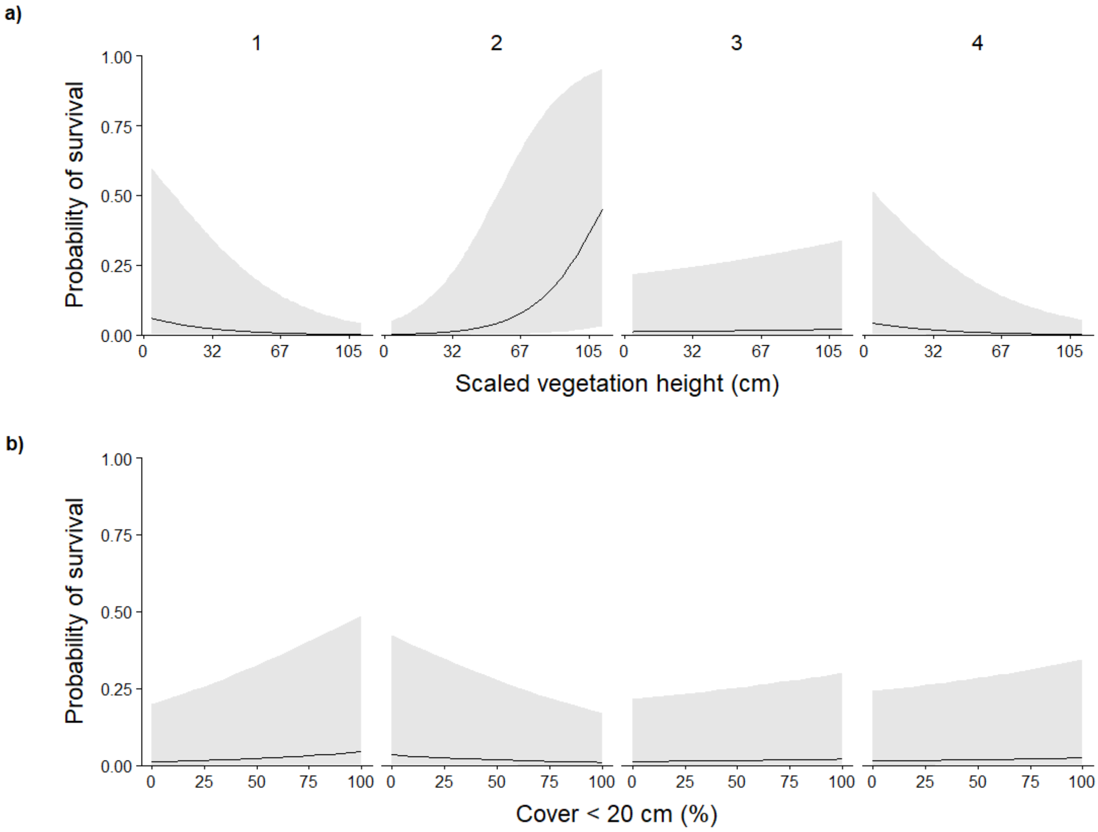


Figure 5: Mean (95% CI) predicted probability of survival for curlew chicks during each of the first four weeks after hatching in relation to (a) vegetation height and (b) percent cover of short (< 20 cm height) vegetation of the vegetation blocks in which they were recorded during each preceding week, in Breckland, eastern England between 2020 and 2022.

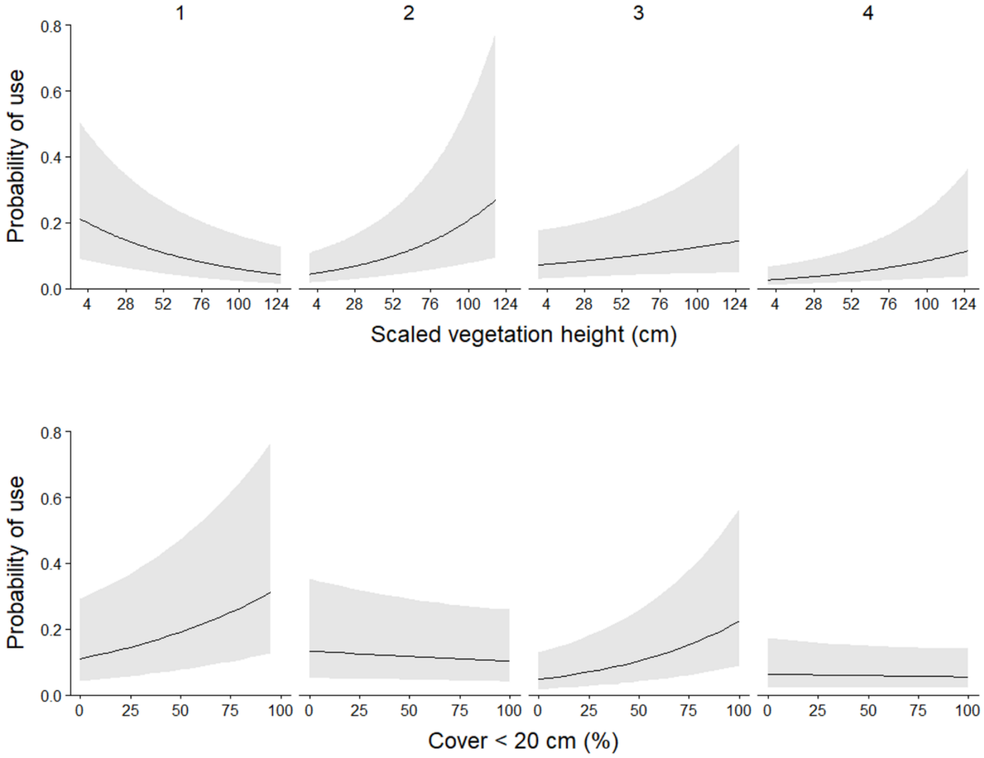


Figure 6: Mean (95% CI) predicted probability of block use in relation to (a) vegetation height and (b) percent cover < 20 cm of curlew broods monitored in Breckland, eastern England 2020-2022.

Discussion

Identifying sources of environmental variation that are associated with variation in demographic rates of threatened species can aid with the design of conservation actions for those species, particularly when the relevant environmental variation can be achieved with conservation management. In Breckland, the vegetation structure used by curlew chicks and the associated survival probabilities varied with age, with chicks less than one week old using short vegetation more and surviving more with greater use of short vegetation, while older chicks used tall vegetation more and survived more with greater use of tall vegetation. Targeted actions to benefit breeding curlew should therefore aim to create heterogeneous vegetation structures (mix of short and tall vegetation) at scales of tens of hectares in areas where conditions currently fail to support sustainable rates of fledging, and to maintain these conditions in areas where they currently exist.

Vegetation heterogeneity is frequently reported to influence the occurrence and demographic success of open-habitat specialists, particularly birds (e.g. Benton *et al.* 2003, Pickett & Siriwardena 2011, Bonari *et al.* 2017, Brüggeshemke *et al.* 2022). For wader chicks, vegetation structure may influence thermoregulation (Carroll *et al.* 2015), foraging efficiency (Pearce-Higgins & Yalden 2004) and ability to hide from predators (Machín *et al.* 2017). For example, reduced shade and moisture in areas of short vegetation is likely to allow younger curlew chicks to stay warm and dry (Carroll *et al.* 2015), while foraging may also be more efficient in these areas while chick body size remains small (e.g. Devereux *et al.* 2004). For older chicks, such thermoregulatory costs may be lower or less important, and may be outweighed by the benefits of cover from predators and/or increased availability of larger bodied invertebrate prey in taller vegetation (Cole *et al.* 2010, Silva-Monteiro *et al.* 2022), which older chicks may be more capable of exploiting and more reliant on, owing to their larger body size (e.g. Schekkerman & Beintema 2007)

In Breckland, a landscape primarily dominated by short vegetation, tall (> 40 cm) vegetation mainly comprised patches of nettle *Urtica dioica* or bracken *Pteridium aquilinum*, or arable crops such as cereals and legumes. As these vegetation types are generally of low conservation value and can have negative effects on biodiversity (e.g. Donald *et al.* 2006, Marrs *et al.* 2007), their contribution to maintaining heterogeneous vegetation structures, and their positive effects on species like curlew, needs to be balanced with other conservation goals such as preventing succession in biodiverse semi-natural habitats (Marrs *et al.* 2007). For nettle and bracken, which are commonly removed as part of conservation management in this landscape, balance could potentially be achieved through identifying spatial and temporal scales of management that would maintain some patches in areas with breeding curlew during the chick-rearing stages. For crops, current rotational farming systems mean that mosaics of bare ground interspersed with short and tall vegetation are typical in these landscapes, which may be particularly important when arable-nesting curlew move chicks into adjacent areas of grassland.

Semi-improved grassland and silage patches also provided areas of tall vegetation used by a small proportion of monitored curlew broods. This habitat is relatively scarce in Breckland, but in other parts of the breeding range curlew commonly use areas of intensive pastoral farming in which grasslands are largely managed with high levels of fertilizer input and used for silage production (Colwell *et al.* 2020). Survival rates of wader chicks in these homogenous and often dense vegetation conditions are typically low, often as a consequence of high levels of starvation or predation (Kentie *et al.* 2013). Provision of suitably heterogenous vegetation structures in these areas for breeding curlew could potentially be achieved through creation of patches of bare ground or short swards within silage fields or, likely more effectively, through conversion from silage to hay production, as flower-rich hay meadows can provide both the open swards for foraging and tall swards for protection from predators (Kentie *et al.* 2015, Loonstra *et al.* 2019), and may also benefit a suite of other threatened grassland species (Wright *et al.* 2012).

Strong effects of vegetation structure on the demography of breeding waders (particularly chick survival) are rarely demonstrated in the literature (Franks *et al.* 2018), likely due to the challenges of monitoring wader chicks and the limited range of vegetation conditions available in many breeding areas. The variation in land management and relatively unique environmental conditions supported in Breckland mean that this region retains a diverse mosaic of habitats and vegetation structures (Dolman *et al.* 2010). Daily observations of broods were sufficient to detect variation in the use and survival of curlew chicks across this diverse landscape because most broods stayed within the nesting areas, and curlew remain sufficiently numerous but breed at sufficiently low densities (Ewing *et al.* 2022) to allow broods to be tracked throughout the pre-fledging period. More studies are required of wader chick use of the vegetation structure available to them and of the costs and benefits associated with differing vegetation heights for chick of differing ages, to further refine grassland management for these increasingly rare species.

Our study demonstrates the potential for management of vegetation structure to enhance survival rates of curlew chicks, however, in each of the four study years too few chicks fledged to reach the rate required to maintain a sustainable population of breeding curlew (0.68 chicks per pair per year; Viana *et al.* 2023). Survival of curlew nests is low in Breckland (Ewing *et al.* 2022) and actions to boost fledging success are only likely to have positive effects on overall breeding productivity in areas where nest survival is high. Deployment of vegetation management in combination with tools to boost hatching success of nests, such as predator-exclusion fencing, could be beneficial, but field trials will be needed to quantify the benefits of such management, ideally across different landscapes. In addition, further research to understand the mechanisms through which vegetation structure can influence predation risk for wader chicks will help to identify the types and scales of vegetation management that might be most beneficial for breeding waders.

Supplementary material to Chapter 3: Survival of Eurasian curlew chicks varies with vegetation structure in a diverse lowland landscape

Table S1: The dominant habitat types (grassland, arable or forest), grassland habitat types and management practices, and presence of cultivated arable land (adjacent to or within sites) and ground-disturbance plots at nine study sites in which curlew chicks were monitored between 2019 and 2022.

Site	Dominant habitat	Grassland habitat	Grassland management	Arable present	Disturbance plot present
1	Grassland	Unimproved grass-heathland	Medium intensity sheep grazing	Yes	Yes
2	Grassland	Unimproved dry grassland	One-cut mow	Yes	No
3	Grassland	Unimproved grass-heathland with small patches of semi-improved grazing pasture and silage	Low-intensity sheep grazing	Yes	Yes
4	Arable	Rough grazing pasture	Medium intensity sheep grazing	Yes	Yes
5	Grassland	Unimproved grass-heathland	High intensity sheep and cattle grazing	No	Yes
6	Arable	Unimproved fallow grassland	None	Yes	Yes
7	Grassland	Semi-improved grazing pasture	Medium intensity sheep grazing	Yes	No
7	Forest	Clear-fell and tree nursery	None	No	No
8	Arable	None	None	Yes	No

Table S2: Breeding evidence categories used to classify curlews detected on surveys as non-breeding, or possible, probably or confirmed breeding.

Non-breeding
• Single, pair or number of birds flying over suspected to be still on migration • Observed but suspected to be summering non-breeder(s)
Possible breeding
• Pair observed in suitable nesting habitat in breeding season on just one occasion • Male present (or bubbling calls heard) in breeding season in suitable breeding habitat
Probable breeding
• Pair observed in suitable nesting habitat in same location on more than one occasion • Permanent territory presumed through territorial behaviour on at least two different occasions • Courtship and display judged to be in or near potential breeding habitat • Pair visiting probable nest site • Agitated behaviour or anxiety calls from adults, suggesting probable presence of nest or young nearby, observed on just one occasion. • Pair nest scraping
Confirmed breeding
• Used nest or eggshells found • Downy young seen • Adults entering or leaving nest-site in circumstances indicating occupied nest or adults seen incubating – sitting is often followed by lowering of the head (disappearing in tall vegetation) followed by periodic raising and looking around • Nest containing eggs • Nest with young seen or heard • Incubation change-over seen - when approaching the nest curlews appear to ‘move with purpose’ without actively feeding, although not necessarily faster or slower than normal • Agitated behaviour or anxiety calls from adults, indicating presence of nest or young nearby, observed on three or more occasions

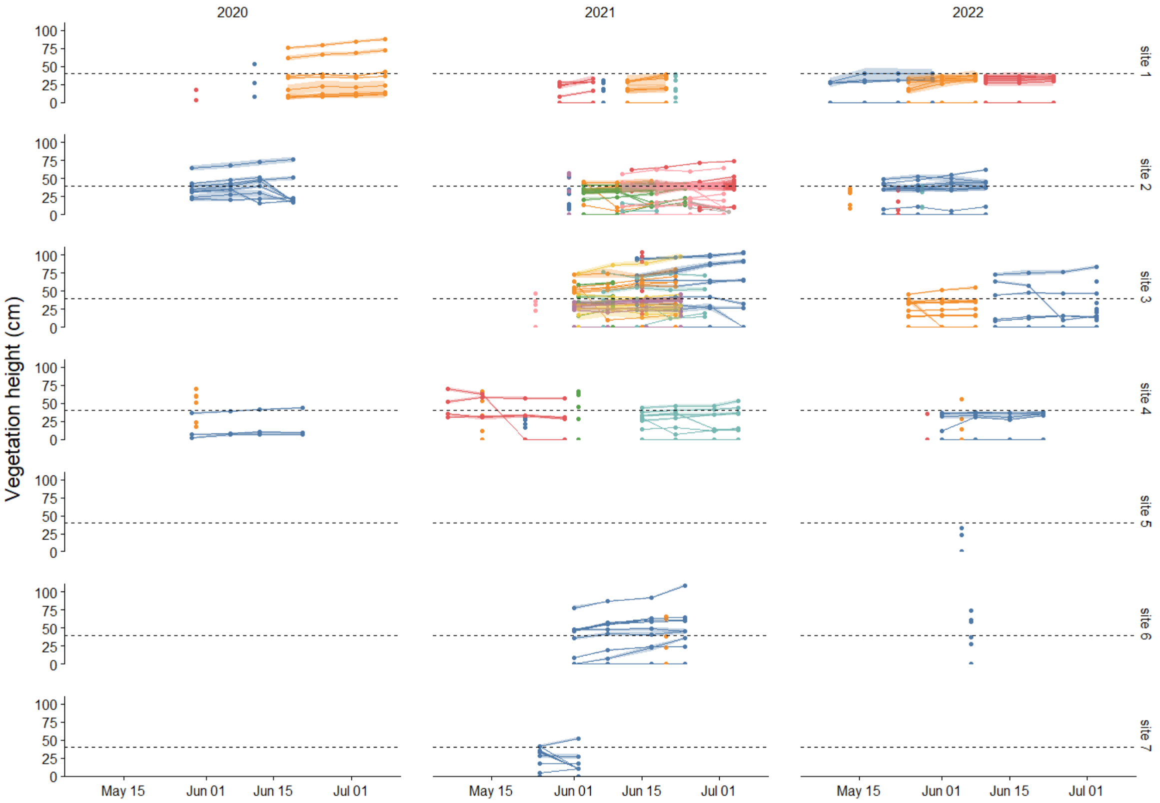


Fig. S1: Mean (± se) height of vegetation blocks (coloured points and lines) in each week for which chicks survived through the chick-rearing period (mid-May to early-July), during the three study years (2020-2022) in which weekly vegetation surveys were conducted across 50 brood landscapes (shown in different colours for clarity), at seven sites in Breckland, eastern England.

.

Chapter 4

Integrating information on occurrence and demography to inform targeting of conservation actions

Abstract

Slowing declines of widespread species requires strategies to target conservation actions effectively. Conservation actions often aim to (1) preserve the conditions in which focal species remain common, (2) create more favourable conditions to attract them, and/or (3) improve conditions to boost occurrence and/or demographic success. However, the situations in which these actions are most appropriate can differ. Here, we develop a conceptual framework to explore how variation in occurrence and demographic success of focal species in different environmental settings can be used to identify appropriate conservation actions. We illustrate this approach with empirical data on breeding Eurasian curlew, Numenius arquata, in relation to landscape composition and configuration in eastern England. Across landscapes comprising grassland, arable and woodland habitats between 2019 and 2022, curlew nests occurred disproportionately in areas with greater grassland cover, lower woodland and arable cover and larger patches of open habitat in the surrounding (500 m radius) landscape. However, these nests rarely hatched or fledged chicks. In contrast, although fewer than 16% of nests occurred in arable-dominated areas, over 31% hatched and 24% fledged. Curlew activity on arable fields was concentrated close to grassland patches. Applying these findings to the conceptual framework suggests a need to (a) preserve habitats and improve curlew productivity on open grasslands and (b) create grassland patches within arable-dominated areas. Considering both occurrence and demography in differing environmental conditions can thus help to identify when actions to preserve, create and/or improve conditions to conserve threatened populations are likely to be most appropriate.

Introduction

The development of the post-2020 strategic plan for the Convention on Biological Diversity potentially represents the last opportunity for governments to set out targets and negotiate actions to slow and reverse biodiversity loss (Hughes *et al.*, 2022). Positive steps have already been taken with over 100 countries formally supporting a drive to protect 30% of land and sea area by 2030 (Carroll and Noss, 2022). While further expansion of protected areas is a positive step towards preserving the > 78% of known threatened species currently persisting without adequate protection (Maxwell *et al.*, 2020), increasing the extent of protected areas alone is unlikely to result in significant biodiversity gains (Bailey *et al.*, 2022; Santangeli *et al.*, 2023). To effectively deliver for nature and ecosystem services, targeted conservation actions to preserve, improve and create favourable management and environmental conditions are required, both within and outwith protected areas (Strassburg *et al.*, 2020).

Traditionally, targeting of conservation actions has been informed by assessing how the occurrence and distribution of individuals varies in relation to a range of environmental conditions (Araújo *et al.*, 2019; Guisan *et al.*, 2013). Conservation actions might then be designed and targeted to preserve and/or create the environmental conditions considered most likely to support high levels of abundance (e.g. Herse *et al.* 2018), species richness (e.g. Ramírez-Albores *et al.* 2021) or diversity (e.g. Lessmann *et al.* 2014). This approach has been particularly crucial for defining protected area boundaries (Pimm *et al.*, 2018) and for restoring important habitats or ecosystems supporting species of conservation concern (Strassburg *et al.*, 2020).

Conservation actions can also be targeted by assessing the demographic rates (survival and/or productivity) achieved by a focal species in different environmental conditions, and designing and deploying specific management actions to boost demographic successes in areas where they are consistently low (Morrison *et al.*, 2022). This method has been used successfully to recover several rare and localised populations including the Mauritius kestrel Falco punctatus (Jones *et al.*, 1995), Iberian lynx Lynx pardinus (Simón *et al.*, 2012) and UK populations of little tern Sternula albifrons (Wilson *et al.*, 2020) and cirl bunting Emberiza cirlus (Davies *et al.*, 2011). However, while such conservation successes make valuable contributions towards the recovery of biodiversity, their impact is increasingly overshadowed by the continued, wide-scale population declines of formerly common and widespread species (Burns *et al.*, 2021; Sánchez-Bayo and Wyckhuys, 2019), for which successful conservation actions have so far been limited (e.g. Pe'er *et al.* 2014, MacDonald *et al.* 2019).

Strategies are urgently required to inform how conservation actions should be targeted to conserve widespread but declining species (Morrison *et al.*, 2021). Such species are often distributed across a range of environmental and management conditions, and retain high levels of variation in local abundance and demographic success (e.g. Silva-Monteiro *et al.* 2021). Using occurrence and demographic data to identify where preservation and improvement of existing conditions, and creation of additional favourable conditions, is required may therefore allow for more appropriate and adequate deployment of conservation actions. For example, in conditions in which a focal species occurs frequently but in which demographic rates are consistently low, preservation of those conditions alone may be insufficient to prevent population declines (e.g. Sergio *et al.* 2021), and improved management promoting greater demographic success will likely be needed (Fig. 1a). Integrating demographic information when deciding which conservation actions to deploy under these conditions potentially helps avoid preservation or creation of sink populations and/or ecological traps, where conditions supporting frequent occurrence are preserved but demographic successes remain infrequent (Furrer and Pasinelli, 2016; Hale and Swearer, 2016).

By contrast, in conditions in which a focal species occurs frequently and also consistently achieves demographic success (e.g. Palmero *et al.* 2021), preservation of those conditions (e.g. through consistent management and/or protected status) may be the most appropriate strategy (Fig. 1b), while conditions in which a species occurs infrequently and rarely achieves demographic success could potentially be improved (Fig. 1c) but are unlikely to be a high priority for conservation action (e.g. Sales *et al.* 2022). Finally, conditions in which a species occurs infrequently but achieves frequent demographic success (e.g. Kamp *et al.* 2015) should likely be both preserved and created to encourage increased occupancy (Fig. 1d). These relatively productive but rarely occupied conditions are quite likely to be neglected if variation in demographic success is not considered when identifying the environmental conditions in which conservation actions should be targeted.

Targeting specific actions to achieve specific goals of preservation, improvement or creation of favourable environmental conditions is likely to aid the effective and efficient use of scarce conservation resources. For example, preserving the management and environmental conditions that already support a relatively high frequency of occurrence and demographic success (Fig. 1b) is likely to be more efficient than designing and deploying actions in conditions in which the species is scarce and demographic success is low (Fig. 1c). However, the effectiveness and efficiency of actions to preserve and create (Fig. 1d) versus actions to preserve occurrence and increase the frequency of demographic successes (Fig.

1a) may be more comparable, depending on the specific circumstances in which the species occurs.

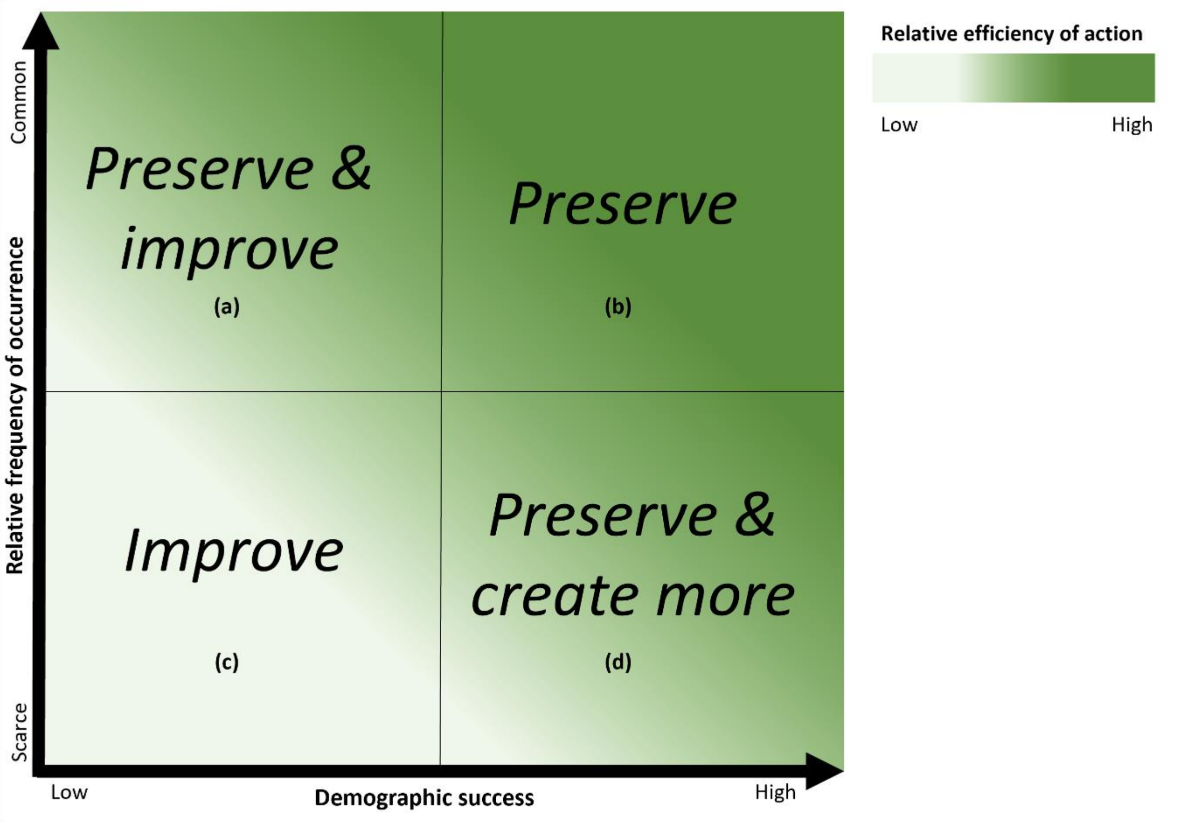


Figure 1: Framework for targeting of appropriate and efficient conservation actions in differing environmental conditions for species of conservation concern, depending on their relative frequency of occurrence and the demographic success typically achieved in those conditions.

Here, we illustrate the application of this conceptual framework using a population of Eurasian curlew Numenius arquata (hereafter, curlew); a widespread wading bird species that breeds across a range of habitats and landscapes but that is rapidly declining because of unsustainably high rates of nest and chick predation (Cook *et al.*, 2021; Franks *et al.*, 2017). We use intensive monitoring of breeding attempts, standardised surveys and remote sensing data to quantify the frequency of curlew occurrence and breeding success (quantified as nests that hatch and nests that fledge chicks) in relation to metrics of landscape composition and configuration likely to influence curlew occurrence and vulnerability to nest and chick predation. We explore how these findings can inform the spatial targeting and prioritisation of conservations actions to preserve, improve and create favourable management and environmental conditions.

Methods

Study area

The study took place in Breckland, a 1019 km2 region of eastern England. Over the last 200 years, wide-scale land-use change has transformed Breckland from a largely semi-natural landscape comprising areas of fallow land and low intensity farmland (Dolman *et al.*, 2010), to a mosaic of varying sized patches comprising intensively managed arable, coniferous plantation and remnant grassland habitat (Fig. 2a), typically managed extensively through one-cut mowing or livestock grazing. Our study area covered 255 km2 of Breckland including woodland and comparable areas of arable and grassland habitat (Table S1; Fig. 2b).

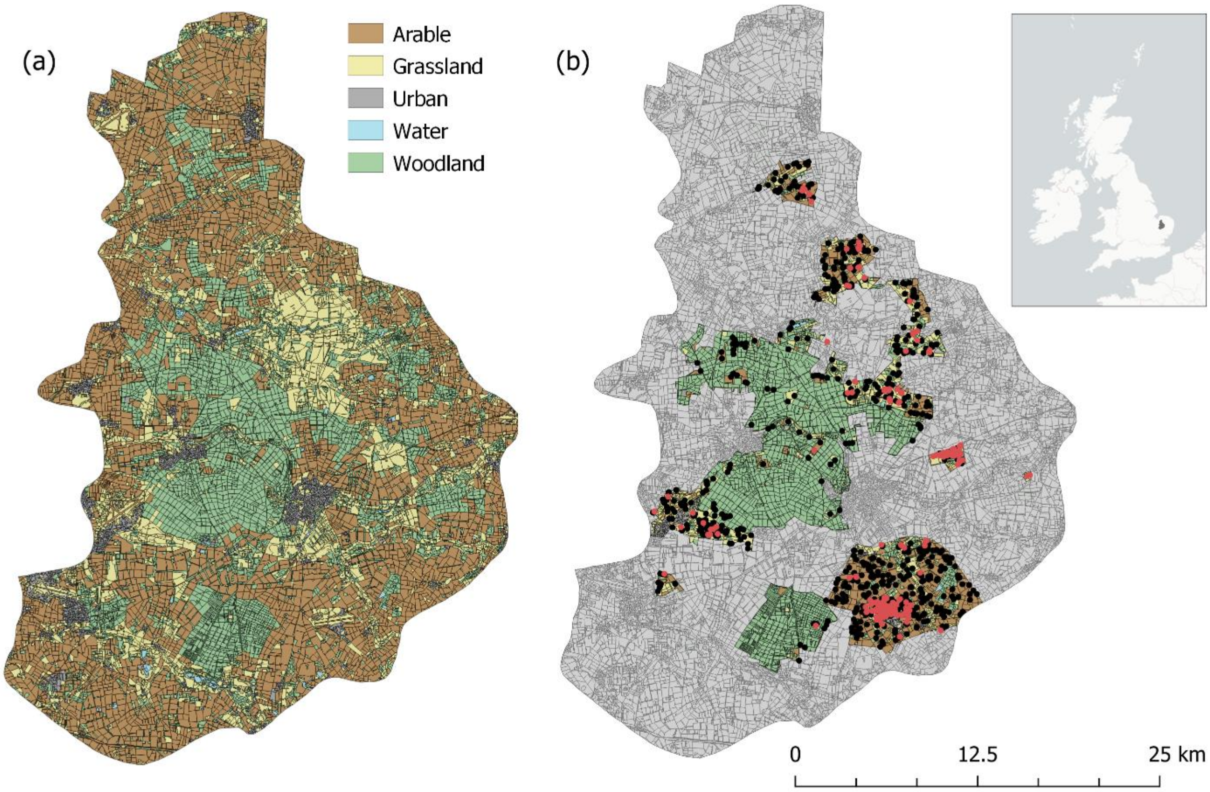


Figure 2: Distribution of (a) arable, grassland, urban, freshwater and woodland habitat (as defined by Centre of Ecology and Hydrology Land Cover 2020 vector data (Morton *et al.* 2021)) across Breckland and (b) used curlew nests (red) and available (black, random points) sites within study areas (colour shades). Inset indicates the location of Breckland within the UK.

Assessing occurrence of breeding curlew

Between 2019 and 2022, curlew pairs were located by conducting three surveys each year between late-March and late-April whereby all open areas within the study area were approached to at least 100 m on foot or by vehicle. All areas in which a curlew pair was observed during the initial surveys were revisited twice per week through the nesting period to confirm the occurrence of breeding attempts by locating active nests. The location of nests were recorded with a GPS device.

Monitoring of curlew breeding attempts

The outcome of nests was determined using iButton temperature loggers and field-based observations, following Ewing *et al.* (2022). Nests were recorded as successful if at least one egg hatched. Curlew broods from hatched nests were monitored following (Chapter 3) by visiting each brood every one to five days in 2019, and daily in 2020-2022, until all chicks in a brood died (dead chicks found or neither chicks nor chick-guarding adults located for three consecutive days) or any surviving chicks fledged.

Landscape composition and configuration

Centre for Ecology and Hydrology Land Cover (CEH LC) 2020 vector data (Morton *et al.*, 2021) were used to define and categorise land parcels into habitat categories and were merged into five groupings (arable, grassland, urban, freshwater and woodland; Table S1; Fig. 2). The simplified habitat classification was ground-truthed by checking 650 of the 6263 land parcels covering the study area during the 2022 field season, which resulted in seven being changed from arable to grassland. Twenty-four parcels covering the full extent of a small grassland site within the study area were changed post-hoc due to all parcels being incorrectly classified as woodland.

In Breckland, pre-fledged curlew chicks generally remain within 500 m of nest sites and have not been recorded moving further than 1000 m (Chapter 3). Metrics of landscape composition and configuration were therefore calculated at spatial resolutions of 500 m and 1000 m around 600 points (Northrup *et al.*, 2013) randomly distributed across open (grassland and arable) areas of the Breckland study area (termed ‘available sites’), 204 known nest locations (‘used nests’; nests observed with at least one egg, found before hatch or failure) and the subsets of monitored used nests that failed (107 ‘failed nests’), hatched (64 ’hatched nests’) and from which broods failed (48 ‘failed broods’) or fledged (16 ‘fledged broods’). Nests that failed for reasons other than predation (e.g. abandonment, mown, trampled; n = 9) and fenced nests (n = 17; defined in Ewing *et al.* 2022) were not included in the failed or hatched subset of nests as landscape structure was unlikely to have influenced their fate. Nests with unknown outcomes (n = 7) were also not included.

Curlew traditionally nest in open landscapes, primarily in grasslands (Franks *et al.*, 2017; Valkama *et al.*, 1998) but also in arable crops (Ewing *et al.* 2022), and are known to avoid areas of woodland (Douglas *et al.*, 2014; Franks *et al.*, 2017; Kaasiku *et al.*, 2022).

Consequently, three measures of landscape composition (percent cover of grassland, arable and woodland) were extracted. The size of the largest open (grassland or arable) habitat patch within the two spatial resolutions was also extracted as a measure of landscape configuration, as breeding waders are known to occur disproportionately in more open landscapes (Gunnarsson *et al.*, 2006; Jóhannesdóttir *et al.*, 2018; Pálsdóttir *et al.*, 2022).

Arable surveys

To explore how the presence of grassland (the habitat primarily used by breeding curlew) influenced the occurrence and distribution of curlew across arable fields during the breeding season, 118 arable fields, grouped in three distance bands around six grassland-dominated sites, were surveyed for curlew during the 2021 breeding season. Early- (mid-March to mid-April), mid- (mid-April to mid-June) and late-season (mid-June to mid-July) surveys were conducted (by EH) to account for potential changes in curlew behaviour and detectability through the season. Fields were either adjacent (within 500 m; n = 40), near (500-2000 m; n = 41) or far (> 2 km; n = 37) from a grassland site (minimum area of 2 km2), measured from the closest edge of the site to the closest edge of the field (Fig. S1).

Ten-minute point count surveys were conducted during each field survey, one survey at each field during the three stages of the season. Points counts were conducted between 09:00 and 12:00, on the edge of fields, in a location of maximum visibility over the field. Point count locations were kept consistent across the season but the order in which fields were visited was randomised between repeat visits. The number of individual curlews seen and heard during surveys was recorded.

Statistical analyses

To describe the landscape structure of areas in which curlew breeding attempts and curlew breeding successes occurred across the Breckland study area, variation in the proportions of used nests, those nests that hatched and those that produced fledged broods (Table 1) was explored in relation to metrics of landscape composition and configuration within binomial Generalised Linear Models (GLMs). Models i-iv included percent cover of grassland and models v-viii percent cover of arable (modelled separately due to collinearity; r > 0.7 in all cases), together with the fixed effects of percent cover of woodland and size of largest open habitat patch (Table 1). Models i-viii were run using landscape metrics calculated at the two spatial resolutions. Results for 500 m resolution are presented in the main text. Results for 1000 m resolution were similar to those at 500 m, and are included in the SOM (Table S2; Fig. S2).

To describe how the distribution of curlew use of arable fields in the breeding season varied in relation to distance from grassland patches, 118 arable fields (Fig. S1) were categorised as either having curlew present in any of the three surveys (n = 11; only two fields were occupied in more than one of the surveys) or absent (n = 107; never recorded in any survey) and modelled in a binomial GLMM, with distance from grassland included as a fixed factor and grass site as a random factor (to account for the non-independence of fields surrounding the same grass site; Table 1; model ix).

Inference was made from maximum models, including all considered effects. All models were run in R (v 4.2.1) using the lme4 package (Bates *et al.* 2015).

Table 1: Description of the model variables used to explain variation in the proportion of used curlew nests, hatched nests and fledged broods, in relation to landscape structure at 500 m and 1000 m resolutions (models i-viii) and, how the presence or absence of curlew in arable fields varied in relation to distance from grassland (model ix).

Type	**Variable**	**Distribution (link)/variable range of values**	**Explanation**
Response	Available sites and used nests	Binomial (logit)	600 available sites (0) and 204 used nests (1)
	Failed nests and hatched nests		107 failed nests (0) and 64 hatched nests (1)
	Failed broods and fledged broods		48 failed broods (0) and 16 fledged broods (1)
	Failed nests and fledged broods		107 failed nests (0) and 16 fledged broods (1)
	Curlew presence		Curlew absence (0) and presence (1)
Explanatory	Largest patch	1.7 – 57 ha	Size of largest open grassland or arable habitat patch with each spatial resolution
	Woodland	0 – 88%	Percent cover of woodland habitat
	Grassland	0 –100%	Percent cover of grassland habitat
	Arable	0 – 100%	Percent cover of arable habitat
	Distance from grassland	Three distance categories	Adjacent (< 500 m), near (500-2000 m) and far (> 2km)
Random	Grass site	Six grass sites	Identity of grassland site

Model	**Response**	**Model structure**
i & v	Available sites and used nests	*i-iv* Largest patch + Woodland + Grassland
ii & vi	Failed and hatched nests	
iii & vii	Failed and fledged broods	*v-viii* Largest patch + Woodland + Arable
iv & viii	Failed nests and fledged broods	
ix	Curlew presence	Distance from grassland + (1|Grass site)

Results

Over 200 curlew breeding attempts were monitored across arable-, grassland- and woodland-dominated areas of our Breckland study area between 2019 and 2022. Despite our study area consisting of > 55% woodland cover and comparable cover of grassland and arable (Table 1), the probability of occurrence of used nests was disproportionately greater as percent cover of grassland increased and percent cover of woodland and arable decreased (Table 2; Fig. 3). Of the used nests, 72% occurred in areas comprising over 50% grassland within 500 m (compared to 31% of available sites) and only two used nests occurred in areas where woodland cover exceeded 50%, while 58 available sites occurred in these conditions. Used nests were also disproportionately more likely to occur as the area of largest open habitat patch increased (Table 2; Fig. 3); over 21% of used nests occurred in areas where the largest open habitat patch was > 30 ha, whereas only 8% of available sites were located in these conditions.

In contrast, the landscapes most likely to support the subsets of used nests that hatched and that fledged broods comprised a significantly lower percent cover of grassland and larger percent cover of arable (Table 2; Fig. 3). Only 59% of hatched nests occurred in areas with > 50% grassland cover compared to 80% of failed nests, and less than half of the fledged broods occurred in areas with grassland cover > 50%. Only 16% of used nests occurred in areas with > 50% arable, whereas 31% of hatched nests and 24% of fledged broods occurred in these areas. Percent cover of woodland and size of largest open patch did not significantly differ between areas with nests that hatched and did not, and broods that fledged and did not (Table 2; Fig. 3). However, despite 44 used nests occurring in areas supporting open patches > 30 ha, only two fledged nests occurred in these areas. Landscape structure did not differ significantly between the areas surrounding failed broods and fledged broods (Table 2; Fig. 3).

Table 2: Results of GLMs exploring variation in the proportion of used curlew nests, hatched nests and fledged broods, in relation to landscape structure in the surrounding 500 m, in Breckland between 2019 and 2022 (see Table 2 for description of model variable and structures). Models i-iv include percent cover of grassland and models v-viii include percent cover of arable. Significant predictors ($p < 0.05$) are highlighted in bold.

Model	Fixed effect	Estimate	se	*p*
i	**(Intercept)**	**-2.342**	**0.278**	**< 0.001**
Available vs Used	**Largest patch**	**0.019**	**0.009**	**0.042**
(with grassland)	**Woodland**	**-0.034**	**0.007**	**< 0.001**
	Grassland	**0.028**	**0.003**	**< 0.001**
ii	(Intercept)	-0.550	0.497	0.267
Failed vs Hatched	Largest patch	0.013	0.016	0.424
(with grassland)	Woodland	0.007	0.015	0.614
	Grassland	**-0.023**	**0.007**	**< 0.001**
iii	(Intercept)	-0.255	0.943	0.787
Failed brood vs Fledged	Largest patch	-0.047	0.039	0.231
(with grassland)	Woodland	0.001	0.022	0.958
	Grassland	-0.006	0.011	0.553
iv	(Intercept)	0.010	0.863	0.902
Failed nest vs Fledged	Largest patch	-0.015	0.033	0.642
(with grassland)	Woodland	0.019	0.024	0.443
	Grassland	**-0.032**	**0.012**	**0.006**
v	(Intercept)	0.136	0.268	0.611
Available vs Used	**Largest patch**	**0.025**	**0.009**	**0.010**
(with arable)	**Woodland**	**-0.057**	**0.008**	**< 0.001**
	Arable	**-0.028**	**0.003**	**< 0.001**
vi	**(Intercept)**	**-1.404**	**0.522**	**0.007**
Failed vs Hatched	Largest patch	0.007	0.016	0.655
(with arable)	Woodland	0.024	0.015	0.118
	Arable	**0.020**	**0.006**	**0.003**
vii	(Intercept)	-0.510	1.105	0.644
Failed brood vs Fledged	Largest patch	-0.047	0.039	0.234
(with arable)	Woodland	0.008	0.024	0.722
	Arable	0.009	0.011	0.375
viii	**(Intercept)**	**-2.866**	**0.993**	**0.004**
Failed nest vs Fledged	Largest patch	-0.019	0.033	0.095
(with arable)	Woodland	0.045	0.027	0.095
	Arable	**0.032**	**0.011**	**0.005**

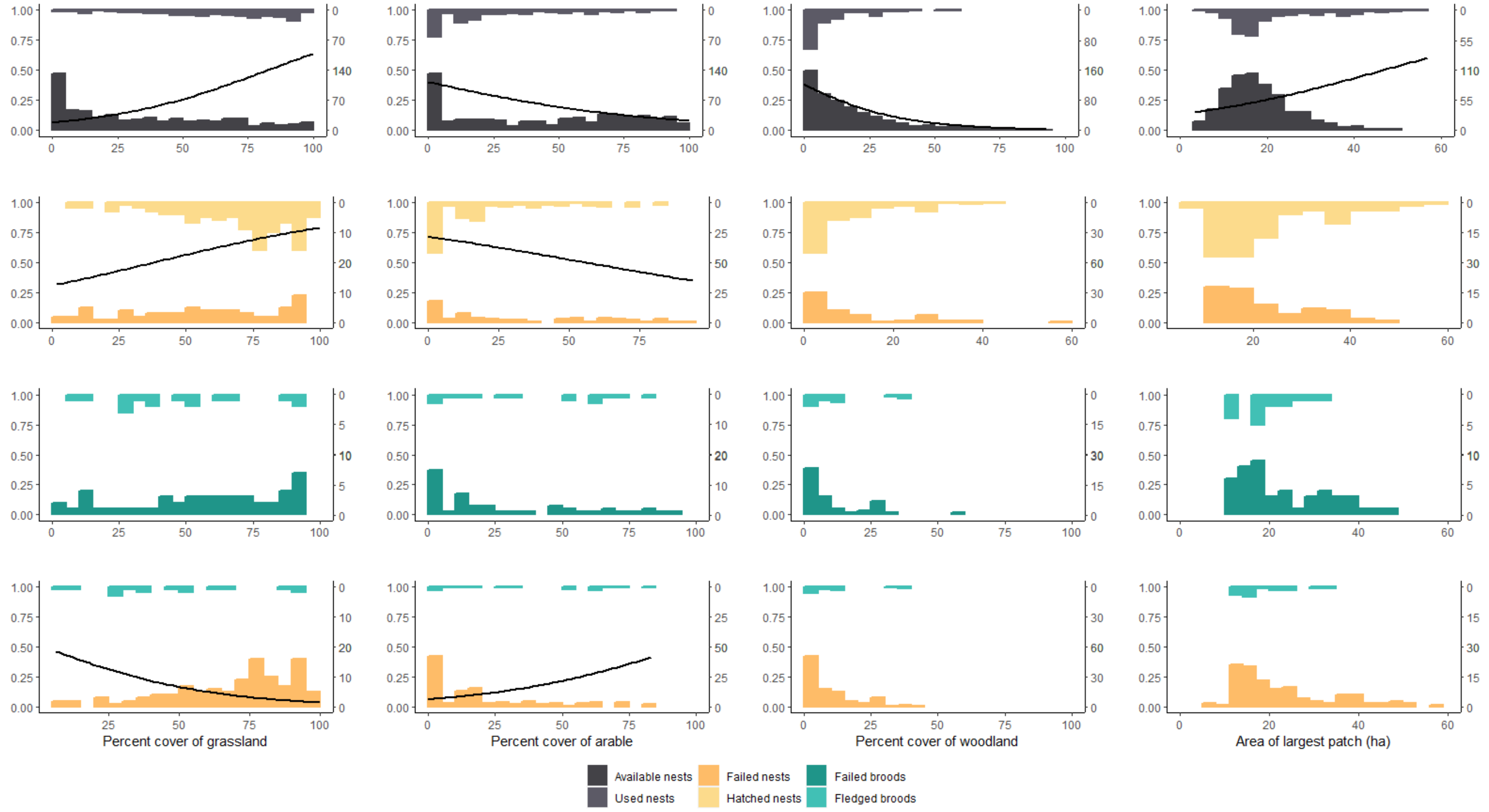


Figure 3: The predicted proportion (lines, left-hand y-axis) and observed frequency of occurrence (bars, right-hand y-axis) of available (randomly located points), used, failed, hatched and fledged curlew nests in relation to percent cover of grassland, arable, woodland and area of largest open habitat patch in the surrounding 500 m, in Breckland (2019-2022). Predicted proportions only presented for significant trends ($p < 0.05$).

Distribution of curlew in arable fields

A total of 19 curlew were recorded in arable fields around four of the six grassland sites during surveys, and these birds occurred on only 9% of surveyed arable fields. A significantly larger proportion of occupied fields were adjacent to grassland than in the near or far distance bands (Table 3, Fig. 4). Only one curlew was observed in an arable field located > 2 km from grassland and 14 of the 19 curlews occurred in fields adjacent to grassland sites.

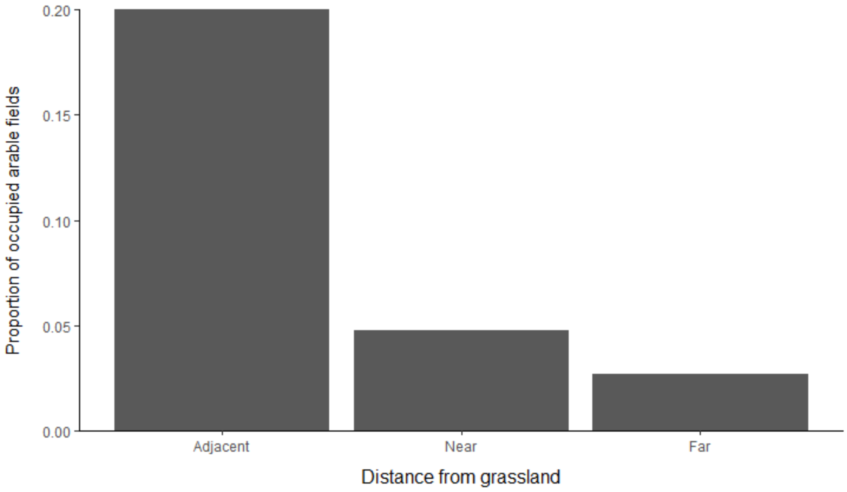


Figure 4: The proportion of arable fields in which curlew occurred at three distances from grassland, surveyed in Breckland between mid-March and mid-July 2021.

Table 3: Results of a GLMM exploring variation in the presence or absence of curlew in arable fields in relation to distance from grassland in Breckland, March to July, 2021 (see Table 2 for description of model variable and structures). Estimates for near and far fields are relative to the intercept (estimate for adjacent fields). Significant predictors ($p < 0.05$) are highlighted in bold.

Model	**Fixed effect**	**Estimate**	**se**	**z**	***p***
ix	(Intercept)	-1.460	0.576	-2.536	**0.011**
	Distance from grassland [Near]	-1.883	0.902	-2.087	**0.037**
	Distance from grassland [Far]	-2.891	1.240	-2.331	**0.020**

Discussion

Appropriate targeting of conservation actions for threatened species can depend on both the conditions in which the species occurs and the conditions in which demographic successes are achieved. In grassland-dominated areas of Breckland, relatively few demographic successes were achieved by curlew at nest and chick stages, despite these areas supporting a disproportionately higher frequency of nesting attempts (i.e. Fig. 1a) while, in arable-dominated areas, curlew occurred less frequently (and primarily in fields adjacent to grassland) but achieved relatively more demographic successes (i.e. Fig. 1c or 1d). For the Breckland curlew population, no current environmental conditions are both frequently used and productive (Fig 1b), and a combination of actions to (1) protect favourable environmental conditions, (2) create more favourable habitats and, (3) enhance demographic success in less productive conditions are likely to be required to maintain this population.

Protected Areas (PAs) are known to have positive impacts on the occurrence and demography of bird populations (Sanderson *et al.* 2022), particularly for rare and declining habitat specialists (Barnes *et al.* 2023). In Breckland, areas comprising large, open habitat patches, away from woodland, in which breeding curlew frequently occur (usually grassland-dominated areas and adjacent arable fields), require protection. This type of open, lowland landscape is constantly under threat from land-use change (Auffret *et al.* 2018, Schils *et al.* 2022), and increasingly, installation of solar panels (Dower 2018) and tree planting (Pálsdóttir *et al.* 2022), as mechanisms of achieving net-zero targets set by the government. Some landscapes supporting high frequencies of breeding curlew in our Breckland study area are already designated as Sites of Special Scientific Interest, and as part of the Breckland Special Protection Areas and/or Special Areas of Conservation, however, no environmental conditions were found to support a high frequency of occurrence and high level of demographic success concurrently. Additionally, none of these PAs specifically include curlew as a designated species and the habitat requirements of curlew may differ from the other species for which Breckland PAs are designated (e.g. stone curlew *Burhinus oedicnemus*; Hawkes *et al.* 2021). This potentially suggests that increasing the extent of PAs is unlikely to be sufficient to support a sustainable population of curlew in Breckland, without actions to also enhance demographic success, specifically targeted at this species.

In Breckland, curlew nest survival is low as a result of high levels of mammalian nest predation (Ewing *et al.* 2022.; Zielonka *et al.* 2020), and too few chicks fledge to maintain a sustainable population (Chapter 3). To enhance the demographic success of breeding curlew, tools such as predator-exclusion fencing (Laidlaw *et al.* 2021) and grassland management (Chapter 3) should be deployed across both grassland- and arable-dominated areas of Breckland, where hatched nests and fledged broods were scarce (despite demographic successes occurring with relatively greater frequency in arable areas). In addition, lethal control of predators can help to boost productivity of ground-nesting birds in some circumstances (Baines *et al.* 2022), although the evidence for consistent benefits at sufficiently large spatial scales is limited (Bolton *et al.* 2007, Douglas *et al.* 2023). To enhance the efficiency of such actions, deployment could be targeted within the few remaining sites supporting high local abundances of curlew in Breckland; a strategy which has potential to substantially enhance the frequency of demographic success (Ewing *et al.* 2022).

Breckland is a primarily arable-dominated landscape and curlew were most commonly recorded in arable fields adjacent to grassland sites. Encouraging increased occurrence of curlew in arable-dominated areas, for example by converting low value arable land to grassland (e.g. Francis and Elliott, 2019), could potentially enhance the productivity of the Breckland population given the relatively greater frequency of demographic successes in these areas. However, as altering the landscape composition of arable-dominated areas could risk jeopardising this slightly higher frequency of demographic success, and encouraging curlew into intensively managed, agriculture areas might increase the proportion of nests and chicks lost to mechanised operations, which is currently low in Breckland (Ewing *et al.* 2022), this is likely to be a lower priority than grassland protection and management. Importantly, grassland protection, creation and management are likely to be most successful in open landscapes, as only two nesting attempts were found in areas with 50% woodland cover, and greater understanding of the grassland characteristics required by curlew (e.g. suitable patch area, sward structure) would aid the design of appropriate management.

The Breckland population of breeding curlew is a good example of how our conceptual framework can be applied to inform the targeting of conservation actions. Despite the use of relatively coarse metrics of landscape structure, this approach effectively demonstrates how co-variation in demography and occurrence can be used to inform targeting of different types of conservation actions. If this framework were to be applied across broader spatial scales it is likely that finer-resolution environmental data would be required to account for variation in management within habitat types. For example, if our framework were to be used to inform targeting of conservation actions for curlew across the whole of the UK, different types of vegetation structure (e.g. silage, hay meadow, heathland) and land-use (e.g. grouse moor, non-grouse moor) should be taken into account (Colwell *et al.* 2020). It might also be necessary to alter the spatial scale over which the impact of landscape structure is assessed, to align with the scale over which the factors influencing occupancy and demography of the focal species operate.

Environmental data are becoming increasingly widely available due to advances in remote sensing technology, and good-quality occurrence data exist for many taxa (particularly birds e.g. Brlík *et al.* 2021; Harris *et al.* 2022), as a result of surveys conducted by dedicated citizen scientists. Opportunities to apply this framework to other threatened populations are therefore likely to be primarily limited by availability of demographic data (Conde *et al.* 2019), which are more challenging to gather. However, designing volunteer-based surveys of demographic rates that capture the range of environment conditions in which populations occur is achievable, particularly for more common, widespread species (e.g. British Trust of Ornithology Nest Record Scheme and Retrapping Adults for Survival scheme; Crick *et al.* 2003; Robinson *et al.* 2008).

Our conceptual framework can potentially be used to target appropriate conservation actions over different spatial scales, for a range of threatened populations, species and communities, particularly those where long-lived individuals are widespread across a range of environmental conditions. Future research to inform the efficient and effective deployment of targeted conservation actions to protect, encourage and/or enhance threatened populations in differing environmental conditions, should aim to integrate demographic and occurrence data, where possible.

Supplementary material to Chapter 4: Integrating frequency of occurrence and demographic success to inform targeting of conservation actions

Table S1: Classification of Centre of Ecology and Hydrology Land Cover 2020 habitat categories and the percent cover of each habitat across the study area.

CEH LC 2020 classification	Simplified classification	Percent cover of Breckland	Percent cover of study area
Broadleaf woodland Coniferous woodland	Woodland	28.71%	55.12%
Arable	Arable	45.62%	22.37%
Improved grassland Semi-natural grassland Mountain, heath and bog	Grassland	20.31%	20.22%
Saltwater Freshwater	Water	0.5%	0.24%
Coastal	N/A	0	0
Built up and gardens	Urban	4.84%	2.04%

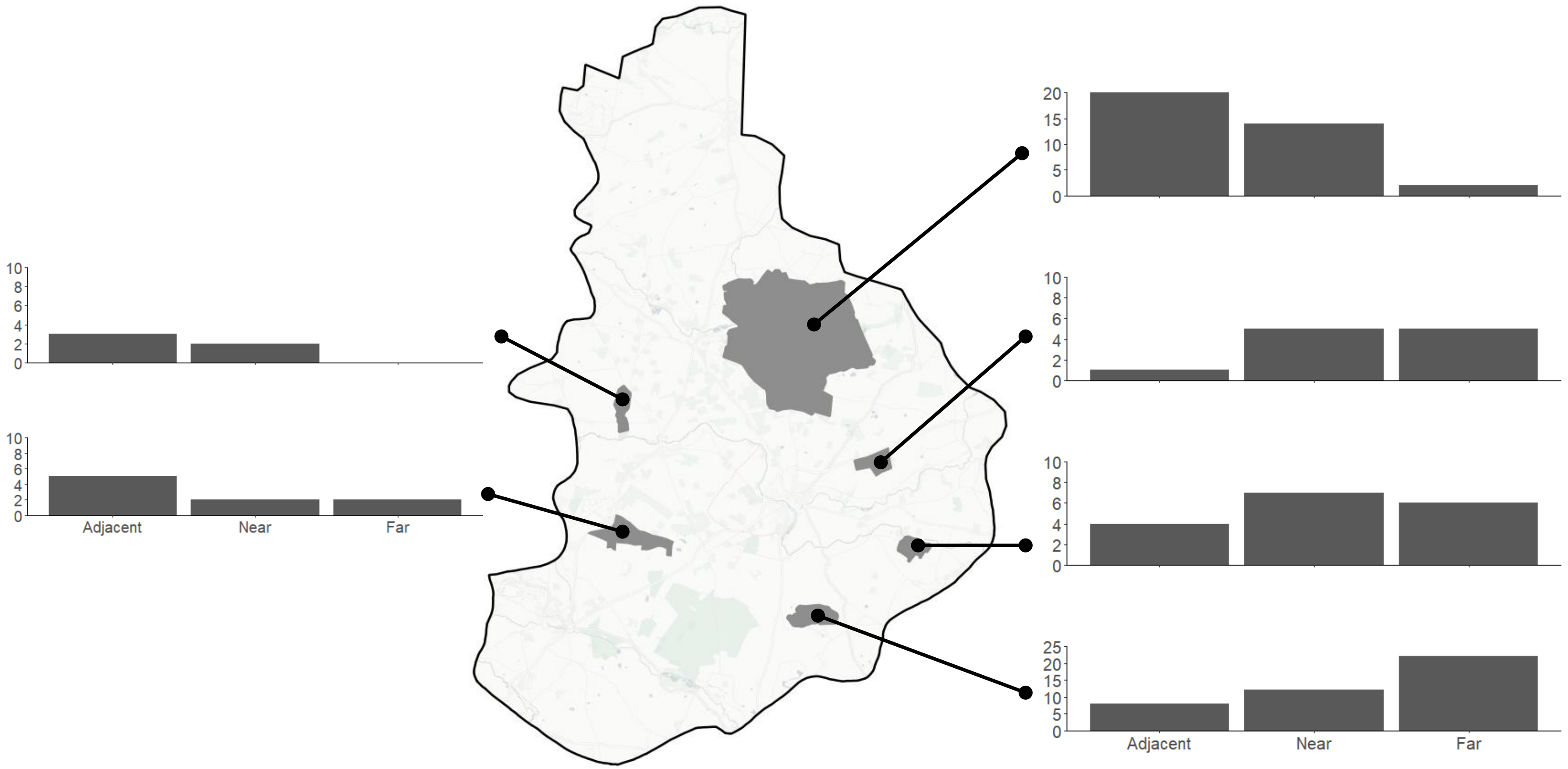


Figure S1: Number of arable fields surveyed (y-axis) across Breckland within each distance category (adjacent, within 500 m; near, 500-2000 m; and far, >2 km), displayed with the associated grassland site.

Table S2: Results of GLMs exploring variation in the proportion of used curlew nests, hatched nests and fledged broods, in relation to landscape structure in the surrounding 1000 m, in Breckland between 2019 and 2022 (see Table 1 for description of model variable and structures). Models i-iv include percent cover of grassland and models v-viii include percent cover of arable. Significant predictors (p < 0.05) are highlighted in bold.

1000m resolution				
i	**(Intercept)**	**-2.042**	**0.268**	**< 0.001**
Available vs Used	Largest patch	0.005	0.006	0.426
(with grassland)	**Woodland**	**-0.022**	**0.006**	**< 0.001**
	Grassland	**0.030**	**0.004**	**< 0.001**
ii	(Intercept)	-0.391	0.497	0.432
Failed vs Hatched	Largest patch	0.003	0.012	0.776
(with grassland)	Woodland	0.009	0.013	0.488
	Grassland	**-0.024**	**0.009**	**0.005**
iii	(Intercept)	-0.016	0.870	0.985
Failed brood vs Fledged	Largest patch	-0.018	0.022	0.413
(with grassland)	Woodland	-0.022	0.023	0.336
	Grassland	-0.003	0.015	0.862
iv	(Intercept)	-1.066	0.798	0.182
Failed nest vs Fledged	Largest patch	-0.010	0.021	0.636
(with grassland)	Woodland	-0.011	0.022	0.633
	Grassland	-0.001	0.013	0.179
v	**(Intercept)**	**0.602**	**0.308**	**0.050**
Available vs Used	Largest patch	0.008	0.006	0.195
(with arable)	**Woodland**	**-0.050**	**0.006**	**< 0.001**
	Arable	**-0.029**	**0.004**	**< 0.001**
vi	**(Intercept)**	**-1.436**	**0.584**	**0.014**
Failed vs Hatched	Largest patch	-0.001	0.012	0.944
(with arable)	Woodland	0.024	0.014	0.094
	Arable	**0.019**	**0.008**	**0.020**
vii	(Intercept)	-0.711	1.094	0.516
Failed brood vs Fledged	Largest patch	-0.017	0.022	0.446
(with arable)	Woodland	-0.013	0.025	0.605
	Arable	0.011	0.013	0.395
viii	**(Intercept)**	**-2.779**	**0.967**	**0.004**
Failed nest vs Fledged	Largest patch	-0.012	0.021	0.565
(with arable)	Woodland	0.006	0.025	0.809
	Arable	0.021	0.012	0.083

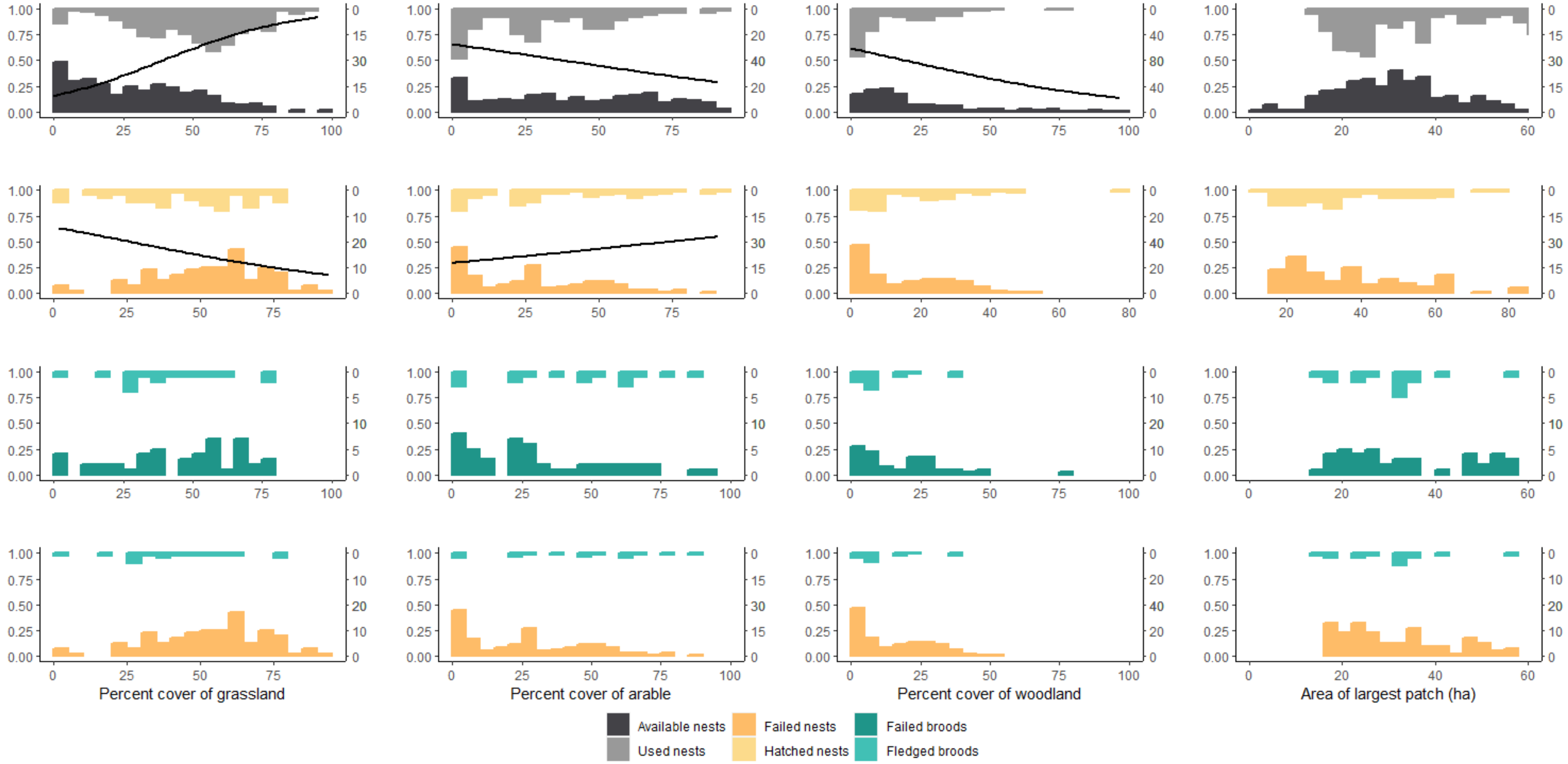


Figure S2: The predicted proportion (lines, left-hand y axis) and observed frequency of occurrence (bars, right-hand y axis) of available (randomly located points), used, failed, hatched and fledged curlew nests in relation to percent cover of grassland, arable, woodland and area of largest open habitat patch in the surrounding 1000 m, in Breckland (2019-2022). Predicted proportions only presented for significant trends ($p < 0.05$).

Chapter 5

Scenarios of conservation actions to boost the breeding productivity of a threatened wader population

Abstract

To address ongoing biodiversity loss, conservation actions to help the growing number of widespread but declining populations are needed, but most actions have so far fallen short of achieving meaningful outcomes. Conservation actions can be designed to boost demographic success at different life stages, and deploying such stage-specific actions in combination could potentially increase their effectiveness, allowing for more efficient use of scarce conservation resources. Empirical opportunities to test the consequences of deploying conservation actions in isolation or combination are rare, and simulation modelling can provide a means of exploring the outcome of differing management scenarios. Here, we use a simulation model to explore the capacity of actions to boost hatching success (predator-exclusion fencing) and fledging success (vegetation management to provide cover for chicks) to achieve the levels of productivity required for population sustainability when delivered in isolation and combination, in a population of Eurasian curlew *Numenius arquata*; a widespread but declining wading bird species that has undergone steep declines across Europe as a result of unsustainably high levels of nest and chick predation. These simulations suggest that sustainable breeding productivity could potentially be achieved with permanent predator-exclusion fencing of ca. 37% of the population, or ~22% of the population if deployed in combination with suitable vegetation structures. By contrast, temporary fencing (for the duration of nest incubation) would only be likely to achieve sustainable levels of productivity if deployed over ~45% of the population and in combination with suitable vegetation structures. This suggests substantial potential benefits of targeting the deployment of predator-proof fencing in areas where vegetation structures that provide cover for chicks exist or could be created, and that field trials of these actions would be worthwhile, while numbers and breeding densities remain sufficiently high to make such trials feasible.

Introduction

Human-induced changes in climate and land-use are driving population declines across the world, threatening global biodiversity (Urban 2015, Powers & Jetz 2019). Conservation efforts to slow or reverse these declines have typically relied on generic environmental management approaches in the hope that these will lead to population recovery (e.g. Batáry *et al.* 2015), but these actions have broadly failed to deliver meaningful outcomes, particularly for widespread, common populations for which declines are becoming increasingly prevalent (Vickery *et al.* 2004, Butler & Norris 2013, Pe'er *et al.* 2014, Burns *et al.* 2021). Addressing these declines effectively requires different strategies, with a growing body of evidence suggesting that more targeted actions are needed (Morrison *et al.* 2021, 2022).

Targeted conservation management can potentially exploit spatio-temporal variation in demographic rates (productivity and/or survival) by deploying specific actions in locations and/or at times when rates are low and can potentially be boosted (Morrison *et al.* 2022). Such actions have to be efficient, to make use of the limited resources available to conservation, while also being capable of delivering sufficient increases in demographic rates to facilitate population sustainability or growth. Opportunities to test conservation actions in the field are limited but, where causes of demographic variation have been quantified and conservation actions to influence those causes are available, simulation modelling of differing scenarios of deployment of actions can be a helpful tool to explore their potential impact (e.g Laidlaw *et al.* 2017). Scenario testing can also help to identify the levels of management required to achieve specific conservation goals, in relation to the magnitude of responses that different management actions might produce (Peterson *et al.* 2003, Nicholson *et al.* 2019), and to inform the design of field trials (Nicholson *et al.* 2019). Consequently, modelling biologically realistic scenarios that can feasibly be delivered, and paramaterising models with demographic data that capture the range of relevant conditions (Nicholson *et al.* 2019), are particularly important.

A group of species for which conservation actions are urgently needed, and demographic data are widely available, are waders *Charadriiform spp*., one of the world's most ubiquitous but threatened avian groups (Colwell 2010, IUCN 2022). The conspicuous behaviours that waders display during both breeding and non-breeding seasons mean that their populations are often well-monitored (e.g. Frost *et al.* 2020, Nagy & Langendoen 2020, Brlík *et al.* 2021, Harris *et al.* 2022). Fine-scale studies of distribution and demography are also common (e.g. Gill *et al.* 2019, Méndez *et al.* 2020, Verhoeven *et al.* 2020) and, consequently, the demographic rates influencing population declines, the spatial and temporal variation in these rates and the drivers of that variation are often quite well understood (e.g. Roodbergen *et al.* 2012, Kentie *et al.* 2018, Laidlaw *et al.* 2020, Kaasiku *et al.* 2022, Pálsdóttir *et al.* 2022).

In western Europe, many studies have linked declines in breeding wader populations to widespread changes in land-use and climate, which have altered environmental conditions (e.g. Verhulst *et al.* 2007, Douglas *et al.* 2014, Kentie *et al.* 2015, Franks *et al.* 2017, Jóhannesdóttir *et al.* 2019, Kaasiku *et al.* 2022, Pálsdóttir *et al.* 2022), resulting in nests and chicks becoming increasingly vulnerable to predation by generalist predators (Macdonald & Bolton 2008, Roodbergen *et al.* 2012, Schroeder *et al.* 2012, Kentie *et al.* 2015). In response, efforts to boost wader populations typically target the nesting and chick-rearing stages of the life-cycle, some of which have had positive effects on local wader abundance and breeding productivity, particularly for populations restricted to nature reserves (Smart *et al.* 2014, Franks *et al.* 2018, Jellesmark *et al.* 2021). However, positive management outcomes have so far been limited for more widely dispersed wader species such as the Eurasian curlew *Numenius arquata* (hereafter, curlew) (Franks *et al.* 2018), which was once a common and widespread species across much of western Europe (Keller *et al.* 2020), but is now a classified as Near Threatened globally (IUCN 2022) and in Europe (BirdLife International 2021).

Like other wader species in western Europe, curlew populations are known to be declining as a result of unsustainably low breeding productivity (Cook *et al.* 2021, Viana *et al.* 2023), caused by high rates of mammalian nest and chick predation (Grant *et al.* 1999, Douglas *et al.* 2014, Zielonka *et al.* 2020, Ewing *et al.* 2022). To restore curlew populations in the long-term, actions to reduce the impacts of mammalian predators are required, but there is not yet an established method that consistently delivers measurable gains in wader breeding productivity across the large spatial scales required for breeding curlew (Douglas *et al.* 2023). Consequently, efforts to boost curlew populations are currently limited to localised actions deployed to prevent extirpration in the short-term (Colwell *et al.* 2020), of which the most frequently used is predator-exclusion fencing.

Predator-exclusion fencing is a flexible tool that can be used to reduce the impact of mammalian predators on ground-nesting bird populations across different temporal (permanent or temporary) and spatial scales (nest-, field- or site-level) (e.g. White & Hirons 2019, Laidlaw *et al.* 2021). A range of fencing strategies have been widely demonstrated to enhance local rates of wader nest survival, and can potentially contribute to increased levels of chick survival when deployed over sufficiently large spatial and temporal scales to protect chicks from mammalian predators through the pre-fledging period (e.g. Rickenbach *et al.* 2011, Malpas *et al.* 2013).

Wader chick survival can also be influenced by vegetation structure. For example, in the Netherlands, survival rates of black-tailed godwit *Limosa limosa* chicks hatched in hay meadows are higher than for chicks hatched in improved grasslands, likely as a result of increased invertebrate food availability and greater ability to evade predators in open, tall swards of hay meadows (Whittingham & Evans 2004, Kentie *et al.* 2013). Similarly, a recent study of Eurasian curlew *Numenius arquata* in Breckland, eastern England found that, in landscapes otherwise comprising short vegetation, the probability of curlew chicks fledging increased from ~11% to ~30% (Chapter 2) when tall (> 50 cm) vegetation occurred within the surrounding (500 m radius) landscape of a hatched curlew nest, likely as a result of the opportunities for concealment from predators provided by tall vegetation.

Targeting conservation actions to boost demographic rates at the life stage/s during which failure is most common is likely to be an effective method of restoring threatened populations (Morrison *et al.* 2021). However, if demographic rates are low across several life stages, then more than one type of stage-specific action may be required to boost overall rates of productivity or survival, and deployment of these actions in combination may be more effective at achieving the required overall demographic rates, and more efficient in terms of required scale and extent of management. Here, we use a simulation model of hatching and fledging success of curlew to assess the impact of predator-exclusion fencing deployed across a range of spatial (proportion of population managed) and temporal (temporary, semi-permanent and permanent) scales, in isolation and in combination with suitable vegetation structures for chick rearing, on the breeding productivity of a threatened curlew population. We use the model to explore the extent (in terms of percentage of population subject to management) of different combinations of actions likely to be required to maintain the curlew population in Breckland, discuss the actions required to deliver this efficiently and the implications for curlew breeding in differing landscapes.

Methods

Simulation model

We constructed a model in R (v 4.2.1) of 1000 breeding female curlew to simulate the effect of different management scenarios on curlew productivity. Each simulation was run 100 times, with different percentages of the population (either 0, 25, 50 or 75%) under one of seven management scenarios. To ensure that biologically realistic values were used in the simulations, the modelled distributions, functions and scenarios were constructed from published and unpublished data on breeding curlew in Breckland, eastern England (Ewing *et al*. 2022, Chapter 2), and other published studies on curlew (Cook *et al.* 2021, Bowgen *et al.* 2022, Viana *et al.* 2023) and other ground-nesting waders in Europe (Malpas *et al.* 2013, Verhoeven *et al.* 2020).

Timing of nesting attempts

In all simulations, each female could complete a maximum of one successful nesting attempt (Bowgen *et al.* 2022). The lay date of each first clutch was determined by sampling randomly from a distribution of days on which first clutches were initiated for curlew nests monitored in Breckland between 2019 and 2022 (Ewing *et al*. unpublished data; Fig. 1a). The success (hatch or fail) of each nesting attempt was determined by a random draw from a binomial distribution, with a predetermined hatching success, either 25% (the observed mean hatching success for this population; Chapter 2) or 75% (published estimate of mean wader hatching success within predator-exclusion fencing; Malpas *et al*. 2013). All eggs in a clutch were assumed to hatch if the nesting attempting was successful. All first nesting attempts that failed were followed by a maximum of one renesting attempt (Verhoeven *et al.* 2020, Bowgen *et al.* 2022). The lay date of renesting attempts was determined by first assigning a nest failure date to each failed attempt, by randomly sampling from a distribution of the number of days between laying and failure (time taken to fail; Ewing *et al*. unpublished data; Fig. 1b), and adding a time gap (renesting gap), also randomly sampled from a distribution of observed renesting gaps (Ewing *et al*. unpublished data; Fig.1c). For each female, this process was continued until either a nesting attempt was successful, the renesting attempt failed, or lay dates exceeded the end of the breeding season on day 75 (75 days is the maximum observed length of breeding season, measured as the difference between the earliest and last date on which a nesting attempt was found to have been initiated across four breeding seasons in Breckland; Ewing *et al*. unpublished data).

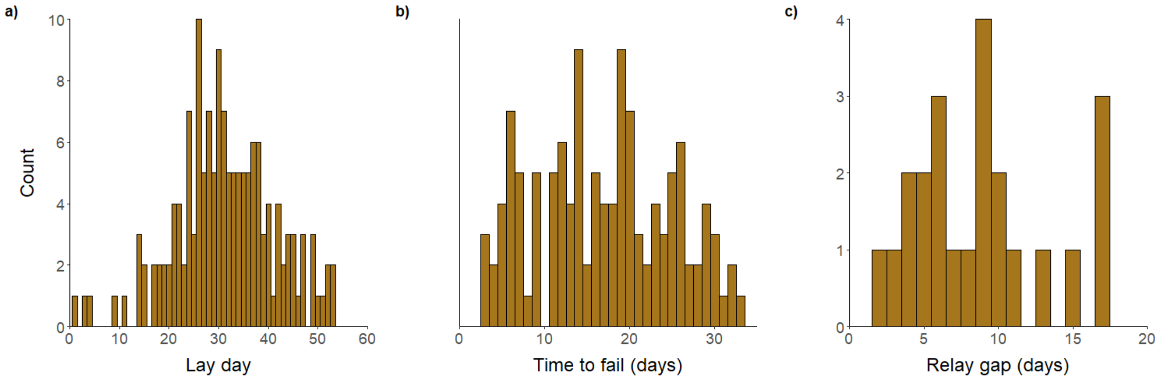


Figure 1: Distributions of (a) first clutch lay day (day of season), (b) number of days between laying and failure (time to fail) and (c) number of days between failure and relaying (relay gap) for curlew nesting attempts monitored in Breckland between 2019 and 2022.

Lay dates were estimated by back-calculating from weights and measures of all eggs in each clutch (164 clutches) and assuming that one egg was laid every 1.5 days (Grant 1996, Ewing *et al.* 2022). As predation is the cause of almost all curlew nest failure (Ewing *et al.* 2022), time taken to fail was estimated for 131 predated curlew nests by calculating the difference between lay dates and failure dates, determined following Ewing *et al.* (2022), and renesting gaps were estimated by calculating the difference between failure dates and lay dates for 23 pairs of first and second clutches (Ewing *et al*. unpublished data). Renesting attempts by the same pairs were identifiable because of the low densities at which curlew breed in Breckland (Ewing *et al.* 2022), the presence of colour-marked breeding adults which could be tracked across the whole breeding season, and the high spatial proximity (typically within 125 m) of first and second clutches of marked individuals.

Simulated management scenarios

Seven management scenarios were simulated, comprising actions to boost hatching success only (temporary predator-exclusion fencing, installed for the incubation period only), hatching success and survival of young chicks (semi-permanent predator-exclusion fencing, spanning the incubation period and the first week of chick growth, when chicks are most vulnerable to predation; Chapter 2) and hatching success and chick survival to fledging (permanent predator-exclusion fencing, covering the incubation and pre-fledging periods), with or without the presence of cover vegetation (> 50 cm height) (Table 1; Chapter 2). The presence of cover vegetation was also simulated in the absence of fencing (Table 1). Each of these scenarios was applied to 0, 25, 50 and 75% of the modelled population.

Simulated effects of management on hatching and fledging rates

In the absence of management, the simulated hatching success of nests was the observed mean rate of 25% (Table 1; Ewing *et al.* 2022) while the simulated hatching success in fenced areas was 75%, following Malpas *et al*. (2013). Chick fledging rates were modelled by sampling at random from observed distributions of the number of chicks fledged per hatched nest without (mean = 0.38 ± 0.3 se; Chapter 2) and with (mean = 1.09 ± 0.84 se; Chapter 2) cover vegetation (Table 1) and, for scenarios including fencing, the mean fledging rate for landscapes with cover vegetation present in 44% of locations (typical of Breckland at present) and absent on the remaining 56% (mean = 0.69 ± 0.23 se), was applied to unfenced nests (to account for existing effects of cover vegetation).

The impact of fencing on chick fledging rates is typically unclear, because of the wide range of (avian and mammalian) predators of chicks and because chicks can leave fenced areas. Consequently, in models of semi-permanent fencing, the effect of fencing on chick survival during the first week of life was explored by randomly sampling from distributions of the number of chicks fledged per hatched nest for which the observed mean (1.6 ± 0.218 se; no effect of cover vegetation is present during this stage; Chapter 2) was increased by either 50% or 100% (followed by the observed probability of fledging from week 2 onwards of 0.4 without, and 0.68 with, cover vegetation; Ewing *et al*. unpublished data). Similarly, in models of permanent fencing, effects of fencing on fledging rates were explored by randomly sampling from distributions for which observed means (0.69 ± 0.23 se without, and 1.09 ± 0.84 se with, cover vegetation; chapter 2) were increased by either 50 or 100% (Table 1).

Table 1: Description of the simulated management scenarios, each of which is applied to 0, 25, 50 and 75% of the modelled population of 1000 female curlew. For each scenario, the hatching success, survival of chicks during week 1 (for semi-permanent fencing) and fledging rates are reported with the % increase (0, 50 or 100) from observed values.

Intervention	*Cover vegetation present*	*Hatching success (% increase)*	*Week 1 chick survival rate (% increase)*	*Fledging rate (% increase)*
Vegetation management	Yes	25 (0)	N/A	1.09 (0)
Temporary fencing	No	75 (150)	N/A	0.69 (0)
Semi-permanent fencing			2.4 (50) 3.2 (100)	0.4 (0)
Permanent fencing			N/A	1.04 (50) 1.38 (100)
Temporary fencing	Yes	75 (150)	N/A	1.09 (0)
Semi-permanent fencing			2.4 (50) 3.2 (100)	0.68 (0)
Permanent fencing			N/A	1.64 (50) 2.18 (100)

For each simulation, the total number of fledged chicks was calculated (sum of chicks fledged from the unmanaged and managed proportions of the population), averaged across the 100 model iterations, and converted to a rate of breeding productivity (number of fledged chicks per female). In figures, these simulated rates of breeding productivity are presented in comparison to two published estimates of the levels required to maintain a sustainable breeding population. The first estimate (0.43 chicks per nest; Cook *et al*. (2021)) was converted to a lower (0.57) and upper (0.72) estimate of chicks per pair by multiplying by the mean number of nests (first attempts and relays) per female calculated for the most optimistic (1.33 (1.26 – 1.37 95% CI) nests per female; 75% of nests fenced, of which 75% hatch successfully, resulting in fewer relays) and most conservative (1.67 (1.59 – 1.85 95% CI) nests per female, no fencing, 25% hatching success and therefore more relays) scenarios. The second estimate was 0.68 fledged chicks per pair (Viana *et al*. 2023).

Results

The increase in breeding productivity that could be achieved by increasing the proportion of the curlew population with access to cover vegetation (> 50 cm height) was relatively modest, and never achieved the estimated levels required to maintain a sustainable population (Fig. 2). The increase in breeding productivity that could be achieved with temporary fencing of nests without additional increases in the presence of cover vegetation (beyond the current presence in 44% of the landscape) also failed to reach the level required to maintain a sustainable population (Fig. 3a). By contrast, sustainable levels could be achieved with temporary fencing of 45.3% (38.4 – 50.8 95% CI) of the population with cover vegetation (Fig. 3d). These levels could also be reached by deploying semi-permanent fencing of 60% (52.4 – 67.2) of the population without cover vegetation or 34.9% (29.8 – 39.2) with cover vegetation, if fences increase chick survival in the first week by 50%, and 42.1% (36.5 – 47.1) of the population without cover vegetation or 23.5% (20.1 – 26.7) with cover vegetation, if chick survival in the first week increased by 100% (Fig. 3b, e). Finally, sustainable levels of breeding productivity could be achieved with permanent fencing of 49.2% (42.7 – 55.5) of the population without cover vegetation or 30.3% (26.4 – 33.96) with cover vegetation, if chick survival increased by 50%, and 37.1% (31.9 – 41.78) of the population without cover vegetation or 21.5% (18.6 – 24.2) with cover vegetation, if chick survival increased by 100% (Fig. 3c, f).

In all fencing scenarios without or with cover vegetation (excluding temporary fencing), the mean percent of the population requiring management only increases slightly from 51.6% (40.9 – 52.9) to 55.6% (47.5 – 64) if the estimated level of breeding productivity required to maintain a sustainable population is 0.68.

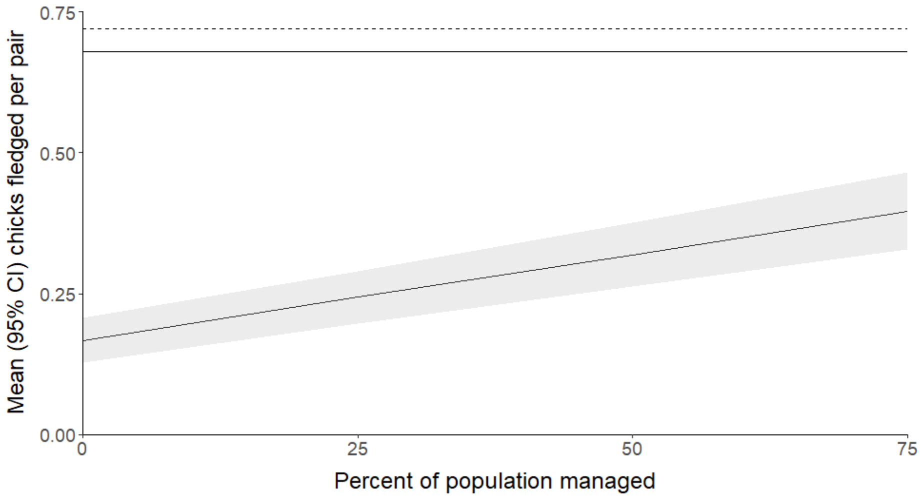


Figure 2: Simulated effects on curlew breeding productivity of management to make cover vegetation available to differing percentages of the population. Horizontal lines indicate estimated rates of sustainable breeding productivity from published studies (solid, Viana *et al*. 2023; and dashed, Cook *et al*. 2021).

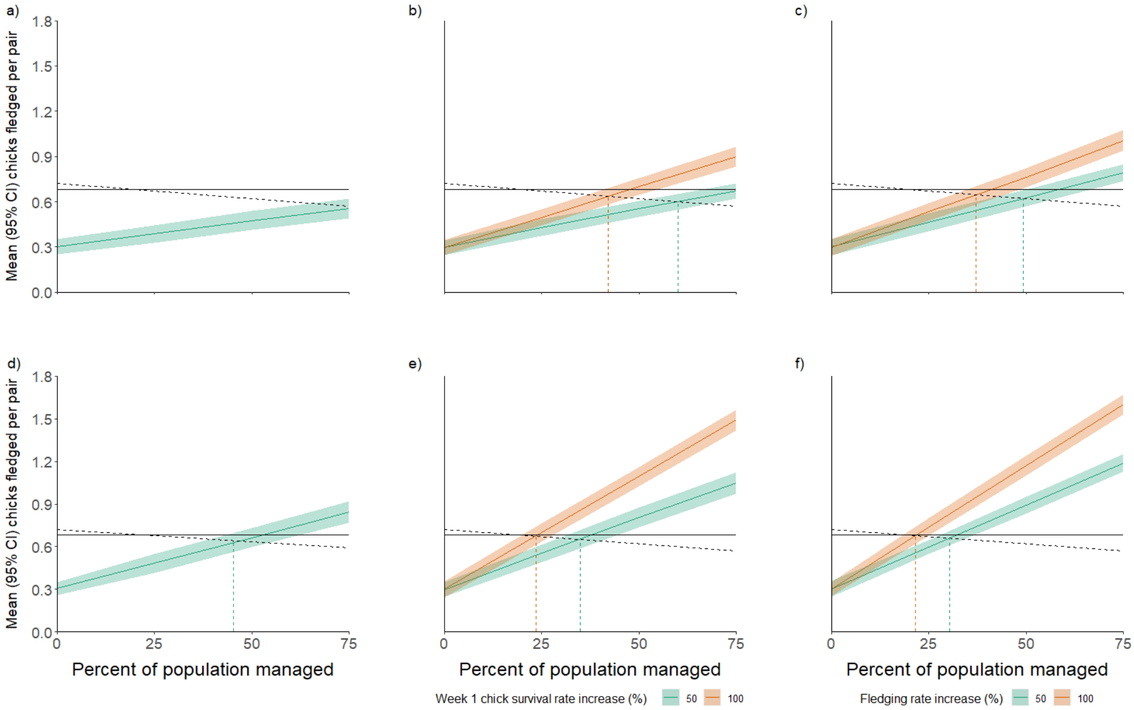


Figure 3: Simulated effects on curlew breeding productivity of management to deploy (a & d) temporary, (b & e) semi-permanent and (c & f) permanent fencing, without (top row) and with (bottom row) cover vegetation, for differing percentages of the population. Black horizontal and sloped lines indicate estimated rates of sustainable breeding productivity from published studies (solid, Viana *et al*. 2023; and dashed, Cook *et al*. 2021) and vertical lines indicate the required percent of the population receiving management to achieve the lowest rate.

Discussion

Many breeding wader populations across Europe are declining as a result of unsustainably low levels of productivity, and targeted actions to boost this crucial demographic rate are urgently needed (Roodbergen *et al.* 2012, Pearce-Higgins *et al.* 2017, Franks *et al.* 2018, Douglas *et al.* 2023). Two possible actions are predator-exclusion fencing, which has been demonstrated to boost hatching success in several species of ground-nesting wader by reducing encounter rates of incubating pairs with mammalian predators (e.g. Rickenbach *et al.* 2011, Smith *et al.* 2011, Malpas *et al.* 2013, Verhoeven *et al.* 2022), and vegetation management as, in landscapes with short vegetation, the presence of cover vegetation (> 50 cm height) is associated with higher levels of chick survival in curlews (Chapter 3). The scenarios explored here suggest that neither vegetation management nor temporary fencing that only captures the incubation period, deployed in isolation, are likely to be sufficient to reach sustainable levels of breeding productivity. However, combining the presence of cover vegetation with fencing could mean that only ~21 – 45%, depending on the temporal scale over which fencing is deployed, of a curlew population would require management to achieve sustainable breeding productivity.

Currently, efforts to boost curlew populations in western Europe, particularly in lowland areas, rely heavily on the deployment of temporary fencing to increase hatching rates (Colwell *et al.* 2020), and high levels of subsequent chick mortality often mean that these efforts have little impact on overall productivity. Temporary fences are capable of boosting hatching success of wader nests (Rickenbach *et al.* 2011, Malpas *et al.* 2013, Verhoeven *et al.* 2022) but, if chick survival and rates of fledging are low, then deployment of temporary fencing in isolation would likely result in only moderate increases in breeding productivity that would be insufficient to support population sustainability. However, combining the deployment of temporary fencing and cover vegetation could potentially achieve sufficient improvements in productivity, but only if deployed over at least ~45% of the population.

In Breckland, around 44% of landscapes into which broods hatch have patches of cover vegetation and the presence of this vegetation is associated with an increased probability of chicks fledging from ~0.11 to ~0.3 (Chapter 3). Open landscapes in Breckland mainly comprise short vegetation (Chapter 3), so targeted actions to increase the presence of cover vegetation would likely aim to maintain or create mosaics of short and tall vegetation. This mix of vegetation heights may provide foraging opportunities and cover from both avian and mammalian predators (Whittingham & Evans 2004), while fencing only excludes medium-sized mammalian predators, such as foxes and badgers (Laidlaw *et al.* 2021). As grassland management and the subsequent vegetation structure are likely to vary across the breeding range of curlew, more studies of the costs and benefits associated with curlew chick use of differing vegetation structure will be needed to inform and refine grassland management elsewhere.

Curlew chicks are most vulnerable to predation during their first week of life, when they also tend to use shorter vegetation (Chapter 2), potentially due to increased foraging opportunities or thermoregulatory benefits (Kentie *et al.* 2013, Carroll *et al.* 2015). Thus, providing an extra level of protection to chicks by using semi-permanent fences that remain in place throughout this period could be beneficial to levels of curlew breeding productivity. However, our models suggest that deployment of semi-permanent fencing in isolation would require management of ~60% of the population to achieve levels of productivity capable of supporting population sustainability, with this type of management only being effective if chicks remained within fenced areas during their first week of growth. Additionally, deploying semi-permanent fencing in combination with vegetation management would still require ~35% of the population to be managed and, given that both temporary and semi-permanent fencing can only be constructed once nests are in place and have been found (White & Hirons 2019), this is likely to be extremely challenging, because of the difficulty of finding so many nests, having the necessary landowner permissions and being able to deploy fences before nests are predated.

The most efficient fencing scenario modelled in our simulations was permanent fencing deployed in combination with cover vegetation, which could potentially achieve sustainable levels of productivity if deployed over ~21.5% of the population. Permanent fencing is capable of boosting hatching success and may also promote increase fledging rates by excluding mammalian predators through the chick rearing period (Malpas *et al.* 2013, Verhoeven *et al.* 2022). Unlike temporary and semi-permanent fencing, permanent fences are typically constructed prior to the breeding season (White & Hirons 2019), in areas very likely to support breeding pairs. Areas in which curlew breed are unlikely to vary much between years due to the high levels of breeding-site fidelity exhibited by monogamous wader species such as curlew (Méndez *et al.* 2018, Kwon *et al.* 2022, Sandercock & Gratto-Trevor 2023). However, nesting locations are only likely to be predictable at the field- or site-level. The most efficient method of deploying permanent fencing is therefore likely to be targeting fields or sites in which multiple pairs of curlew breed, to protect as many breeding attempts as possible across multiple breeding seasons. Permanent fencing is also likely to be most efficient when deployed in combination with lethal predator control, targeted to eliminate the threat of any mammalian predators enclosed within the fenced area.

Simulation modelling can be a helpful tool to explore potential outcomes of management scenarios, and thus to inform future management strategies, particularly when appropriate data are available for model parameterisation (Nicholson *et al.* 2019). For wading birds, one of the most challenging aspects of demography to measure is the number of breeding attempts made by pairs within each breeding season, as re-nesting following nest failure is common across temperate-to-high latitudes (e.g. Morrison *et al.* 2019). Studies of tagged individual black-tailed godwits suggest that numbers of nesting attempts may be underestimated in field studies, as early-season nest failures are often missed (Verhoeven *et al.* 2020). For this reason, our model assumed that curlew always renest after a failed first clutch, and that the field estimates of hatching and fledging rates are accurate. This could potentially result in breeding productivity being overestimated if renesting does not always occur and/or if some nesting attempts were not found. In addition, more work may be needed to refine current estimates of the level of breeding productivity required for population sustainability, and how annual variation in productivity might influence these estimates. To maintain a sustainable breeding population, long-lived species such as curlew may only require occasional years in which overall productivity is high, and the associated conditions may not have been captured during the four-year study period of this project. Consequently, there is continuing need for monitoring and collection of demographic data over long-time periods, particularly as environmental conditions change in response to ongoing changes in climate and land-use.

Currently levels of curlew breeding productivity in Breckland appear to be well below those required to maintain a sustainable breeding population (Chapter 3) and, as one of the largest remaining populations in the English southern lowlands (Colwell *et al.* 2020), it is a crucial population to maintain. The findings of the simulations presented here suggest that deploying fencing in areas with cover vegetation is a potentially feasible tool to boost productivity, particularly if large numbers of nests could be protected within permanent fences. Field trials are urgently required to test the efficacy of these actions in Breckland and in different landscapes, while curlew populations remain sufficiently high to make such actions feasible. It is also crucial that further analyses incorporate the economic costs of deploying and maintaining different interventions as a comparator of feasibility. Given that curlew are generally widespread and occur at highest density in privately managed sites (Ewing *et al.* 2022), partnerships with private landowners will be an essential part of delivering meaningful outcomes for breeding curlew.

Chapter 6

Thesis discussion

Thesis conclusions

Efforts to tackle the global biodiversity crisis have so far mainly involved designation of protected areas, with the aim of preserving important and unique ecosystems and habitats (Silva *et al.* 2018, Geldmann *et al.* 2019, Dietz *et al.* 2020, Bailey *et al.* 2022), single-species recovery programmes aimed at saving highly endangered, often rare and range restricted populations (e.g. Davies *et al.* 2011, Simón *et al.* 2012, Nicoll *et al.* 2021) or generic management aimed at improving environmental conditions in highly modified landscapes, through increasing resource availability for a group of species such as farmland birds (e.g. Butler & Norris 2013, Batáry *et al.* 2015, Boetzl *et al.* 2021, Redhead *et al.* 2022, Roilo *et al.* 2023). While these approaches all make highly valuable contributions to biodiversity conservation, there has also been a gradual but persistent decline in populations of more widespread, formerly common species (e.g. Kamp *et al.* 2015, Bell & Calladine 2017, Burns *et al.* 2021), symptomatic of deep-rooted anthropogenic influences on our environment. Conservation management to restore these increasingly threatened populations have so far fallen short of achieving meaningful outcomes and new approaches are required.

Targeting conservation actions to boost specific demographic rate/s in locations, or during periods of time, when they are low, could be an effective use of conservation resources for widespread but declining species (Morrison *et al.* 2021, 2022). The chapters within this thesis were designed to complement each other by quantifying spatial and temporal variation in different components of productivity of the globally Near Threatened but widespread Eurasian curlew (Chapters 2, 3), developing a conceptual framework to identify the situations in which different types of action are likely to be most appropriate and applying this to breeding curlew (Chapters 4), and constructing a simulation model to explore the scale of delivery of such actions that would be required to achieve levels of productivity likely to be needed for population sustainability (Chapter 5) and how best to deliver them in human-modified landscapes.

Impact and management of generalist mesopredators

Evidence from across Europe has demonstrated that wader populations are declining as a result of low breeding productivity, with numerous studies linking this to high rates of nest and chick predation (e.g. Macdonald & Bolton 2008, Roodbergen *et al.* 2012, Kentie *et al.* 2015, Laidlaw *et al.* 2015, Kaasiku *et al.* 2022, Pálsdóttir *et al.* 2022). For curlew in Breckland, the story is no different. We found that the probability of a curlew nest surviving incubation was only ~0.25, with 86% of nest failure resulting from (primarily nocturnal) predation (Chapter 2), and rates of breeding productivity did not exceed the levels required for a sustainable population in any of the four years of study (Chapter 3). Owing to the widespread distribution of curlew in the region and the generally low densities at which they breed, actions to limit the impact of predation on this population would likely require landscape-scale approaches (Chapter 2).

There is a large body of evidence to suggest that mammalian mesopredators have become more prevalent across European landscapes in the last 40 years (Deinet *et al.* 2013, Newton 2017, Roos *et al.* 2018). These are typically generalist species, enabling them to exploit human-modified landscapes, often to the detriment of more specialised prey species such as ground-nesting birds (Roos *et al.* 2018). Reducing the impact of predation on threatened prey species is an ongoing conservation challenge, with successes largely being confined to islands, where projects can eradicate populations of destructive non-native species without continued immigration from surrounding landscapes (Oppel *et al.* 2011, Russell *et al.* 2016), and nature reserves where land-use can more easily accommodate tools such as predator-exclusion fencing (e.g. Malpas *et al.* 2013, Verhoeven *et al.* 2022). However, as yet, a strategy that consistently, sustainably and legally reduces the impact of mesopredators at a landscape-scale has not been developed. The challenges associated with managing predators of ground-nesting birds were addressed in a workshop held during this PhD, the findings of which were published and are presented as an appendix to this thesis (Laidlaw *et al.* 2021).

Currently, design and delivery of effective actions to manage predator populations is constrained by limited understanding of their distribution, demography, movement ecology and population dynamics (e.g. Glen & Dickman 2005). Mesopredators are often nocturnal and elusive, and their ecology can be complex and non-intuitive (Glen & Dickman 2005). This complexity has major implications for the management of such species to reduce their impact on threatened populations, as removal or exclusion of mesopredators can potentially have unintended consequences for other predator species, and for the threatened populations being protected. For example, localised removal of feral ferrets *Mustela furo* to protect an important seabird population led to enhanced survival of juvenile ferrets and subsequent increases in ferret populations (Bodey *et al.* 2011a). Similarly, removal of domestic cats from a New Zealand island reserve initially resulted in increased rat abundance and a subsequent decrease in breeding success of Cook’s petrel *Pterodroma cookie* (Rayner *et al.* 2007). Finally, and more counter-intuitively, common ravens *Corvus corax* ranged more widely and predated artificial nests more rapidly after removal of the comparatively smaller hooded crow *Corvus cornix* (Bodey *et al.* 2009). These examples emphasise the importance of considering ecosystem-wide effects of predator management and highlight the complexity of attempting to manage one element (generalist mammalian predators) of complex food webs.

More research is urgently required to improve understanding of predator-prey systems and how management actions can be used effectively to manipulate encounter rates between predators and threatened prey species. For ground-nesting waders in Europe, particular attention should be given to the red fox *Vulpes vulpes*, which is widely considered as the major predator of nests in the region (Macdonald & Bolton 2008). In addition, further studies to quantify the contribution of different predator species to wader chick mortality are needed, as most studies consider only nest predator impacts and associated actions. Identifying chick predators is challenging (despite highly intensive monitoring of curlew broods during our study (Chapter 3), no predation events were observed), but studies could take advantage of the increased miniaturisation of tracking devices to collect the high-resolution data of chicks needed to identify where and when predation events occur.

Ultimately, limiting the impact of mesopredators on widespread species such as curlew will be challenging, particularly in highly anthropomorphised landscapes, such as Breckland, and deploying effective strategies to do this at the appropriate scales is likely to be a long and complex process, involving partnership working with many different land-owners. To prevent extirpations in the short-term, more immediate, emergency measures may be required.

The importance of grasslands for lowland-breeding curlew

Actions to boost threatened wader populations in Europe have generally achieved most successful outcomes in nature reserves (Smart *et al.* 2014, Franks *et al.* 2018, Jellesmark *et al.* 2021). As wader populations have become increasingly threatened by nest and chick predation, the breeding range of many species has contracted into these protected areas, where land can be managed to create attractive conditions for breeding (Silva-Monteiro *et al.* 2021). In contrast, most breeding curlew occur outwith reserves, in areas managed for agriculture but, despite low levels of productivity being reported in most areas, some higher density breeding sites still persist (Ewing *et al.* 2022).

In Breckland, we found most curlew to be breeding at very low densities across a range of different habitats and conditions, but two grassland sites still host densities comparable to those supported in the UK uplands (Chapter 2; Baines *et al*. 2022). The first site is a ~2 km^2 area of grass-heath managed by a private estate primarily for deer stalking, but also as part of an estate-wide land sparing policy. This site hosted a density of 3.3 pairs per km^2 but, of 42 curlew nests monitored at this site over four years, only 18 hatched and only four chicks fledged successfully (Chapter 2, 3). The second site is an RAF base, used primarily for training new recruits and logistics. This site (~3 km^2) hosts potentially the highest density of breeding curlew in the southern lowlands of England, with a minimum of 7.4 breeding pairs per km^2 (Chapter 2). However, breeding productivity here was also low, with only 22/70 monitored nests hatching across four years, from which only 10 chicks fledged (Chapter 2, 3).

These two sites potentially represent a unique opportunity to maintain and enhance the Breckland curlew population by deploying actions at only two sites, rather than at sites across the region which would be far more logistically challenging. In chapter 5, simulations suggested that the most efficient means of achieving sustainable levels of breeding productivity were likely to involve a combination of vegetation management (maintenance or provision of cover vegetation) and permanent predator-exclusion fencing, with only ~21.5% of the population requiring such management to reach sustainable levels. Currently, ~36 pairs of curlew breed across these two sites, equating to around 24% of the estimated curlew population in Breckland (~150 pairs). Fencing and maintaining or encouraging cover vegetation at these two sites could thus be an effective means of enhancing curlew productivity in Breckland. If such actions were deployed and were successful at improving breeding productivity, these sites could potentially act as source populations, supplementing losses in the wider Breckland population where curlew likely breed at too low a density to be managed efficiently and effectively (Ewing *et al.* 2022).

These two sites also demonstrate the importance of integrating demographic data alongside occurrence data when targeting and prioritising conservation actions (Chapter 4). Using occurrence data alone might suggest that these sites only require protection to maintain current conditions (Chapter 4). However, integrating demographic data into this type of decision-making highlights the additional need for actions to boost productivity, as current levels appear to be too low to allow these populations to persist in the long term.

It remains to be seen how many other sites support high densities of breeding curlew in the southern lowlands of England, but it is likely that these will be hard to detect using citizen-based surveys. Curlew are a highly mobile species during the breeding season (Bowgen *et al.* 2022) and are also very secretive, particularly when laying and incubating eggs. For example, prior to the start of this PhD, BTO BirdTrack data suggested a maximum of five breeding pairs at RAF Honington, subsequent intensive field monitoring revealed the current population to be 25 – 30 pairs.

The vast majority of curlew in Breckland breed on the few remaining large areas of grassland, and even the few pairs that nest on arable crops do so in the fields adjacent to grasslands (Chapter 4). However, semi-natural grasslands are an increasingly scarce habitat across the UK as many have been lost to development or intensification of agricultural (Vickery *et al.* 2001, Ridding *et al.* 2015). Much of the remaining semi-natural grassland in the UK is privately owned (Ridding *et al.* 2015) and, although some of these sites are covered by standardised citizen science schemes such as the BTO Breeding Bird Survey, few will be monitored at the intensity required to accurately estimate numbers of breeding curlew and some will not be surveyed at all owing to restricted public access.

Collaborating for curlew

One of the UK's largest landowners is the Ministry of Defence (MOD), managing ~1.4% of the country's land area, including some of the largest remaining semi-natural dry grasslands in western Europe and large numbers of grassland airfields (MOD 2009). Although only a few of these sites are subject to biodiversity monitoring, the presence of breeding curlew on many of these sites is becoming increasingly clear and, on active airfields, has led to conflict between conservation of this threatened species and air safety (Natural England 2022).

Curlew are considered to be at high risk of striking aircrafts and, while the MOD have a duty of care to the wildlife supported on their sites, air safety is prioritised. Consequently, under license, adult curlew can be shot if they pose in imminent threat to aircraft and large numbers of nests are destroyed each year in an attempt to reduce curlew activity on bases (Natural England 2022). To mitigate these actions, headstarting projects have recently been established, whereby eggs laid on RAF bases that are due to be destroyed are instead removed, reared in captivity and released at the point of fledging.

Headstarting is an increasingly well-recognised tool that can be used to boost the breeding productivity of highly threatened wader populations (Pain *et al.* 2018). In most cases, headstarting is a last resort, used primarily when a population reaches a critical level at which it would go extinct before levels of breeding productivity can be boosted sufficiently in the wild (Ross *et al.* 2021, Wijewardena *et al.* 2023). The curlew headstarting project is primarily a way to mitigate conflict with RAF bases, but also provides a unique opportunity to answer some important questions about curlew biology relevant to the species' conservation, and to explore whether release of headstarted juveniles can be used as a tool to encourage colonisation of new breeding sites in areas where conditions can be more easily managed.

Currently, headstarted curlew are being released at a range of sites and their subsequent movements are tracked through a mix of GPS-tagging, radio-tracking and surveys for colour-ringed individuals. The findings from these studies should help to identify factors influencing the recruitment of juveniles into breeding locations, and thus to inform future headstarting releases. For example, it is possible that recruitment rates may vary between release sites with and without established breeding curlew populations, as recruitment may be linked to conspecific social cues (Gill 2019). Proximity to the coast could also influence recruitment, with juveniles potentially joining passage or overwintering birds on migration to other breeding sites (Gill *et al.* 2019), and environmental conditions at release sites could also influence recruitment and subsequent likelihood of successful breeding (e.g. Laidlaw *et al.* 2015, Kaasiku *et al.* 2022)

More research is required to fully understand the importance of RAF bases to the UK curlew population, particularly in the lowlands, and whether the current management of curlew on these sites (headstarting) is having the desired effect (reduced risk of bird strike). If other bases in southern England also support high densities of breeding curlew, particularly if they have low levels of air traffic, it might be possible to target conservation actions in these sites to further mitigate the impact of nest destruction on more active bases, which might be a more cost-effective option and attractive for the MOD in the long-term. Currently, there are very few NGO-run sites that support breeding curlew in lowland England and thus opportunities to protect existing populations are limited.

Field trials

To inform the deployment of appropriate and adequate, curlew-specific agri-environment prescriptions in farmed landscapes, and conservation approaches in non-agricultural settings (e.g., airfields), interventions need to be robustly trialed across the range of landscapes in which curlew breed in the UK.

Field trials of predator-exclusion fencing over different temporal (permanent or temporary) and spatial scales (nest-, field- or site-level) should be prioritised due to the potential of this tool to boost the hatching rate and overall breeding productivity (e.g., Rickenbach *et al*. 2011, Smith *et al*. 2011, Malpas *et al*. 2013, Verhoeven *et al*. 2022). Fencing should be trialed experimentally in landscapes with and without vegetation structure promoting chick survival (Chapter 3 and 5), and in combination with lethal mammalian predator control within larger fenced areas.

During fieldwork, grassland patches of as little as 1.5 ha were observed being used to successfully rear chicks in arable-dominated areas of Breckland however, it is unclear whether this patch size would be sufficient to encourage recruiting curlew pairs to breed within arable-dominated landscapes in which demographic successes are slightly more common (Chapter 4). Additional field trials could be designed whereby grassland patches of varying sizes (1 – 100 ha) and suitably heterogeneous vegetation structure are created within arable-dominated areas to identify the area of grassland required to encourage additional recruitment into these areas.

Remaining knowledge gaps

This project has primarily focused on the curlew population breeding in Breckland, a lowland area of eastern England. One of the main reasons for targeting effort in this region was that information from successive Breeding Bird Atlases (Balmer *et al.* 2013) suggested that the population was stable or possibly growing slowly. Focusing research efforts in areas in which threatened populations are not (yet) in decline can potentially help to identity the conditions promoting such trends, which can then be used to inform management. However, our findings suggest that productivity in Breckland is low, despite the apparent population stability.

This project has also been conducted over four years, a relatively short period over which to study a long-lived species which may only require very occasional successful breeding seasons to maintain population stability. Long-term monitoring is required for threatened curlew populations to fully understand annual variation in demographic rates and the conditions influencing such variation. Alternatively, a good year now might represent what an average year constituted during periods of population stability or growth, and populations may only be persisting in Breckland because of adult longevity. Rapid declines could therefore be on the horizon as adults senesce or die, increasing the urgency for immediate deployment of actions.

Finland hosts the second largest curlew population in Europe. As the Finnish population is thought to be stable and the majority of birds breed in lowland areas (Brown 2015), this could potentially provide a good opportunity to identify the conditions promoting population stability or growth in lowland breeding curlew, which could be used to inform management of more threatened populations in the UK. Greater attention should also be given to strategies aimed at reducing the impact of afforestation in the UK uplands, which hosts over 85% of the UK breeding population (Brown 2015). Afforestation can have substantial, negative effects on breeding wader populations (e.g. Kaasiku *et al.* 2022, Pálsdóttir *et al.* 2022) and is likely to be the greatest emerging threat facing curlew in the UK.

Curlew are a very well-loved species in the UK, and using this to our advantage will be key in gaining the support of important stakeholders, such as the RAF and owners of other large estates with areas of open grassland. Curlew have the potential to act as a flagship species for grassland management in the UK, and conservation of such habitats needs to be prioritised in order to restore curlew populations.

Finally, integrated, evidence-based actions are required to maintain and restore curlew populations and ultimately save this iconic but increasingly threatened species from extinction. To deliver these actions, we need a robust agenda for action that mobilises large-scale, multistakeholder nature recovery, narrows the disconnect between actions to conserve nature and actions leading to loss of nature, and complements and generates further support from both the public and private sectors (Sutherland *et al.* 2004, Strassburg *et al.* 2020, Milner-Gulland *et al.* 2021, Pettorelli *et al.* 2021, Leadley *et al.* 2022, Chan *et al.* 2023).

Appendix 1

Predator management for breeding waders: a review of current evidence and priority knowledge gaps

Predator management for breeding waders: a review of current evidence and priority knowledge gaps

Rebecca A. Laidlaw[1*], Jennifer Smart[1,2], Harry Ewing[1], Samantha E. Franks[3], Heinrich Belting[4], Lynda Donaldson[5], Geoff M. Hilton[5], Nicola Hiscock[5], Andrew N. Hoodless[6], Baz Hughes[5], Nigel S. Jarrett[5], Rosemarie Kentie[7,8], Erik Kleyheeg[9], Rebecca Lee[5], Maja Roodbergen[9], Dawn M. Scott[10], Mike J. Short[6], Evgeny E. Syroechkovskiy[11], Wolf Teunissen[9], Hannah Ward[12], Graham White[13] & Jennifer A. Gill[1]

[1]School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich, UK

[2] Royal Society for the Protection of Birds, RSPB England, Stalham House, 65 Thorpe Rd, Norwich, UK

[3]British Trust for Ornithology, The Nunnery, Thetford, UK

[4]NLWKN - Betriebsstellen Brake-Oldenburg und Hannover-Hildesheim, Germany

[5]Wildfowl & Wetlands Trust, Slimbridge, Gloucester, UK

[6]Game & Wildlife Conservation Trust, Fordingbridge, Hampshire, UK

[7]Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Utrecht University, Texel, The Netherlands

[8]Theoretical and Computational Ecology, IBED, University of Amsterdam, Science Park 904, 1090GE, Amsterdam, The Netherlands

[9]Sovon Dutch Centre for Field Ornithology, Nijmegen, The Netherlands

[10]School of Life Sciences, Keele University, Keele, UK

[11]BirdsRussia, Moscow, Russia

[12]Centre for Conservation Science, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, UK

[13] Royal Society for the Protection of Birds, The Lodge, Sandy,, UK

The design and delivery of the workshop from which the data used in this paper were collected and the writing of the manuscript were led by RAL, HE, SEF, ANH, JS & JAG, with additional contributions from other co-authors.

Published in *Wader Study*, April 2021, 128: 44-55

Abstract

Rapid declines in breeding wader populations across the world have prompted the development of a series of conservation tools, many of which are designed to influence productivity. Across western Europe, efforts to reverse population declines are typically limited by high levels of nest and chick predation and, managing this predator impact has been a major research focus in the last two decades. A workshop held at the 2019 International Wader Study Group conference aimed to synthesise current understanding of predator management tools and to use expert knowledge to identify and prioritise important knowledge gaps in this area. Here we review the four predator management tools that were described (predator diversion, exclusion, lethal control and headstarting), together with insights into the potential responses of mammalian predators to these management tools. The expert assessment of important areas for future work highlighted the need to increase our knowledge of predators and their responses to management interventions; to ensure our science connects to policy, practitioners and members of the public; and the need for clear and consistent goals for the future of breeding wader populations to inform the development and deployment of these management tools.

Introduction

Across western Europe, widespread drainage and agricultural intensification have driven declines in wetland biodiversity, and breeding wader populations have been a particularly prominent casualty of these processes (Wilson *et al.* 2004, Smart *et al.* 2008). Once common and widespread, breeding wader populations are increasingly confined to nature reserves (Smart *et al.* 2006), and have continued to decline despite the creation and management of conditions suitable for breeding in nature reserves and, through agri-environment schemes, in the wider countryside (O'Brien & Wilson 2011, Smart *et al.* 2014). The life history of waders is generally characterised by low fecundity and high adult survival but, while variation in survival rates contributes greatly to population dynamics, manipulating survival is rarely feasible. By contrast, management to enhance productivity is common, with the ultimate goal of increasing numbers of breeding individuals. One of the primary reasons associated with the failure of declining wader populations to recover is unsustainably high levels of nest and chick predation, and consequent low levels of recruitment into breeding populations (MacDonald & Bolton 2008a, Laidlaw *et al.* 2017, Kentie *et al.* 2018). There is evidence that nest predation rates have increased in recent decades (Roodbergen *et al.* 2012), and a recent review of predator impacts on bird populations found that waders were commonly limited by predation (Roos *et al.* 2018). The predators of wader eggs and chicks are typically generalist mammalian and avian predators and, consequently, managing their impacts on specific populations (which may comprise only a small part of their diet) is challenging. In addition, several of the avian predators that can be important predators of wader chicks (Mason *et al.* 2018) are themselves of protected conservation status (especially raptors). A series of different conservation tools have been used to try to reduce predator impacts on breeding waders (e.g. see Colwell (2019) for *Charadrius* Plover examples). The aim of a recent predator management workshop held during the 2019 International Wader Study Group (IWSG) conference was to synthesise current understanding of the deployment and effectiveness of a selection of these tools, and to identify and prioritise knowledge gaps that need to be addressed.

The predator management tools considered at the workshop included (1) diversionary techniques, which aim to reduce levels of nest and chick predation by altering the relative attractiveness of the landscape or resource base; (2) exclusion techniques, which aim to create barriers between predators and nesting waders; and (3) lethal control techniques which aim to reduce local predator abundance. Our understanding of these tools are summarised below, together with details of their design and deployment. Studies of these tools have focussed almost entirely on their effectiveness at reducing predation levels, and very little attention has been paid to how predators might respond to the use of these tools. Consequently, this issue is also considered below. Finally, a more recently developed emergency intervention tool for increasing hatching, fledging and recruitment rates is headstarting, which involves removing eggs and rearing chicks in captivity through the period of greatest vulnerability to predation. This technique is also described.

Attendees at the workshop spanned a broad range of stakeholders in breeding wader conservation, and included researchers, landowners, conservationists and representatives of organisations involved in the development of conservation policy. Following presentations on each of four predator management techniques, attendee discussion was used to identify knowledge gaps and the long-list of questions resulting from this process was subsequently reduced to 12 through round-table discussion by the plenaries. Attendees were then asked to rank each of the 12 short-listed questions on three criteria; urgency, importance and feasibility (Table 1). The resulting scores (numbers of attendees ranking high, medium or low for each criterion applied to each question) were then synthesised and discussed. Here we present (i) reviews of the evidence for the effectiveness of each of the predator management techniques, including potential implications for the responses of mammalian predators to these activities, and (ii) for each identified question, the outcome of the scoring of criteria and the main points arising from the discussion of these issues.

Table 1: Table showing the criteria for being prioritised as high, medium or low priority for the different classifications of urgency, importance and feasibility. Feasibility included a range of attributes: whether there was existing data availability (need for additional empirical studies), the logistics, cost, scale and time requirements and also the legal constraints (licensing requirements etc.).

	Urgency	**Importance**	**Feasibility**
High	Likely to require swift action	Has potential to greatly influence outcomes of interventions, or alter current practices	Relevant data exist or could be easily gathered (low cost / time / logistic requirements), with few / no legal constraints
Medium	May require swift action in some or all aspects	May influence some or all aspects of outcomes of interventions, or alter some or all current practices	Some relevant data exist and / or could be gathered but some logistic or legal aspects likely to be complex / challenging
Low	Unlikely to require swift action	Unlikely to greatly influence outcomes of interventions or current practices	Relevant data not available and gathering those data would be complex / challenging

1. Predator Diversion

Managing breeding wader habitat

Strategic habitat management in landscapes that support breeding waders is likely to influence how predators interact with waders and other prey. Relatively simple forms of strategic habitat management aim to reduce accessibility of sites to predators, availability of predator breeding locations (e.g. trees, dry banks or reedbeds) and/or opportunities for predators to hunt effectively (e.g. through removal of perches for avian predators).

Landscape-scale habitat management can potentially be used to influence the impact of predators on breeding waders. In Dutch grasslands, numbers of breeding black-tailed godwits *Limosa limosa limosa* are declining rapidly (Kentie *et al.* 2016, Roodbergen & Teunissen 2019), and densities increase along a gradient of land-use intensity from herb-poor meadows and grassland monocultures to herb-rich meadows (Groen *et al.* 2012), with important habitat-specific differences in demographic rates. black-tailed godwits breeding in monocultures tend to experience lower nest survival (Kentie *et al.* 2015) and lower survival of chicks, possibly due to a combination of low food availability and higher predation rate (Kentie *et al.* 2013), compared to herb-rich meadows where population growth rates can be positive (Kentie *et al.* 2018). In this example, landscape-scale variation in land-use intensity is having population-level effects through complex interactions between management, predation and breeding success, and strategic management of landscape structure could potentially be used to alter these relationships. Similar processes also operate in other species and study systems. For example, the abundance of wet features positively influences the breeding density of some wader species on wet grasslands (e.g. Smart *et al.* 2006, Eglington *et al.* 2008) with important density-dependent reductions in predation rates of nests and chicks (MacDonald & Bolton 2008b, Eglington *et al.* 2009, Laidlaw *et al.* 2017). Reducing the accessibility of wader breeding areas, for example by surrounding them with water, may deter some mammalian predators, although both European badgers *Meles meles* (hereafter, badgers) and foxes can and do swim, if necessary.

Managing non-wader prey

The availability of small mammal prey in wader landscapes could also have important implications for the generalist predators that prey on small mammals and waders (e.g. foxes, stoats *Mustela erminea*, weasels *M. nivalis* and raptors), so understanding how management influences small mammal distribution is important. For example, the presence and activity of common voles *Microtus arvalis* can vary across grazing regimes, and grazing management can be used to manipulate vole presence (Lagendijk *et al.* 2019). There is also a need to understand the influence of agricultural activities on the availability of key resources for predators (Pringle *et al.* 2019).

Wet grasslands managed for waders are generally unsuitable for small mammals (too short and wet), which mostly occur in the taller and denser vegetation of verges outside of grazed fields (Laidlaw *et al.* 2013). Northern lapwing *Vanellus vanellus* (hereafter lapwing) nest predation rates have been shown to be lower on wet grassland fields with more surrounding verge habitat (Laidlaw *et al.* 2015), and the magnitude of this effect is such that increasing the amount of verge in wet grassland landscapes could, in theory, reduce nest predation rates by up to ~20%, but only in areas with high lapwing nesting densities (Laidlaw *et al.* 2017). Managing habitat to benefit the non-wader prey of key predators could therefore have implications for wader demography.

Potential predator responses to diversion techniques

In the case of raptors, which are species of conservation importance protected by law but important predators of wader chicks (Mason *et al.* 2018), diversionary techniques to reduce their impact may be most appropriate, particularly when raptor predation pressure is localised and substantial. In these situations, providing diversionary food directly to focal raptors during the breeding season, with the aim of reducing their need to hunt, has been shown to significantly reduce predation rates on chicks (e.g. red kites *Milvus milvus* predating Lapwings: RSPB unpublished data; kestrels *Falco tinnunculus* predating little terns *Sternula albifrons*: Smart & Amar 2018). There are other potential methods for diverting avian predators away from important breeding areas. For example, laser-hazing involves directing a laser beam at the body of the predator to dissuade them from hunting, but trials of the efficacy of this method (at tern colonies) have thus far been inconclusive because it has proven difficult to haze a sufficiently large proportion of predators, and there appear to be inconsistent effects of hazing on predation attempts and success (RSPB unpublished data).

In the case of mammalian predators, the cover provided by shrubs and trees, and the availability of suitable areas for breeding (e.g. subterranean earths for foxes) can be very important, and removal of these features could potentially divert them away from wader breeding areas. However, the area over which such features may have to be removed could be extensive and, may therefore not be financially or practically feasible. Reducing the attractiveness to predators of wader breeding areas through, for example, provision of alternative high quality and accessible foraging habitats could, in theory, encourage predators to focus their activity away from wader breeding areas (Mukherjee *et al.* 2009), but predator dissuasion is likely to depend on predator abundance and the spatial and temporal distribution of resources.

Manipulating habitats to enhance small mammal populations could have the unintended effect of allowing the area to support higher densities of predators due to an increase in prey abundance, and changes in the availability of key prey species could influence mammalian predator responses to diversion techniques. For example, rabbits *Oryctolagus cuniculus* and small mammals are a key component of the diet of rural foxes (Soe *et al.* 2017), and rabbit populations have declined across Europe (Smith & Boyer 2007); in the UK, a 62% decline has been reported between 1996 and 2017 (Harris *et al.* 2019), in part linked to the recent occurrence of Rabbit Haemorrhagic Disease (RHD). Blanco-Aguiar *et al.* (2012) documented an avian predatory switch from rabbits to gamebirds as a consequence of rabbit declines from RHD in Spain. Additionally, water voles *Arvicola amphibius*, a wetland vole species which are likely to have been alternative prey for foxes foraging in wetland habitats (Short & Porteus 2018), have seen dramatic declines in distribution and numbers in the UK (90% decline since 1970's; Jefferies *et al.* 2003). It is unknown if current mammalian prey declines are causing shifts in the diet of predators towards breeding waders.

While there has been considerable research into some aspects of predator diversion tools there are still several important questions that need to be addressed. Key knowledge gaps include the behavioural and demographic responses of predators to the deployment of these tools, especially increased provision of non-wader prey, the potential for predator dietary shifts in relation to changes in prey availability, and the scale of deployment of habitat management, diversionary feeding, or predator dissuasion that would be required to achieve local population growth of waders.

2. Predator exclusion

Over the last two decades, the potential for predator fencing to improve wader breeding success by excluding mammalian predators (particularly foxes and badgers) from nesting areas has been widely explored. A variety of fence types and designs have been employed, to address a wide range of contexts. In particular, fences can be designed to operate at different spatial and temporal scales. Spatially, fences to exclude large mammalian predators can be deployed from individual nests up to whole sites, and temporally, deployment can range from temporary (e.g. covering only the period when nests are active) to seasonal (e.g. covering some or all of the breeding season) to permanent (Fig.1). In addition, fences can operate through electrification or by creating a physical barrier that is impenetrable to the larger mammalian predators of nests and chicks. Nest enclosures (i.e. physical barriers to predators placed directly over nests) can enhance hatching success, but nest abandonment and predation of incubating adults have also been recorded (Isaksson *et al.* 2007, Barber *et al.* 2010), and so the overall benefit of this management approach remains unclear.

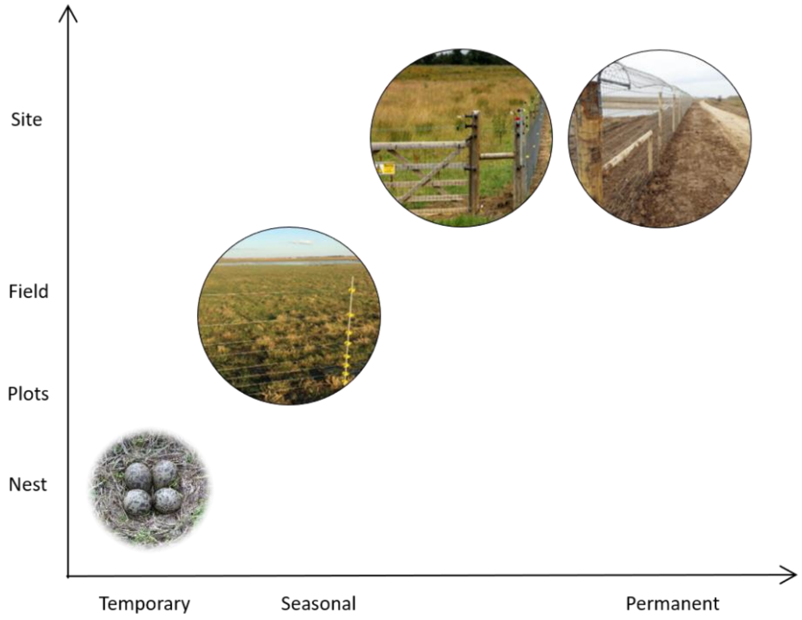


Figure 1: Plot showing relative spatial and temporal scales for the different fence types. Photos of combination and barrier fences from (White & Hirons 2019).

Temporary fencing at smaller spatial scales (individual nests to fields) tends to involve electrified fences that are easy to construct and move around (e.g. stranded wire livestock fences) while permanent, site-scale fencing tends to involve barrier fencing, which can be of sufficient height and/or buried depth to exclude mammals capable of jumping and/or digging, or existing permanent livestock fences can be electrified (the latter are often termed ‘combination’ fences). Combination fences provide both a physical and an electric barrier and are commonly used in conservation settings. Further details on fencing design, installation and maintenance together with the advantages and disadvantages of different fence types can be found in the detailed guidance produced by the RSPB (White & Hirons 2019). In general, temporary electrified fences are relatively cheap and easy to deploy but require reliable electricity supplies (mains or battery, potentially with solar panel charging) and regular monitoring, and batteries can drain rapidly if vegetation is not kept sufficiently short to avoid contact with the fences. By contrast, permanent barrier or combination fences are generally more durable and easier to maintain but are also more expensive to construct and can restrict movements of non-target species. Fence designs have developed greatly in recent years and following the most recent guidelines closely is likely to be extremely important. In addition, ongoing maintenance and management of all fence types is essential to ensure that an effective barrier is maintained.

Several studies have explored the effectiveness of fences at excluding mammalian nest predators, typically by comparing either fenced and unfenced areas, or comparing areas before and after fence deployment. These studies typically report substantial improvements in hatching success inside fences for all scales and types of fences, with hatching success rates of around 80% being regularly reported in fenced areas (Maslo & Lockwood 2009, Rickenbach *et al.* 2011, Malpas *et al.* 2013). Consequently, fencing has rapidly become a key component of breeding wader conservation actions across western Europe. Fences do not exclude avian predators and smaller mammalian predators (e.g. mustelids) and so the consistently high hatching success achieved within fences supports the previous evidence that larger mammals are responsible for the majority of wader nest predation in these areas. A much larger range of predators (including avian predators) can be responsible for chick predation. Fences do not exclude many of these chick predators and the precocial chicks of waders can leave fenced areas, but the evidence to-date suggests that the increase in hatching success achieved with fencing can translate into high levels of fledging (Rickenbach *et al.* 2011, Malpas *et al.* 2013), although this is not always the case (Hoodless & MacDonald 2016).

While a great deal of trialling and testing of predator-exclusion fencing has been conducted, and while there is strong evidence of the effectiveness of fences as a nest protection tool, several important questions have yet to be addressed. These include the capacity of fences to facilitate breeding wader population recovery, the deployment strategies that could deliver such a goal and the extent to which fences need to be deployed in combination with other predator management techniques (e.g. lethal predator control to reduce predator pressure and/or predator diversion techniques to avoid high levels of chick predation).

Potential predator responses to exclusion

Fencing is one of the most effective exclusion interventions for mammalian predators (Khorozyan & Waltert 2019), but it’s effectiveness could potentially be improved by being used in combination with predator dissuasive tools, e.g. acoustic (high pitched sounds), visual (e.g. flashing lights) or chemical (scent based), that aim to deter predators by overwhelming their senses. The success of these deterrents is typically context-dependent, and over-exposure can sometimes lead to habituation (Khorozyan & Waltert 2019), and the effects of such deterrents on breeding waders is unknown. Temporary fencing could potentially exclude mammalian predators from areas which were previously part of a home range, which could result in range shifts and increased between-group aggression, reductions in body condition and survival and increases in stress and disease occurrence (Williamson & Williamson 1984). If the patch excluded is large and/or high quality this could result in tenacity to penetrate the barrier. For some terrestrial predators, persistence can result in individuals assessing fences for weak spots where fences can be breached. Fencing without consideration of the quality and extent of the remaining landscape for predator use may therefore increase risks of fence breaches.

3. Predator exclusion

The concept of increasing wader productivity and population size through lethal control of predators stems from wild gamebird management, where culling of predators is regarded as fundamental, alongside the provision of nesting and brood-rearing cover (Potts 1980). Control typically involves the removal of foxes and corvids from the area where waders breed, and often from a buffer strip of 500-1,000 m surrounding this core area. It may also involve control of small native mustelids (stoat and weasel) or the invasive American mink *Neovison vison* which, as an exotic predator, potentially renders evolved defence mechanisms of waders less effective. Methods and seasonal timing of control vary between countries owing to differences in national and regional legislation. Methods used include day/night shooting and various live-capture traps and neck-snares for foxes, shooting and cage-trapping for corvids, and killing or live-capture traps for mustelids. During the last five years, night vision and thermal-imaging rifle-scopes have become more widely used and have started to replace traditional spotlighting for fox control (GWCT, unpublished data). These new technologies, in combination with the use of trail cameras to detect predator presence and trap alarm systems, have generally led to improved efficiency of predator control.

When implemented at the landscape level, lethal control can result in local and regional predator suppression (Heydon *et al.* 2000, Heydon & Reynolds 2000a, b, Porteus *et al.* 2019). Lethal control has been shown to be effective at increasing breeding productivity of several wader species above the level required for stable populations in different countries and situations (Niemczynowicz *et al.* 2017). In the UK uplands, for example, experimental control of foxes, corvids and small mustelids resulted in an average threefold increase in the breeding success of lapwing, golden plover *Pluvialis apricaria* and curlew *Numenius* *arquata*. Importantly, greater breeding success translated into increases in breeding numbers (≥ 14% per annum) for these three species, compared to ongoing declines in numbers (≥ 17% per annum) in the absence of predator control, although no effect was recorded for snipe *Gallinago gallinago* (Fletcher *et al.* 2010). Large-scale surveys indicate that predator control on grouse moors in the UK uplands leads to higher breeding wader densities than on moorland with no predator control, and increases in wader populations have been documented following the reinstatement of predator control (Tharme *et al.* 2001, Littlewood *et al.* 2019, Ludwig *et al.* 2019).

On lowland wet grassland at the Dümmer reserve, NW Germany, black-tailed godwit fledging success during six years of fox control averaged 0.83 chick/pair (n = 136 pairs), compared to 0.27 chick/pair (n = 62 pairs) over seven years without fox control (Belting pers. comm.). Across Lower Saxony, monitoring of 2,537 pairs of black-tailed godwit over 14 sites during 2012-2017 revealed fledging success greater than 0.7 chick/pair only at the four sites, supporting 853 pairs, where efficient fox control was undertaken (Belting pers. comm.). However, an effect of predator control is not always apparent (Bodey *et al.* 2011b). In an eight-year experiment across 11 nature reserves, (Bolton *et al.* 2007) found that reducing fox and carrion crow *Corvus corone* numbers had no overall effect on lapwing nest survival rates or population trends, although twice as many pairs fledged young at six sites during periods of predator control. In addition, reductions in nest survival in the presence of predator control were apparent when controlling for the background density of foxes and carrion crows, indicating that the impact of predator control on nest survival rates may vary depending on the density of predators present at that time (Bolton *et al.* 2007) .

Several meta-analyses of the effect of lethal control on bird populations, all including studies on breeding waders and other ground-nesting birds, have concluded that the average overall effect is positive but that there is great variation in effect sizes among species and locations (Côté & Sutherland 1997, Holt *et al.* 2008, Smith *et al.* 2010). There are many possible causes for these variable responses to predator removal, including annual variation in the abundance of predators or alternative prey, abiotic factors, such as poor weather at hatching or catastrophic losses due to flooding, an impact from other predators which have not been targeted, density-dependent effects, individual variation in predator behaviour, or inefficient predator control.

Lethal control is the most emotive and controversial of the conservation tools for increasing wader productivity but may be the only feasible option in certain landscapes and for species which breed at low density and whose broods wander over large areas. For instance, exclusion fencing is largely impractical for lapwings nesting in arable fields and for curlews in upland areas, whereas lethal control has the advantage that it affords protection to both nests and chicks. In situations where a wader population is critically low, lethal control can buy time to address habitat issues and, if conducted efficiently at a large enough scale, it might reduce the predation problem at the landscape scale (Heydon *et al.* 2000). The need for lethal control also needs to be clearly explained, to maintain support for a recovery project. Disadvantages are that it requires competent practitioners following best practice and, even then, some methods risk the capture of non-target species. The outcome of lethal control in a given location is difficult to predict, and there is a risk that by removing foxes and corvids, predation by species that are protected (e.g. badger, buzzard *Buteo buteo*) or more difficult to control (e.g. stoat) increases. It is therefore essential to undertake adequate monitoring of predation rates, to avoid unintended consequences such as compensatory predation (Dion *et al.* 1999).

Monitoring before, during and after deployment of lethal control is important to check that predation is the main cause of low wader productivity, to identify the predator species responsible, and then to ensure that lethal control results in the desired outcome. In some cases, the main predator may be a legally protected species and alternative management tools will have to be considered. If lethal control is identified as a necessary tool to boost a wader population, clear aims should be defined at the outset, encompassing the methods to be used, scale, timeframe, cost and method of measuring the outcome. Where legislation permits, control leading up to and during the wader breeding period (January-July) is considered most appropriate as the aim should be seasonal predator suppression rather than local eradication. In the study by (Fletcher *et al.* 2010), for example, the increase in wader numbers was achieved with a 43% reduction in spring fox numbers and a 78% reduction in carrion crows. Implementation of lethal control must be legal, proportionate and, because it is controversial, with the potential for detrimental impact on a project or conservation organisation, justifiable. Collection of data on wader productivity, predator density and numbers of predators killed is, therefore, essential so that the approach taken can be evaluated and justified. For example, while the RSPB considers fox control to be important on some of its key breeding wader reserves, it has a policy of ensuring that practitioners must ensure no orphaning of dependent cubs. Monitoring on its reserves during 2012-2018 showed that annual lapwing productivity on reserves with fox control averaged 0.78 ± 0.15 chick/pair compared with 0.47 ± 0.06 chick/pair on reserves with no fox control, which, in conjunction with the number of foxes removed, justified this approach.

Ultimately, to reduce the need for lethal control, and possibly other interventions, it is important to investigate why generalist predators occur at such high densities in the landscape and what has driven increases in their numbers, and impacts on ground-nesting birds, over the last 30-40 years. Better understanding of predator populations will inform the development of more sustainable solutions for recovery of declining wader populations in the long-term. In the short-term, the focus should be on filling knowledge gaps that will help make lethal control more efficient and effective. More studies are needed on the behaviour and detectability of predator species, including how predators use landscapes, which may enable practitioners to target their management better (Reynolds *et al.* 2004) and measure its impact. Further research is needed on the effects of controlling predators on the wider ecological community. For example, it is currently unclear whether controlling some predators, particularly foxes, results in functional or numerical responses of other mesopredators, leading to compensatory predation on wader eggs and chicks (Trewby *et al.* 2008, Ritchie & Johnson 2009). Mesopredator increases would be especially detrimental to wader populations if the new suite of predators were legally protected and/or could not be controlled effectively. Finally, it is important to understand the situations in which lethal control is most effective and when it should be combined with other techniques, such as exclusion fencing.

Potential predator responses to control

In the UK, the National Game Bag Census suggests fox numbers are relatively stable after a period of increase during 1960-early 1990s (Aebischer *et al.* 2011). Foxes are territorial with a social group that defends the territory against surrounding groups. In addition, there is often a smaller proportion of itinerant individuals that do not hold a home range but move across multiple social groups (Storm *et al.* 1976). Loss of an individual in a territorial social group through culling can affect the social unit, leading to changes in movements and territories (Ham *et al.* 2019) and potentially breeding opportunities. Dependent cubs could also perish, likely through starvation and dehydration, although there is usually a sex bias towards males during culling (Kämmerle *et al.* 2019). Lethal control can reduce social group size and thus group capacity to defend the territory, potentially creating a territory vacuum or ‘sink’ into which new individuals can move, with consequences for the level of culling likely to be required to maintain suppressed fox numbers (Porteus *et al.* 2019). In studies of badgers, culls have been shown to result in greater movement of individuals between social groups (Tuyttens *et al.* 2000). Understanding the economic costs of culling and its relative effectiveness needs to be compared to other non-lethal approaches, alongside the ethical considerations of culling one native species to protect another native species. Finally, culling one predator type can potentially lead to increases in other predators within the community, through competitor release and changes in trophic interactions (e.g. (Molsher *et al.* 2017).

4. Headstarting

Headstarting waders to increase the productivity of a wild population is a relatively new concept but this technique has been used in the amphibian, reptile and fish world for over 50 years (Huff 1989, Heppell *et al.* 1996, Fraser 2008). There are various definitions of ‘headstarting’ but of most relevance to waders is “a conservation technique in which young animals are raised artificially and subsequently released into the wild. The technique allows a greater proportion of young to reach independence, without predation or loss to other natural causes” (Alberts *et al.* 2004). Species and populations that are most suited to headstarting are those that: (i) experience high mortality during early growth stages, (ii) can be successfully raised in captivity with a high fledging rate, (iii) have relatively high survival in later life stages and are long-lived, (iv) mature quickly, (v) would be expected to recruit to the release population or area (i.e. show a degree of natal philopatry) and (vi) where the number of headstarted individuals contribute a reasonable proportion of the population size to which they are expected to recruit.

Headstarting has been used in various forms for a variety of wader species, including piping plover *Charadrius melodus* (Powell *et al.* 1997), American oystercatcher *Haematopus palliatus* (Collins *et al.* 2016), spoon-billed sandpiper *Calidris pygmaea* (Pain *et al.* 2018), black-tailed godwit and curlew. The impact of headstarting will vary depending on the size of the target population, productivity in the wild, and the ability of captive operations to increase the survival of eggs and/or chicks and release healthy birds capable of survival in the wild. Preliminary analysis suggests headstarting, often involving early removal of clutches from just 10 adult pairs per year who then go on to re-lay in the wild, may be slowing the global decline of the spoon-billed sandpiper (Clark *et al.* 2018) and is increasing the productivity of UK black-tailed godwits from 0.34 to 1.1 fledglings per pair (RSPB/WWT unpublished data). These projects both involve marking and tracking of headstarted individuals and, for both these migratory species, headstarted individuals have migrated successfully and returned to project areas to breed and have produced their own young.

While headstarting can be a powerful conservation tool, it is associated with a number of significant risks and, like other conservation methods, will only result in long-term benefits if conducted as part of a wider conservation effort that addresses the underlying cause(s) of decline. Risks include inadequate care or housing during the captive phase that results in mortality or low fitness in released birds, behavioural modifications, infectious disease, lack of imprinting on natal areas and negative impacts on the source population. Many of these risks can be successfully managed by ensuring headstarting operations (i) are conducted by experienced, multi-disciplinary teams (including animal care specialists, veterinarians, site managers and scientists), (ii) are well-planned and based on a clear conservation case determined using population modelling, and (iii) include comprehensive disease management and post-release monitoring.

The high-degree of uncertainty associated with headstarting raises many questions such as will released birds return, survive as well as their wild counter-parts, breed successfully or will their treatment in captivity affect later behaviour? The uncertainty of headstarting presents two key challenges, the first of which is good decision-making, ensuring that headstarting is undertaken in circumstances where it can be effective ,but also ensuring opportunities to benefit a population through headstarting are not missed. Taking a risk-based approach, using population modelling and completing a comprehensive feasibility assessment can aid decision-making. The second key challenge is increasing our understanding of headstarting when experiments are often not possible due to the target population being threatened, and time and resources being limited. As such, it is vital that headstarting efforts are designed as trials and learning is maximised through close monitoring and detailed reporting of the failures as well as the successes.

There are a number of guidance documents available to help manage the risks and meet the challenges associated with headstarting (Lee *et al.* 2012, IUCN/SSC 2013, National Species Reintroduction Forum 2014a, b). Fig.2 presents a set of processes that should be followed from project initiation through to monitoring outcomes (specifically marking and tracking of headstarted individuals to quantify subsequent survival and recruitment), adapted from the Scottish Code for Translocations (National Species Reintroduction Forum 2014a).

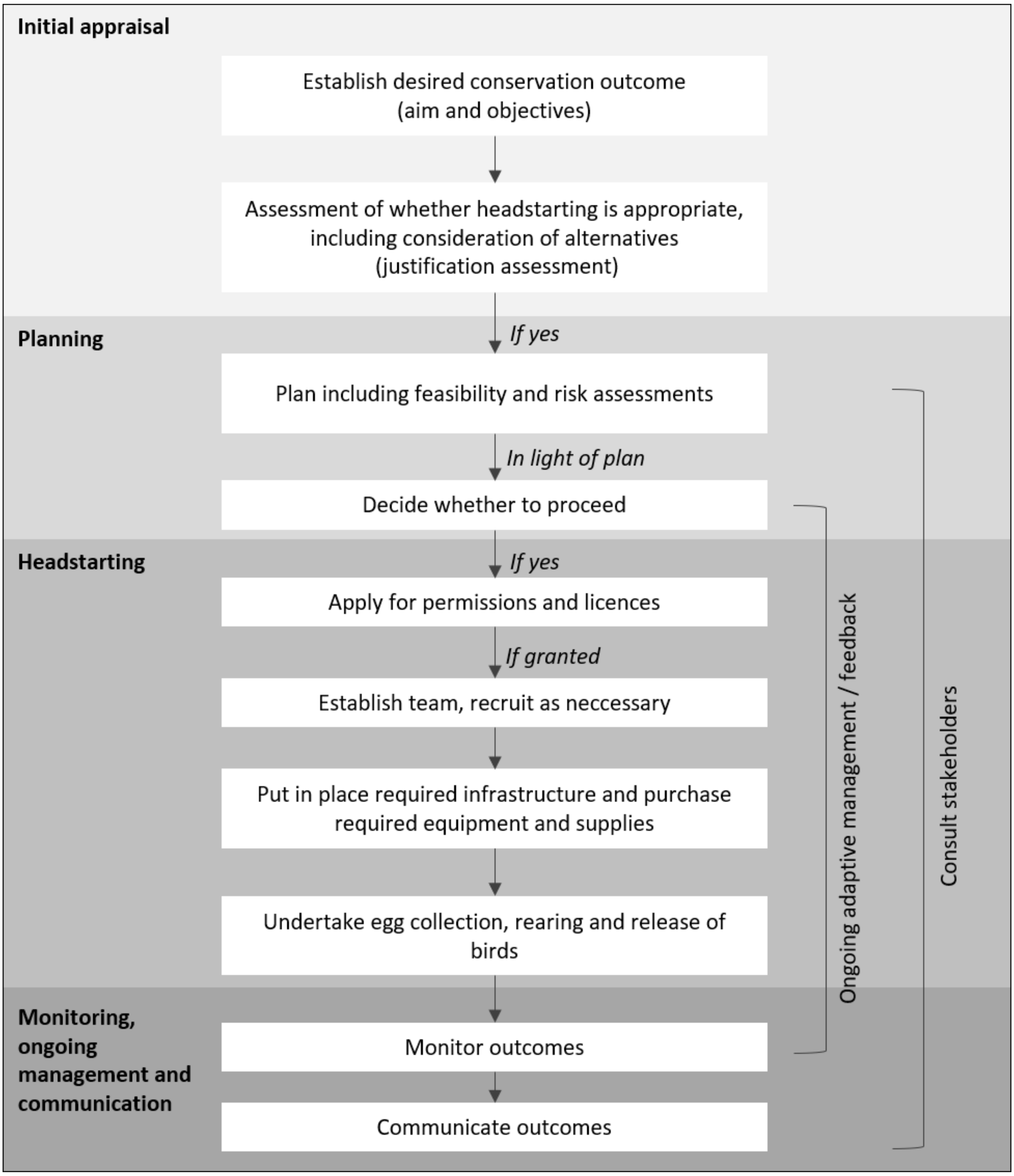
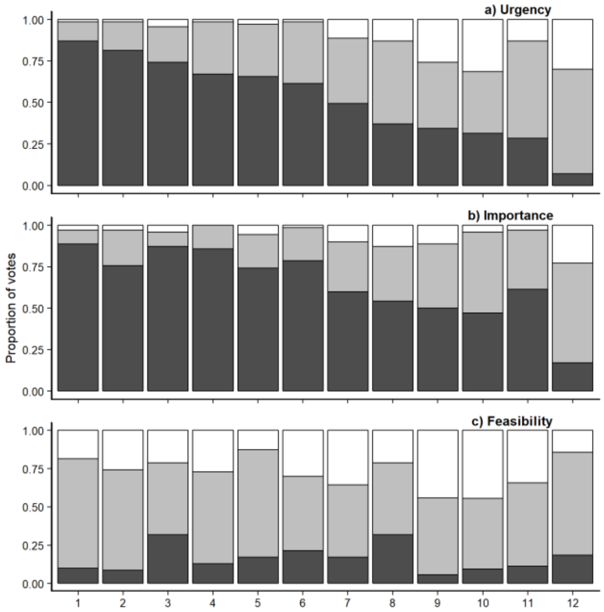


Figure 2: A flow chart of the processes that should be followed for any headstarting project from initial concept through planning, doing and monitoring outcomes. Adapted from the Scottish Code for Translocations (National Species Reintroduction Forum 2014a).

Discussion of knowledge gaps

Workshop attendees were asked to rank each of the 12 short-listed questions on three criteria: urgency, importance and feasibility (Table 1). These questions were derived through plenary discussion from the knowledge gaps raised during the presentations and group discussions. Attendees assigned high, medium or low classifications for each criterion applied to each question (Fig.3). We present the knowledge gaps in order of the proportion of the audience that considered the urgency to address that knowledge gap to be high (Fig.3). The scores assigned to the questions for urgency and importance were broadly similar, indicating that questions tended to be considered as high in both urgency and importance, or medium/low in both urgency and importance (Fig.3a & b). Most questions were considered to have medium or low feasibility, with none receiving a majority score of highly feasible (Fig.3c). The process of determining and prioritising knowledge gaps revealed that there was particular importance assigned to determining an appropriate and achievable vision for breeding wader populations in the future, which we address initially below. We then discuss the remaining knowledge gaps that are focused around three topic areas: (i) increasing our understanding of predator responses to management, (ii) connecting to policy, uptake and transferability of management options and (iii) the wider implications of predator management.

Determining an appropriate and achievable future vision for breeding waders and predator management is integral to determining whether we are carrying out the most urgent and important work required to attain our desired outcome (Fig.3; [Q11], with square brackets hereafter referring to numbered knowledge gap). While targets and goals provide something to aim for, they are often narrow in focus and concentrate on site, landscape or regional levels. While it may seem comfortable to have a realistic target of a certain number of pairs in a local population, the setting of targets will likely be influenced by our preconceptions, and ultimately it may not be the place of practitioners alone to determine these targets. Achieving the goal of increasing local populations on managed areas using the management tools discussed here may be feasible, but if our fundamental objective is to re-establish wader populations in the wider countryside, then we are likely to need to extend beyond the currently available management tools (Lyons *et al.* 2008). Having an appropriate *vision* for the future may also allow us to harness the efforts of people working or living across different countries and habitats towards the same outcomes. Consideration of our collective vision is an important first step as it has the potential to influence how questions concerning the remaining knowledge gaps we present might be framed.



1) Why do high predator densities occur?
2) What influences predator behaviour / detectability?
3) How can predator management interventions be supported by policy?
4) How do predator communities respond to predator management interventions?
5) How does the deployment of management interventions influence our capacity to achieve our target?
6) How do we influence the uptake, use and understanding of these tools?
7) How do waders respond to management interventions?
8) How can predator management interventions be used to influence public perception and behaviour?
9) What impacts do apex predators have on meso-predator effects on waders?
10) How transferable is our current knowledge of predator impacts on waders?
11) What should be our vision?
12) When should predator management interventions be combined?

Figure 3: Proportion of the 70 workshop attendees that voted for each of the 12 knowledge gaps over the three classifications of a) urgency, b) importance and c) feasibility on the three priority levels of high (dark grey), medium (light grey) and low (white; see Table 1 for definitions). The knowledge gaps are in descending order of high urgency vote proportion.

Increasing our understanding of predator responses to management

The knowledge gaps concerning predator responses to management were focussed on understanding the causes of high predator densities [Q1], and the potential role of gamebird releases in parts of Europe in which they occur was highlighted. Determining factors that influence predator behaviour and predator detectability [Q2] and how predator communities respond to predator management interventions [Q4], which includes the possibility of mesopredator release (Crooks & Soulé 1999), were also important areas of future research that could greatly influence the design and deployment of predator management tools. Three of the four knowledge gaps that scored highest on urgency and importance concerned the need for improved understanding of predators ([Q1], [Q2] and [Q4]). Attendees considered there to be particularly low feasibility for determining the impact of apex predators on mesopredator effects on waders ([Q9]; highest number of votes given to “low”; Table 1).

Connecting to policy and transferability of knowledge

Knowledge gaps that were concerned with dissemination of information regarding predator management were also highlighted during discussions. How interventions can be supported by policy [Q3], and how we can influence the uptake, use and understanding of these tools

[Q6] both scored highly on the metrics of urgency and importance (Fig.3). Determining how information regarding predator management could be used to influence public perception and behaviour [Q8] and how transferrable our current knowledge is [Q10] to other habitats and species facing the issue of predation were also issues considered important, but slightly less urgent than other issues.

The three knowledge gaps with the highest degree of agreed feasibility (largest proportion of audience considering there to be high feasibility) were those regarding the dissemination of information through policy support, update and understanding of management tools and influencing public perception of management ([Q3], [Q6] and [Q8]; Fig.3). However, attendees considered there to be particularly low feasibility for how transferrable our current knowledge of predator impacts on waders is to other systems [Q10].

Wider impacts of predator management

Consideration of the wider impacts of predator management focussed on how deployment strategies can be designed to achieve specific goals [Q5] and when they should be combined for greater impact [Q12]. The response of waders to both management interventions [Q7] and to mesopredators in the presence of apex predators [Q9] were also key knowledge gaps exploring beyond the direct impacts of management upon predators. Discussion of these issues highlighted the importance of identifying the goals of predator management for breeding waders, as this will influence the design, the spatial and temporal scales of deployment and the geographical targeting of management approaches.

Summary

This workshop provided a very valuable opportunity to identify the most pressing questions in this issue of fundamental importance to recovering breeding wader populations in western Europe. We consider all 12 knowledge gaps to be priorities, especially as their importance, urgency or feasibility may vary geographically. We hope that this work provides a platform for the rapid development of studies to address many of these knowledge gaps and will help to facilitate the collaborations that will undoubtedly be needed to reduce predator impacts on breeding waders before it is too late.

Acknowledgements

We thank all participants at the workshop on 23rd September 2019 who contributed and voted during the day. We also thank the International Wader Study Group conference organising committee for allowing our workshop to be part of the IWSG conference at Morecombe 2019, with special thanks to Jacquie Clarke and Richard du Feu. We thank Mark Colwell and Brett Sandercock for valuable comments that improved the manuscript. The workshop and RAL were funded by NERC (grant number NE/P002986/1).

References

Aebischer, N.J., Bailey, C.M., Gibbons, D.W., Morris, A.J., Peach, W.J. & Stoate, C. 2016. Twenty years of local farmland bird conservation: the effects of management on avian abundance at two UK demonstration sites. *Bird Study* 63: 10–30.

Aebischer, N.J., Davey, P.D. & Kingdon, N.G. 2011. *National Gamebag Census: Mammal Trends to 2009. Game & Wildlife Conservation Trust, Fordingbridge (www.gwct.org.uk/ngcmammals).*

Alberts, A.C., Lemm, J.M., Grant, T.D. & Jackintell, L.A. 2004. Testing the utility of headstarting as a conservation strategy for West Indian iguanas. In: *Iguanas: Biology and Conservation* (A. Alberts, R. Carter, W. Hayes, & E. Martins, eds), pp. 210–219. University of California Press, Berkeley, California.

Alves, J.A. & Dias, M.P. 2020. Portugal's airport plans threaten wetlands. *Science* 369: 1440–1440.

Alves, J.A., Dias, M.P., Méndez, V., Katrínardóttir, B. & Gunnarsson, T.G. 2016. Very rapid long-distance sea crossing by a migratory bird. *Scientific Reports* 6: 1–6.

Alves, J.A., Gunnarsson, T.G., Sutherland, W.J., Potts, P.M. & Gill, J.A. 2019. Linking warming effects on phenology, demography, and range expansion in a migratory bird population. *Ecology and evolution* 9: 2365–2375.

Amano, T., Székely, T., Koyama, K., Amano, H. & Sutherland, W.J. 2010. A framework for monitoring the status of populations: an example from wader populations in the East Asian–Australasian flyway. *Biological conservation* 143: 2238–2247.

Amar, A., Grant, M., Buchanan, G., Sim, I., Wilson, J., Pearce-Higgins, J.W. & Redpath, S. 2011. Exploring the relationships between wader declines and current land-use in the British uplands. *Bird Study* 58: 13–26.

Andres, B.A., Moore, L., Cox, A.R., Frei, B. & Roy, C. 2022. A preliminary assessment of shorebird harvest in coastal Guyana. *Wader Study* 129: 39–47.

Angelstam, P., Manton, M., Stjernquist, I., Gunnarsson, T.G., Ottvall, R., Rosenberg, M., Thorup, O., Wedholm, P., Elts, J. & Gruberts, D. 2022. Barriers and bridges for sustaining functional habitat networks: A macroecological system analysis of wet grassland landscapes. *Ecology and Evolution* 12.

Anteau, M.J., Swift, R.J., Sherfy, M.H., Koons, D.N., Ellis, K.S., Shaffer, T.L., Toy, D.L. & Ring, M.M. 2022. Experimental evaluation of predator exclosures on nest, chick, and adult survival of piping plovers. *The Journal of Wildlife Management* 86.

Araújo, M.B., Anderson, R.P., Márcia Barbosa, A., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R.B., Zimmermann, N.E. & Rahbek, C. 2019. Standards for distribution models in biodiversity assessments. *Science Advances* 5.

Atkinson, P.W., Clark, N.A., Bell, M.C., Dare, P.J., Clark, J.A. & Ireland, P.L. 2003. Changes in commercially fished shellfish stocks and shorebird populations in the Wash, England. *Biological Conservation* 114: 127–141.

Auffret, A.G., Kimberley, A., Plue, J. & Waldén, E. 2018. Super-regional land-use change and effects on the grassland specialist flora. *Nat Commun* 9: 3464.

Bailey, J., Schéré, C.M., Metcalfe, C.A., Griffin, D.C., Hoppit, G., Turner, R.K., Travers, T., Hill, J.K. & Sinnadurai, P. 2022. Protected Areas and Nature Recovery: Achieving the goal to protect 30% of UK land and seas for nature by 2030.

Baillie, J., Böhm, M., Collen, B. & Kemp, R. 2012. Spineless: status and trends of the world's invertebrates.

Bainbridge, I.P. & Minton, C. 1978. The migration and mortality of the Curlew in Britain and Ireland. *Bird Study* 25: 39–50.

Baines, D., Fletcher, K., Hesford, N., Newborn, D. & Richardson, M. 2022. Lethal predator control on UK moorland is associated with high breeding success of curlew, a globally near-threatened wader. *Eur J Wildl Res* 69: 6.

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 Thetford.

Barbier, E.B., Burgess, J.C. & Dean, T.J. 2018. How to pay for saving biodiversity. *Science* 360: 486–488.

Barbier, E.B., Lozano, R., Rodríguez, C.M. & Troëng, S. 2020. Adopt a carbon tax to protect tropical forests. *Nature* 578: 213–216.

Barbosa, A. & Moreno, E. 1999. Evolution of foraging strategies in shorebirds: an ecomorphological approach. *The Auk* 116: 712–725.

Bardgett, R.D., Bullock, J.M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., Chomel, M., Durigan, G., L. Fry, E., Johnson, D., Lavallee, J.M., Le Provost, G., Luo, S., Png, K., Sankaran, M., Hou, X., Zhou, H., Ma, L., Ren, W., Li, X., Ding, Y., Li, Y. & Shi, H. 2021. Combatting global grassland degradation. *Nat Rev Earth Environ* 2: 720–735.

Barnes, A.E., Davies, J.G., Martay, B., Boersch-Supan, P.H., Harris, S.J., Noble, D.G., Pearce-Higgins, J.W. & Robinson, R.A. 2023. Rare and declining bird species benefit most from designating protected areas for conservation in the UK. *Nat Ecol Evol* 7: 92–101.

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.

Battley, P.F., Warnock, N., Tibbitts, T.L., Gill Jr, R.E., Piersma, T., Hassell, C.J., Douglas, D.C., Mulcahy, D.M., Gartrell, B.D., Schuckard, R., Melville, D.S. & Riegen, A.C. 2012. Contrasting extreme long-distance migration patterns in bar-tailed godwits Limosa lapponica. *Journal of Avian Biology* 43: 21–32.

Bell, M.V. & Calladine, J. 2017. The decline of a population of farmland breeding waders: a twenty-five-year case study. *Bird Study* 64: 264–273.

Bellebaum, J. & Bock, C.D. 2008. Influence of ground predators and water levels on Lapwing Vanellus vanellus breeding success in two continental wetlands. *Journal of Ornithology*, doi: 10.1007/s10336-008-0341-7.

Bengtsson, J., Bullock, J.M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P.J., Smith, H.G. & Lindborg, R. 2019. Grasslands—more important for ecosystem services than you might think. *Ecosphere* 10: e02582.

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

Berg, A. 1992. Factors Affecting Nest-Site Choice and Reproductive Success of Curlews Numenius-Arquata on Farmland. *Ibis* 134: 44–51.

Berg, Å. 1994. Maintenance of populations and causes of population changes of curlews Numenius arquata breeding on farmland. *Biological Conservation* 67: 233–238.

Bodey, T.W., Bearhop, S. & McDonald, R.A. 2011a. Localised control of an introduced predator: creating problems for the future? *Biol Invasions* 13: 2817–2828.

Bodey, T.W., McDonald, R.A. & Bearhop, S. 2009. Mesopredators constrain a top predator: competitive release of ravens after culling crows. *Biology Letters* 5: 617–620.

Bodey, T.W., Mcdonald, R.A., Sheldon, R.D. & Bearhop, S. 2011b. Absence of effects of predator control on nesting success of Northern Lapwings *Vanellus vanellus*: Implications for conservation. *Ibis* 153: 543–555.

Bodey, T.W., Smart, J., Smart, M.A., Gregory, R., Boatman, N., Green, M., Holland, J., Marshall, J., Renwick, A. & Siriwardena, G. 2010. Reducing the impacts of predation on ground-nesting waders: a new landscape-scale solution. *Asp. Appl. Biol* 100: 167–174.

Boere, G.C. & Stroud, D.A. 2006. The flyway concept: what it is and what it isn't. *Waterbirds around the world* 40–47.

Boetzl, F.A., Krauss, J., Heinze, J., Hoffmann, H., Juffa, J., König, S., Krimmer, E., Prante, M., Martin, E.A., Holzschuh, A. & Steffan-Dewenter, I. 2021. A multitaxa assessment of the effectiveness of agri-environmental schemes for biodiversity management. *PNAS* 118.

Bolton, M., Tyler, G., Smith, K. & Bamford, R. 2007a. The impact of predator control on lapwing Vanellus vanellus breeding success on wet grassland nature reserves. *J Appl Ecol* 44: 534–544.

Bonari, G., Fajmon, K., Malenovský, I., Zelený, D., Holuša, J., Jongepierová, I., Kočárek, P., Konvička, O., Uřičář, J. & Chytrý, M. 2017. Management of semi-natural grasslands benefiting both plant and insect diversity: The importance of heterogeneity and tradition. *Agriculture, Ecosystems & Environment* 246: 243–252.

Boschert, M. & Rupp, J. 1993. Brutbiologie des Großen Brachvogels Numenius arquata in einem Brutgebiet am südlichen Oberrhein. *Vogelwelt* 114: 199–221.

Bowgen, K.M., Dodd, S.G., Lindley, P., Burton, N.H.K. & Taylor, R.C. 2022. Curves for Curlew: Identifying Curlew breeding status from GPS tracking data. *Ecology and Evolution* 12: e9509.

Boyd, C., Brooks, T.M., Butchart, S.H.M., Edgar, G.J., Da Fonseca, G.A.B., 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.

Boyd, H. 1962. Mortality and fertility of European Charadrii. *Ibis* 104: 368–387.

Bretagnolle, V., Villers, A., Denonfoux, L., Cornulier, T., Inchausti, P. & Badenhausser, I. 2011. Rapid recovery of a depleted population of Little Bustards Tetrax tetrax following provision of alfalfa through an agri-environment scheme. *Ibis* 153: 4–13.

Brlík, V., Šilarová, E., Škorpilová, J., Alonso, H., Anton, M., Aunins, A., Benkö, Z., Biver, G., Busch, M., Chodkiewicz, T., Chylarecki, P., Coombes, D., de Carli, E., del Moral, J.C., Derouaux, A., Escandell, V., Eskildsen, D.P., Fontaine, B., Foppen, R.P.B., Gamero, A., Gregory, R.D., Harris, S., Herrando, S., Hristov, I., Husby, M., Ieronymidou, C., Jiquet, F., Kålås, J.A., Kamp, J., Kmecl, P., Kurlavičius, P., Lehikoinen, A., Lewis, L., Lindström, Å., Manolopoulos, A., Martí, D., Massimino, D., Moshøj, C., Nellis, R., Noble, D., Paquet, A., Paquet, J.-Y., Portolou, D., Ramírez, I., Redel, C., Reif, J., Ridzoň, J., Schmid, H., Seaman, B., Silva, L., Soldaat, L., Spasov, S., Staneva, A., Szép, T., Florenzano, G.T., Teufelbauer, N., Trautmann, S., van der Meij, T., van Strien, A., van Turnhout, C., Vermeersch, G., Vermouzek, Z., Vikstrøm, T., Voříšek, P., Weiserbs, A. & Klvaňová, A. 2021. Long-term and large-scale multispecies dataset tracking population changes of common European breeding birds. *Sci Data* 8: 21.

Brown, D. 2015. International Single Species Action Plan for the Conservation of the Eurasian Curlew Numenius arquata arquata, N. a. orientalis and N. a. suschkini. *AEWA Technical Series* 58.

Brown, D., Wilson, J., Douglas, D., Thompson, P., Foster, S., McCulloch, N., Phillips, J., Stroud, D., Whitehead, S. & Crockford, N. 2015. The Eurasian Curlew–the most pressing bird conservation priority in the UK. *British Birds* 108: 660–668.

Brüggeshemke, J., Drung, M., Löffler, F. & Fartmann, T. 2022. Effects of local climate and habitat heterogeneity on breeding-bird assemblages of semi-natural grasslands. *J Ornithol* 163: 695–707.

Buchanan, G.M., Pearce-Higgins, J.W., Douglas, D.J.T. & Grant, M.C. 2017. Quantifying the importance of multi-scale management and environmental variables on moorland bird abundance. *Ibis* 159: 744–756.

Burfield, I.J. 2008. The conservation status and trends of raptors and owls in Europe. *AMBIO: A Journal of the Human Environment* 37: 401–407.

Burgess, M.D., Black, R.A., Nicoll, M. a. C., Jones, C.G. & Norris, K. 2009. The use of agricultural, open and forest habitats by juvenile Mauritius Kestrels Falco punctatus. *Ibis* 151: 63–76.

Burns, F., Eaton, M.A., Burfield, I.J., Klvaňová, A., Šilarová, E., Staneva, A. & Gregory, R.D. 2021. Abundance decline in the avifauna of the European Union reveals cross-continental similarities in biodiversity change. *Ecology and Evolution* 11: 16647–16660.

Butchart, S.H.M., Di Marco, M. & Watson, J.E.M. 2016. Formulating Smart Commitments on Biodiversity: Lessons from the Aichi Targets. *Conservation Letters* 9: 457–468.

Butler, R.W. & Kaiser, G.W. 1995. Migration Chronology, Sex Ratio, and Body Mass of Least Sandpipers in British Columbia. *The Wilson Bulletin* 107: 413–422.

Butler, S.J. & Norris, K. 2013. Functional space and the population dynamics of birds in agro-ecosystems. *Agriculture, Ecosystems & Environment* 164: 200–208.

Calladine, J., Humphreys, E.M., Gilbert, L., Furness, R.W., Robinson, R.A., Fuller, R.J., Littlewood, N.A., Pakeman, R.J., Ferguson, J. & Thompson, C. 2017. Continuing influences of introduced hedgehogs Erinaceus europaeus as a predator of wader (Charadrii) eggs four decades after their release on the Outer Hebrides, Scotland. *Biol Invasions* 19: 1981–1987.

Cao, L., Zhang, Y., Barter, M. & Lei, G. 2010. Anatidae in eastern China during the non-breeding season: Geographical distributions and protection status. *Biological Conservation* 143: 650–659.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. 2012. Biodiversity loss and its impact on humanity. *Nature* 486: 59–67.

Carneiro, C., Gunnarsson, T.G. & Alves, J.A. 2019. Why Are Whimbrels Not Advancing Their Arrival Dates Into Iceland? Exploring Seasonal and Sex-Specific Variation in Consistency of Individual Timing During the Annual Cycle. *Front Ecol Evol* 7.

Carrié, R., Lopes, M., Ouin, A. & Andrieu, E. 2018. Bee diversity in crop fields is influenced by remotely-sensed nesting resources in surrounding permanent grasslands. *Ecological Indicators* 90: 606–614.

Carroll, C. & Noss, R.F. 2022. How percentage-protected targets can support positive biodiversity outcomes. *Conservation Biology* 36: e13869.

Carroll, J.M., Davis, C.A., Elmore, R.D., Fuhlendorf, S.D. & Thacker, E.T. 2015. Thermal patterns constrain diurnal behavior of a ground-dwelling bird. *Ecosphere* 6: art222.

Catry, T., Alves, J.A., Andrade, J., Costa, H., Dias, M.P., Fernandes, P., Leal, A., Lourenco, P.M., Martins, R.C., Moniz, F., Pardal, S., Rocha, A., Santos, C.D., Encarnacao, V. & Granadeiro, J.P. 2011. Long-term declines of wader populations at the Tagus estuary, Portugal: a response to global or local factors? *Bird Conserv Int* 21: 438–453.

Catry, T., Ventura, F., Dias, M.P., Santos, C.D., Martins, R.C., Palmeirim, J.M. & Granadeiro, J.P. 2022. Estimating the conservation cost of the projected new international Lisbon airport for migratory shorebirds of the Tagus estuary, Portugal. *Bird Conservation International* 32: 232–245.

Cazalis, V., Princé, K., Mihoub, J.-B., Kelly, J., Butchart, S.H.M. & Rodrigues, A.S.L. 2020. Effectiveness of protected areas in conserving tropical forest birds. *Nat Commun* 11: 4461.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., Garcia, A., Pringle, R.M. & Palmer, T.M. 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Sci Adv* 1.

Chan, S., Bauer, S., Betsill, M.M., Biermann, F., Boran, I., Bridgewater, P., Bulkeley, H., Bustamente, M.M.C., Deprez, A., Dodds, F., Hoffmann, M., Hornidge, A.-K., Hughes, A., Imbach, P., Ivanova, M., Köberle, A., Kok, M.T.J., Lwasa, S., Morrison, T., Pörtner, H.-O., Sari, A.P., VanDeveer, S.D., Vollmer, D., Widerberg, O. & Pettorelli, N. 2023. The global biodiversity framework needs a robust action agenda. *Nat Ecol Evol* 7: 172–173.

Chowdhury, S.U., Foysal, M. & Green, R.E. 2022. Accelerating decline of an important wintering population of the critically endangered Spoon-billed Sandpiper Calidris pygmaea at Sonadia Island, Bangladesh. *Journal of Ornithology* 163: 891–901.

Clark, N.A. 2006. Tidal Barrages and Birds. *Ibis* 148: 152–157.

Clark, N.A., Anderson, G.Q.A., Li, J., Syroechkovskiy, E.E., Tomkovich, P.S., Zöckler, C., Lee, R. & Green, R.E. 2018. First formal estimate of the world population of the Critically Endangered Spoon-billed Sandpiper Calidris pygmaea. *Oryx* 52: 137–146.

Coad, L., Watson, J.E., Geldmann, J., Burgess, N.D., Leverington, F., Hockings, M., Knights, K. & Di Marco, M. 2019. Widespread shortfalls in protected area resourcing undermine efforts to conserve biodiversity. *Frontiers in Ecology and the Environment* 17: 259–264.

Colhoun, K., Flannelly, F., O’Neill, J., Phelan, E., Servignat, H., O’Donoghue, B. & Kelly, S. 2022. Status and distribution of breeding Eurasian Curlew in Ireland 2021.

Collins, S.A., Sanders, F.J. & Jodice, P.G.R. 2016. Assessing conservation tools for an at-risk shorebird: Feasibility of headstarting for American Oystercatchers *Haematopus palliatus*. *Bird Conservation International* 26: 451–465.

Colwell, M. 2018. *Curlew Moon*. HarperCollins UK.

Colwell, M., Hilton, G., Smart, M. & Sheldrake, P. 2020. Saving England's lowland Eurasian Curlews. *British Birds* 14.

Colwell, M.A. 2010. *Shorebird ecology, conservation, and management*. Univ of California Press.

Conde, D.A., Staerk, J., Colchero, F., da Silva, R., Schöley, J., Baden, H.M., Jouvet, L., Fa, J.E., Syed, H., Jongejans, E., Meiri, S., Gaillard, J.-M., Chamberlain, S., Wilcken, J., Jones, O.R., Dahlgren, J.P., Steiner, U.K., Bland, L.M., Gomez-Mestre, I., Lebreton, J.-D., González Vargas, J., Flesness, N., Canudas-Romo, V., Salguero-Gómez, R., Byers, O., Berg, T.B., Scheuerlein, A., Devillard, S., Schigel, D.S., Ryder, O.A., Possingham, H.P., Baudisch, A. & Vaupel, J.W. 2019. Data gaps and opportunities for comparative and conservation biology. *Proceedings of the National Academy of Sciences* 116: 9658–9664.

Conklin, J.R. 2019. Evolutionary and ecological flexibility in migration of Charadrius plovers. In: *The Population Ecology and Conservation of Charadrius Plovers*, pp. 149–182. CRC Press.

Cook, A.S.C.P., Burton, N.H.K., Dodd, S.G., Foster, S., Pell, R.J., Ward, R.M., Wright, L.J. & Robinson, R.A. 2021. Temperature and density influence survival in a rapidly declining migratory shorebird. *Biological Conservation* 260: 109198.

Coomber, F.G., Smith, B.R., August, T.A., Harrower, C.A., Powney, G.D. & Mathews, F. 2021. Using biological records to infer long-term occupancy trends of mammals in the UK. *Biological Conservation* 264: 109362.

Cooper, N.W., Rushing, C.S. & Marra, P.P. 2019. Reducing the conservation reliance of the endangered Kirtland's warbler through adaptive management. *The Journal of Wildlife Management* 83: 1297–1305.

Côté, I.M. & Sutherland, W.J. 1997. The effectiveness of removing predators to protect bird populations. *Conservation Biology* 11: 395–405.

Cramp, S., Simmons, K.L., editors, Brooks, D., Collar, N., Dunn, E., Gillmor, R., Hollom, P., Hudson, R., Nicholson, E. & Ogilvie, M. 1983. *Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic: 3. Waders to gulls*.

Crick, H.Q.P., Baillie, S.R. & Leech, D.I. 2003. The UK Nest Record Scheme: its value for science and conservation. *Bird Study* 50: 254–270.

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

Currie, D., Valkama, J., Berg, A., Boschert, M., Norrdahl, K., Hänninen, M., Korpimäki, E., Pöyri, v. & Hemminki, O. 2001. Sex roles, parental effort and offspring desertion in the monogamous Eurasian Curlew Numenius arquata. *Ibis* 143: 642–650.

Dallimer, M., Marini, L., Skinner, A.M., Hanley, N., Armsworth, P.R. & Gaston, K.J. 2010. Agricultural land-use in the surrounding landscape affects moorland bird diversity. *Agriculture, ecosystems & environment* 139: 578–583.

Davies, M., Grice, P., Evans, A., Jeffs, C., Lock, L. & Wotton, S. 2011. The Cirl Bunting recovery story. Celebrating the success of a model species recovery project. *British Wildlife* 22: 263.

Deinet, S., Ieronymidou, C., McRae, L., Burfield, I.J., Foppen, R.P., Collen, B. & Böhm, M. 2013. Wildlife comeback in Europe: The recovery of selected mammal and bird species.

Delany, S., Scott, D., Dodman, T. & Stroud, D. 2009. An atlas of wader populations in Africa and Western Eurasia. *British Birds* 102: 639–642.

Díaz, S.M., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K. & Butchart, S. 2019. The global assessment report on biodiversity and ecosystem services: Summary for policy makers.

Dicks, L.V., Breeze, T.D., Ngo, H.T., Senapathi, D., An, J., Aizen, M.A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L.A., Gemmill-Herren, B., Howlett, B.G., Imperatriz-Fonseca, V.L., Johnson, S.D., Kovács-Hostyánszki, A., Kwon, Y.J., Lattorff, H.M.G., Lungharwo, T., Seymour, C.L., Vanbergen, A.J. & Potts, S.G. 2021. A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nat Ecol Evol* 5: 1453–1461.

Dietz, M.S., Belote, R.T., Gage, J. & Hahn, B.A. 2020. An assessment of vulnerable wildlife, their habitats, and protected areas in the contiguous United States. *Biological Conservation* 248: 108646.

Dinerstein, E., Vynne, C., Sala, E., Joshi, A.R., Fernando, S., Lovejoy, T.E., Mayorga, J., Olson, D., Asner, G.P., Baillie, J.E.M., Burgess, N.D., Burkart, K., Noss, R.F., Zhang, Y.P., Baccini, A., Birch, T., Hahn, N., Joppa, L.N. & Wikramanayake, E. 2019. A Global Deal For Nature: Guiding principles, milestones, and targets. *Science Advances* 5: eaaw2869.

Dion, N., Hobson, K.A. & Larivière, S. 1999. Effects of removing duck-nest predators on nesting success of grassland songbirds. *Canadian Journal of Zoology* 77: 1801–1806.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. 2014. Defaunation in the Anthropocene. *Science* 345: 401–406.

Dolman, P.M., Panter, C. & Mossman, H.L. 2010. Securing biodiversity in Breckland: guidance for conservation and research. *First report of the Breckland biodiversity audit*.

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.

Dornberger, W. n.d. Ranftl. H. 1986. Breeding populations of Curlew, Redshank and Blacktailed Godwit in northern Bavaria (West Germany) 1977-1986. *Anzeiger der Ornithologischen Gesellschaft in Bayern* 25: 189–194.

Douglas, D.J.T., Bellamy, P.E., Stephen, L.S., Pearce-Higgins, J.W., Wilson, J.D. & Grant, M.C. 2014. Upland land use predicts population decline in a globally near-threatened wader. *J Appl Ecol* 51: 194–203.

Douglas, D.J.T. & Pearce-Higgins, J.W. 2014. Relative importance of prey abundance and habitat structure as drivers of shorebird breeding success and abundance. *Animal Conservation* 17: 535–543.

Douglas, D.J.T., Tománková, I., Gullett, P., Dodd, S.G., Brown, D., Clift, M., Russell, N., Warnock, N., Smart, J. & Sanders, S. 2023. Varying response of breeding waders to experimental manipulation of their habitat and predators. *Journal for Nature Conservation* 126353.

Dower, B. 2018. 19 - Solar Panels in the Landscape. In: *A Comprehensive Guide to Solar Energy Systems* (T. M. Letcher & V. M. Fthenakis, eds), pp. 373–389. Academic Press.

Downey, H., Amano, T., Cadotte, M., Cook, C.N., Cooke, S.J., Haddaway, N.R., Jones, J.P.G., Littlewood, N., Walsh, J.C., Abrahams, M.I., Adum, G., Akasaka, M., Alves, J.A., Antwis, R.E., Arellano, E.C., Axmacher, J., Barclay, H., Batty, L., Benítez-López, A., Bennett, J.R., Berg, M.J., Bertolino, S., Biggs, D., Bolam, F.C., Bray, T., Brook, B.W., Bull, J.W., Burivalova, Z., Cabeza, M., Chauvenet, A.L.M., Christie, A.P., Cole, L., Cotton, A.J., Cotton, S., Cousins, S.A.O., Craven, D., Cresswell, W., Cusack, J.J., Dalrymple, S.E., Davies, Z.G., Diaz, A., Dodd, J.A., Felton, A., Fleishman, E., Gardner, C.J., Garside, R., Ghoddousi, A., Gilroy, J.J., Gill, D.A., Gill, J.A., Glew, L., Grainger, M.J., Grass, A.A., Greshon, S., Gundry, J., Hart, T., Hopkins, C.R., Howe, C., Johnson, A., Jones, K.W., Jordan, N.R., Kadoya, T., Kerhoas, D., Koricheva, J., Lee, T.M., Lengyel, S., Livingstone, S.W., Lyons, A., McCabe, G., Millett, J., Strevens, C.M., Moolna, A., Mossman, H.L., Mukherjee, N., Muñoz-Sáez, A., Negrões, N., Norfolk, O., Osawa, T., Papworth, S., Park, K.J., Pellet, J., Phillott, A.D., Plotnik, J.M., Priatna, D., Ramos, A.G., Randall, N., Richards, R.M., Ritchie, E.G., Roberts, D.L., Rocha, R., Rodríguez, J.P., Sanderson, R., Sasaki, T., Savilaakso, S., Sayer, C., Sekercioglu, C., Senzaki, M., Smith, G., Smith, R.J., Soga, M., Soulsbury, C.D., Steer, M.D., Stewart, G., Strange, E.F., Suggitt, A.J., Thompson, R.R.J., Thompson, S., Thornhill, I., Trevelyan, R.J., Usieta, H.O., Venter, O., Webber, A.D., White, R.L., Whittingham, M.J., Wilby, A., Yarnell, R.W., Zamora-Gutierrez, V. & Sutherland, W.J. 2021. Training future generations to deliver evidence-based conservation and ecosystem management. *Ecological Solutions and Evidence* 2: e12032.

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 grassland. *J Appl Ecol* 45: 305–314.

Eglington, S.M., Gill, J.A., Smart, Mark.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.

Eichenberg, D., Bowler, D.E., Bonn, A., Bruelheide, H., Grescho, V., Harter, D., Jandt, U., May, R., Winter, M. & Jansen, F. 2021. Widespread decline in Central European plant diversity across six decades. *Global Change Biology* 27: 1097–1110.

Evans, P. & Pienkowski, M. 1984. Population dynamics of shorebirds. *Shorebirds: breeding behavior and populations* 83–123.

Ewing, H., Franks, S., Smart, J., Burton, N. & Gill, J.A. 2022. Nest survival of threatened Eurasian Curlew (Numenius arquata) breeding at low densities across a human-modified landscape. *Ibis*.

Exo, K.-M., Wellbrock, A.H.J., 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.

Eycott, A.E., Watkinson, A.R. & Dolman, P.M. 2006. Ecological patterns of plant diversity in a plantation forest managed by clearfelling. *J Appl Ecol* 43: 1160–1171.

Fletcher, K., Aebischer, N.J., Baines, D., Foster, R. & Hoodless, A.N. 2010a. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *J Appl Ecol* 47: 263–272.

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.

Fluet-Chouinard, E., Stocker, B.D., Zhang, Z., Malhotra, A., Melton, J.R., Poulter, B., Kaplan, J.O., Goldewijk, K.K., Siebert, S., Minayeva, T., Hugelius, G., Joosten, H., Barthelmes, A., Prigent, C., Aires, F., Hoyt, A.M., Davidson, N., Finlayson, C.M., Lehner, B., Jackson, R.B. & McIntyre, P.B. 2023. Extensive global wetland loss over the past three centuries. *Nature* 614: 281–286.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. 2005. Global Consequences of Land Use. *Science* 309: 570–574.

Fouquet, M. 2013. Plan National de Gestion (2014-2018)–Courlis cendré (Numenius arquata).

Francis, A. & Elliott, J. 2019. New routes to decarbonise land use with Natural Infrastructure Schemes. *Green Alliance and National Trust*.

Franklin, J., Serra-Diaz, J.M., Syphard, A.D. & Regan, H.M. 2016. Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences* 113: 3725–3734.

Franks, S.E., Douglas, D.J., Gillings, S. & Pearce-Higgins, J.W. 2017. Environmental correlates of breeding abundance and population change of Eurasian Curlew Numenius arquata in Britain. *Bird Study* 64: 393–409.

Franks, S.E., Roodbergen, M., Teunissen, W., Carrington Cotton, A. & Pearce-Higgins, J.W. 2018. Evaluating the effectiveness of conservation measures for European grassland-breeding waders. *Ecology and evolution* 8: 10555–10568.

Fraser, D.J. 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications* 1: 535–586.

Frost, T., Calbrade, N., Birtles, G., Mellan, H., Hall, C., Robinson, A., Wotton, S., Balmer, D. & Austin, G. 2020. Waterbirds in the UK 2018/19: The wetland bird survey. *Ann Arbor, MI: Thetford*.

Fuller, R.J., Williamson, T., Barnes, G. & Dolman, P.M. 2017. Human activities and biodiversity opportunities in pre-industrial cultural landscapes: relevance to conservation. *Journal of Applied Ecology* 54: 459–469.

Gaitán, J.J., Oliva, G.E., Bran, D.E., Maestre, F.T., Aguiar, M.R., Jobbágy, E.G., Buono, G.G., Ferrante, D., Nakamatsu, V.B., Ciari, G., Salomone, J.M. & Massara, V. 2014. Vegetation structure is as important as climate for explaining ecosystem function across Patagonian rangelands. *Journal of Ecology* 102: 1419–1428.

Galewski, T. & Devictor, V. 2016. When Common Birds Became Rare: Historical Records Shed Light on Long-Term Responses of Bird Communities to Global Change in the Largest Wetland of France. *PLOS ONE* 11: e0165542.

Gallo-Cajiao, E., Morrison, T.H., Woodworth, B.K., Lees, A.C., Naves, L.C., Yong, D.L., Choi, C.-Y., Mundkur, T., Bird, J., Jain, A., Klokov, K., Syroechkovskiy, E., Chowdhury, S.U., Fu, V.W.K., Watson, J.E.M. & Fuller, R.A. 2020. Extent and potential impact of hunting on migratory shorebirds in the Asia-Pacific. *Biological Conservation* 246: 108582.

Galtbalt, B., Lilleyman, A., Coleman, J.T., Cheng, C., Ma, Z., Rogers, D.I., Woodworth, B.K., Fuller, R.A., Garnett, S.T. & Klaassen, M. 2021. Far eastern curlew and whimbrel prefer flying low-wind support and good visibility appear only secondary factors in determining migratory flight altitude. *Movement ecology* 9: 1–12.

Gameiro, J., Franco, A.M.A., Catry, T., Palmeirim, J.M. & Catry, I. 2020. Long-term persistence of conservation-reliant species: Challenges and opportunities. *Biological Conservation* 243: 108452.

Gaston, K.J. & Blackburn, T.M. 1995. Birds, body size and the threat of extinction. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 347: 205–212.

Geldmann, J., Manica, A., Burgess, N.D., Coad, L. & Balmford, A. 2019. A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. *Proceedings of the National Academy of Sciences* 116: 23209–23215.

Gerasimov, Y.N., Artukhin, Y.B. & Gerasimov, N. 1997. The eastern curlew Numenius madagascariensis in Kamchatka, Russia. *The Stilt* 30: 14–15.

Gerritsen, G. 2021. De broedbiologie van Wulpen in West-Overijssel. *Limosa* 94: 19–29.

Gill, D.A., Mascia, M.B., Ahmadia, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S., Free, C.M., Geldmann, J., Holst, S., Jensen, O.P., White, A.T., Basurto, X., Coad, L., Gates, R.D., Guannel, G., Mumby, P.J., Thomas, H., Whitmee, S., Woodley, S. & Fox, H.E. 2017. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* 543: 665–669.

Gill, J. 2019. Does competition really drive population distributions? *Wader Study Group Bulletin* 126: 166–168.

Gill, J.A., Alves, J.A. & Gunnarsson, T.G. 2019. Mechanisms driving phenological and range change in migratory species. *Philosophical Transactions of the Royal Society B* 374: 20180047.

Gill, R.E., Jr., Piersma, T., Hufford, G., Servranckx, R. & Riegen, A. 2005. Crossing the Ultimate Ecological Barrier: Evidence for an 11 000-km-Long Nonstop Flight from Alaska to New Zealand and Eastern Australia by Bar-Tailed Godwits. *The Condor* 107: 1–20.

Glen, A.S. & Dickman, C.R. 2005. Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biological Reviews* 80: 387–401.

Grant, M.C. 1996. Predicting the hatching dates of Curlew Numenius arquata clutches. *Wader Study Group Bulletin* 80: 53–54.

Grant, M.C., Orsman, C., Easton, J., Lodge, C., Smith, M., Thompson, G., Rodwell, S. & Moore, N. 1999. Breeding success and causes of breeding failure of curlew Numenius arquata in Northern Ireland. *J Appl Ecol* 36: 59–74.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P. & Buckley, Y.M. 2013. Predicting species distributions for conservation decisions. *Ecology Letters* 16: 1424–1435.

Gunnarsson, T.G., Gill, J.A., Appleton, G.F., Gíslason, H., Gardarsson, A., Watkinson, A.R. & Sutherland, W.J. 2006. Large-scale habitat associations of birds in lowland Iceland: implications for conservation. *Biological conservation* 128: 265–275.

Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M.H. & Tilman, D. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12: 1029–1039.

Ham, C., Donnelly, C.A., Astley, K.L., Jackson, S.Y.B. & Woodroffe, R. 2019. Effect of culling on individual Badger *Meles meles* behaviour: Potential implications for bovine tuberculosis transmission. *Journal of Applied Ecology* 56: 2390–2399.

Hancock, M.H., Klein, D. & Cowie, N.R. 2020. Guild-level responses by mammalian predators to afforestation and subsequent restoration in a formerly treeless peatland landscape. *Restoration Ecology* 28: 1113–1123.

Handler, A., Lonsdorf, E.V. & Ardia, D.R. 2020. Evidence for red fox (Vulpes vulpes) exploitation of anthropogenic food sources along an urbanization gradient using stable isotope analysis. *Canadian Journal of Zoology* 98: 79–87.

Harris, S., Massimino, D., Balmer, D., Kelly, L., Noble, D., Pearce-Higgins, J., Woodcock, P., Wotton, S. & Gillings, S. 2022. The breeding bird survey 2021. *BTO research report* 745.

Hawkes, R.W., Smart, J., Brown, A., Green, R.E., Jones, H. & Dolman, P.M. 2021. Effects of experimental land management on habitat use by Eurasian Stone-curlews. *Animal Conservation* 24: 743–755.

Hawkes, R.W., Smart, J., Brown, A., Jones, H., Lane, S., Wells, D. & Dolman, P.M. 2019. Multi-taxa consequences of management for an avian umbrella species. *Biological Conservation* 236: 192–201.

Haworth, P. & Thompson, D. 1990. Factors associated with the breeding distribution of upland birds in the South Pennines, England. *Journal of Applied Ecology* 562–577.

Hayhow, D., Eaton, M., Stanbury, A., Burns, F., Kirby, W., Bailey, N., Beckmann, B., Bedford, J., Boersch-Supan, P. & Coomber, F. 2019. State of nature 2019.

Hemerik, L., Klok, C. & Roodbergen, M. 2009. Diagnosing declining grassland wader populations using simple matrix models. *Animal Biology* 59: 127–144.

Heppell, S.S., Crowder, L.B. & Crouse, D.T. 1996. Models to evaluate headstarting as a management tool for long-lived turtles. *Ecological Applications* 6: 556–565.

Herse, M.R., With, K.A. & Boyle, W.A. 2018. The importance of core habitat for a threatened species in changing landscapes. *Journal of Applied Ecology* 55: 2241–2252.

Heydon, M.J. & Reynolds, J.C. 2000a. Demography of rural Foxes (Vulpes vulpes) in relation to cull intensity in three contrasting regions of Britain. *Journal of Zoology* 251: 265–276.

Heydon, M.J. & Reynolds, J.C. 2000b. Fox (*Vulpes vulpes*) management in three contrasting regions of Britain, in relation to agricultural and sporting interests. *Journal of Zoology* 251: 237–252.

Heydon, M.J., Reynolds, J.C. & Short, M.J. 2000. Variation in abundance of Foxes (Vulpes vulpes) between three regions of rural Britain, in relation to landscape and other variables. *Journal of Zoology* 251: 253–264.

Holt, A.R., Davies, Z.G., Tyler, C. & Staddon, S. 2008. Meta-analysis of the effects of predation on animal prey abundance: evidence from UK vertebrates. *PLoS One* 3: e2400.

Hoodless, A.N. & MacDonald, M.A. 2016. Evaluation of electric fencing as a means of increasing Lapwing chick survival and overall productivity on fallow plots. *Defra Research Report on Project LM0108*.

Hötker, H., Jeromin, H. & Melter, J. 2007. Development of populations of meadow waders breeding in Germany-results of a new monitoring approach for scarce bird species. *VOGELWELT-BERLIN-* 128: 49.

Hovick, T.J., Elmore, R.D. & Fuhlendorf, S.D. 2014. Structural heterogeneity increases diversity of non-breeding grassland birds. *Ecosphere* 5: art62.

Hua, N., Tan, K., Chen, Y. & Ma, Z. 2015. Key research issues concerning the conservation of migratory shorebirds in the Yellow Sea region. *Bird Conservation International* 25: 38–52.

Huff, J.A. 1989. Marine Turtle Newsletter. *Marine Turtle Newsletter* 46: 1–2.

Hughes, A., Shen, X., Corlett, R., Li, L., Luo, M., Woodley, S., Zhang, Y. & Ma, K. 2022. Challenges and possible solutions to creating an achievable and effective Post-2020 Global Biodiversity Framework. *Ecosystem Health and Sustainability* 8: 2124196.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S. & Loreau, M. 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477: 199–202.

IUCN. 2022. The IUCN Red List of Threatened Species.

IUCN/SSC. 2013. Guidelines for reintroductions and other conservation translocations. *Version 1.0. Gland, Switzerland: IUCN Species Survival Commission* viiii + 57 pp.

Jackson, D. & Green, R. 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.

Jellesmark, S., Ausden, M., Blackburn, T.M., Gregory, R.D., Hoffmann, M., Massimino, D., McRae, L. & Visconti, P. 2021. A counterfactual approach to measure the impact of wet grassland conservation on U.K. breeding bird populations. *Conservation Biology* 35: 1575–1585.

Jensen, F. & Lutz, M. 2007. Management plan for Curlew (Numenius arquata) 2007–2009. *European Communities, Luxembourg*.

Jiguet, F., Duby, D., Bourgeois, A., Robin, F., Rousseau, P., Nijs, G., Fuchs, J., Lorrillière, R. & Bocher, P. 2021. Investigation into the illegal killing of a tagged Eurasian Curlew. *Forensic Science International: Animals and Environments* 1: 100005.

Jóhannesdóttir, L., Alves, J.A., Gill, J.A. & Gunnarsson, T.G. 2018. Use of agricultural land by breeding waders in low-intensity farming landscapes. *Animal Conservation* 21: 291–301.

Jóhannesdóttir, L., Gill, J.A., Alves, J.A., Brink, S.H., Arnalds, Ó., Méndez, V. & Gunnarsson, T.G. 2019. Interacting effects of agriculture and landscape on breeding wader populations. *Agriculture, Ecosystems & Environment* 272: 246–253.

Johnson, C.A., Sutherland, G.D., Neave, E., Leblond, M., Kirby, P., Superbie, C. & McLoughlin, P.D. 2020. Science to inform policy: Linking population dynamics to habitat for a threatened species in Canada. *Journal of Applied Ecology* 57: 1314–1327.

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L. & Wilmshurst, J.M. 2017. Biodiversity losses and conservation responses in the Anthropocene. *Science* 356: 270–275.

Johnstone, I. 2007. The population status and nesting-success of Curlews Numenius arquata in Wales in 2006. *Welsh Birds* 5: 78–87.

Jones, C.G., Heck, W., Lewis, R.E., Mungroo, Y., Slade, G. & Cade, T. 1995. The restoration of the Mauritius Kestrel Falco punctatus population. *Ibis* 137: S173–S180.

Julliard, R., Jiguet, F. & Couvet, D. 2004. Common birds facing global changes: what makes a species at risk? *Global Change Biology* 10: 148–154.

Kaasiku, T., Rannap, R. & Männil, P. 2022. Predation-mediated edge effects reduce survival of wader nests at a wet grassland-forest edge. *Animal Conservation* n/a.

Kämmerle, J., Niekrenz, S. & Storch, I. 2019. No evidence for spatial variation in predation risk following restricted-area Fox culling. *BMC Ecology* 19: 17.

Kamp, J., Oppel, S., Ananin, A.A., Durnev, Y.A., Gashev, S.N., Hölzel, N., Mishchenko, A.L., Pessa, J., Smirenski, S.M., Strelnikov, E.G., Timonen, S., Wolanska, K. & Chan, S. 2015a. Global population collapse in a superabundant migratory bird and illegal trapping in China. *Conservation Biology* 29: 1684–1694.

Kamp, J., Pelster, A., Gaedicke, L., Karthäuser, J., Dieker, P. & Mantel, K. 2015b. High nest survival and productivity of Northern Lapwings Vanellus vanellus breeding on urban brownfield sites. *J Ornithol* 156: 179–190.

Kämpfer, S. & Fartmann, T. 2022. Natural coastal dunes on Wadden Sea islands as a refuge for an endangered wader species. *J Coast Conserv* 26: 53.

Kedward, K., Ryan-Collins, J. & Chenet, H. 2022. Biodiversity loss and climate change interactions: financial stability implications for central banks and financial supervisors. *Climate Policy* 0: 1–19.

Keller, V., Herrando, S., Voríšek, P., Franch, M., Kipson, M., Milanesi, P., Martí, D., Anton, M., Klvanová, A. & Kalyakin, M.V. 2020. *European breeding bird atlas 2: Distribution, abundance and change*.

Kempenaers, B. & Valcu, M. 2017. Breeding site sampling across the Arctic by individual males of a polygynous shorebird. *Nature* 541: 528–531.

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

Kentie, R., Coulson, T., Hooijmeijer, J.C.E.W., Howison, R.A., Loonstra, A.H.J., Verhoeven, M.A., Both, C. & Piersma, T. 2018. Warming springs and habitat alteration interact to impact timing of breeding and population dynamics in a migratory bird. *Global Change Biology* 24: 5292–5303.

Kentie, R., Hooijmeijer, J.C., Trimbos, K.B., Groen, N.M. & Piersma, T. 2013. Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks. *J Appl Ecol* 50: 243–251.

Khorozyan, I. & Waltert, M. 2019. How long do anti-predator interventions remain effective? Patterns, thresholds and uncertainty. *Royal Society Open Science* 6: 190826.

Kipp, C. & Kipp, M. 2009. Zur Bestandsentwicklung des Großen Brachvogels Numenius arquata in der „Wüste “bei Schwege. *Charadrius* 45: 27–32.

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.

Krüger, H., Väänänen, V.-M., Holopainen, S. & Nummi, P. 2018. The new faces of nest predation in agricultural landscapes—a wildlife camera survey with artificial nests. *Eur J Wildl Res* 64: 76.

Kwon, E., Valcu, M., Cragnolini, M., Bulla, M., Lyon, B. & Kempenaers, B. 2022. Breeding site fidelity is lower in polygamous shorebirds and male-biased in monogamous species. *Behavioral Ecology* 33: 592–605.

Laidlaw, R., Smart, J., Ewing, H., Franks, S., Belting, H., Donaldson, L., Hilton, G., Hiscock, N., Hoodless, A., Hughes, B., Jarrett, N., Kentie, R., Kleyheeg, E., Lee, R., Roodbergen, M., Scott, D., Short, M., Syroeschkovskiy, E., Teunissen, W., Ward, H., White, G. & Gill, J. 2021. Predator management for breeding waders: a review of current evidence and priority knowledge gaps. *Wader Study* 128: 44–55.

Laidlaw, R.A., Gunnarsson, T.G., Méndez, V., Carneiro, C., Þórisson, B., Wentworth, A., Gill, J.A. & Alves, J.A. 2020. Vegetation structure influences predation rates of early nests in subarctic breeding waders. *Ibis*.

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.

Laidlaw, R.A., Smart, J., Smart, M.A. & Gill, J.A. 2017. Scenarios of habitat management options to reduce predator impacts on nesting waders. *J Appl Ecol* 54: 1219–1229.

Le Saout, S., Hoffmann, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T.M., Bertzky, B., Butchart, S.H.M., Stuart, S.N., Badman, T. & Rodrigues, A.S.L. 2013. Protected Areas and Effective Biodiversity Conservation. *Science* 342: 803–805.

Leadley, P., Gonzalez, A., Obura, D., Krug, C.B., Londoño-Murcia, M.C., Millette, K.L., Radulovici, A., Rankovic, A., Shannon, L.J., Archer, E., Armah, F.A., Bax, N., Chaudhari, K., Costello, M.J., Dávalos, L.M., Roque, F. de O., DeClerck, F., Dee, L.E., Essl, F., Ferrier, S., Genovesi, P., Guariguata, M.R., Hashimoto, S., Ifejika Speranza, C., Isbell, F., Kok, M., Lavery, S.D., Leclère, D., Loyola, R., Lwasa, S., McGeoch, M., Mori, A.S., Nicholson, E., Ochoa, J.M., Öllerer, K., Polasky, S., Rondinini, C., Schroer, S., Selomane, O., Shen, X., Strassburg, B., Sumaila, U.R., Tittensor, D.P., Turak, E., Urbina, L., Vallejos, M., Vázquez-Domínguez, E., Verburg, P.H., Visconti, P., Woodley, S. & Xu, J. 2022. Achieving global biodiversity goals by 2050 requires urgent and integrated actions. *One Earth* 5: 597–603.

Lee, R., Cranswick, P.A., Cromie, R.L., Hilton, G.M., Jarrett, N.S. & Hughes, B. 2012. AEWA Guidelines for the Translocation of Waterbirds for Conservation Purposes: Complementing the IUCN Guidelines. AEWA Conservation Guidelines No. 13, AEWA Technical Series No. 49. Bonn, Germany.

Lees, A.C., Newton, I. & Balmford, A. 2013. Pheasants, buzzards, and trophic cascades. *Conservation Letters* 6: 141–144.

Lessmann, J., Muñoz, J. & Bonaccorso, E. 2014. Maximizing species conservation in continental Ecuador: a case of systematic conservation planning for biodiverse regions. *Ecology and Evolution* 4: 2410–2422.

Littlewood, N.A., Mason, T.H.E., Hughes, M., Jaques, R., Whittingham, M.J. & Willis, S.G. 2019. The influence of different aspects of grouse moorland management on nontarget bird assemblages. *Ecology and Evolution* 9: 11089–11101.

Loktionov, E.Y., Digby, R.A., Yakushev, N.N., Shepelev, I.A., Clements, J.P., Tomkovich, P.S., Jarrett, N.S., Clark, N.A., Green, R.E. & Lappo, E.G. 2023. Evaluating the Impacts of Headstarting on the Critically En-dangered Spoon-Billed Sandpiper Calidris Pygmaea.

Loonstra, A.H.J., Verhoeven, M.A., Senner, N.R., Hooijmeijer, J.C.E.W., Piersma, T. & Kentie, R. 2019. Natal habitat and sex-specific survival rates result in a male-biased adult sex ratio. *Behavioral Ecology* 30: 843–851.

Ludwig, S.C., Roos, S. & Baines, D. 2019. Responses of breeding waders to restoration of grouse management on a moor in South-West Scotland. *J Ornithol* 160: 789–797.

Lyons, J.E., Runge, M.C., Laskowski, H.P. & Kendall, W.L. 2008. Monitoring in the context of structured decision-making and adaptive management. *Journal of Wildlife Management* 72: 1683–1692.

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

Mace, G.M., Barrett, M., Burgess, N.D., Cornell, S.E., Freeman, R., Grooten, M. & Purvis, A. 2018. Aiming higher to bend the curve of biodiversity loss. *Nature Sustainability* 1: 448–451.

Malpas, L.R., Kennerley, R.J., Hirons, G.J., 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.

Marrs, R.H., Galtress, K., Tong, C., Cox, E.S., Blackbird, S.J., Heyes, T.J., Pakeman, R.J. & Le Duc, M.G. 2007. Competing conservation goals, biodiversity or ecosystem services: Element losses and species recruitment in a managed moorland–bracken model system. *Journal of Environmental Management* 85: 1034–1047.

Marzluff, J.M. & Neatherlin, E. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biological conservation* 130: 301–314.

Maslo, B. & Lockwood, J.L. 2009. Evidence-based decisions on the use of predator exclosures in shorebird conservation. *Biological Conservation* 142: 3213–3218.

Maslovsky, K.S., Maleko, P.N., Pronkevich, V.V., Slaght, J.C. & Powell, A.N. 2023. First nests of Endangered Nordmann's Greenshank Tringa guttifer found in over 40 years indicate nesting plasticity. *Bird Conservation International* 33: e43.

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.

Maxwell, S.L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A.S.L., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B.B.N., Wenger, A., Jonas, H.D., Venter, O. & Watson, J.E.M. 2020. Area-based conservation in the twenty-first century. *Nature* 586: 217–227.

McCarthy, D.P., Donald, P.F., Scharlemann, J.P.W., Buchanan, G.M., Balmford, A., Green, J.M.H., Bennun, L.A., Burgess, N.D., Fishpool, L.D.C., Garnett, S.T., Leonard, D.L., Maloney, R.F., Morling, P., Schaefer, H.M., Symes, A., Wiedenfeld, D.A. & Butchart, S.H.M. 2012. Financial Costs of Meeting Global Biodiversity Conservation Targets: Current Spending and Unmet Needs. *Science* 338: 946–949.

McHugh, N.M., Bown, B.L. & Clark, J.E. 2018. Use of field margins managed under an agri-environment scheme by foraging Barn Swallows Hirundo rustica. *Bird Study* 65: 329–337.

Méndez, V., Alves, J.A., Gill, J.A. & Gunnarsson, T.G. 2018. Patterns and processes in shorebird survival rates: a global review. *Ibis* 160: 723–741.

Méndez, V., Alves, J.A., Gill, J.A., Þórisson, B., Carneiro, C., Pálsdóttir, A.E., Vignisson, S.R. & Gunnarsson, T.G. 2022. Effects of pair migratory behavior on breeding phenology and success in a partially migratory shorebird population. *Ecology and Evolution* 12: e9184.

Méndez, V., Alves, J.A., Þórisson, B., Marca, A., Gunnarsson, T.G. & Gill, J.A. 2020. Individual variation in migratory behavior in a subarctic partial migrant shorebird. *Behavioral Ecology*.

Mérő, T.O., Žuljević, A. & Lengyel, S. 2023. The role of reed management and habitat quality on brood parasitism and chick survival of the brood parasitic Common Cuckoo. *Ecology and Evolution* 13: e9705.

Milner-Gulland, E., Addison, P., Arlidge, W.N., Baker, J., Booth, H., Brooks, T., Bull, J.W., Burgass, M.J., Ekstrom, J. & zu Ermgassen, S.O. 2021. Four steps for the Earth: mainstreaming the post-2020 global biodiversity framework. *One Earth* 4: 75–87.

Minton, C., Jessop, R., Collins, P. & Standen, R. 2011. The migration of Eastern Curlew Numenius madagascariensis to and from Australia. *Stilt* 59: 6–16.

Mitsch, W.J., Bernal, B., Nahlik, A.M., Mander, Ü., Zhang, L., Anderson, C.J., Jørgensen, S.E. & Brix, H. 2013. Wetlands, carbon, and climate change. *Landscape Ecol* 28: 583–597.

Molsher, R., Newsome, A.E., Newsome, T.M. & Dickman, C.R. 2017. Mesopredator management: Effects of Red Fox control on the abundance, diet and use of space by feral cats. *PLoS ONE* 12: e0168460.

Morrison, C.A., Alves, J.A., Gunnarsson, T.G., Þórisson, B. & Gill, J.A. 2019. Why do earlier-arriving migratory birds have better breeding success? *Ecology and Evolution* 9: 8856–8864.

Morrison, C.A., Butler, S.J., Clark, J.A., Arizaga, J., Baltà, O., Cepák, J., Nebot, A.L., Piha, M., Thorup, K., Wenninger, T., Robinson, R.A. & Gill, J.A. 2022. Demographic variation in space and time: implications for conservation targeting. *Royal Society Open Science* 9: 211671.

Morrison, C.A., Butler, S.J., Robinson, R.A., Clark, J.A., Arizaga, J., Aunins, A., Baltà, O., Cepák, J., Chodkiewicz, T., Escandell, V., Foppen, R.P.B., Gregory, R.D., Husby, M., Jiguet, F., Kålås, J.A., Lehikoinen, A., Lindström, Å., Moshøj, C.M., Nagy, K., Nebot, A.L., Piha, M., Reif, J., Sattler, T., Škorpilová, J., Szép, T., Teufelbauer, N., Thorup, K., van Turnhout, C., Wenninger, T. & Gill, J.A. 2021. Covariation in population trends and demography reveals targets for conservation action. *Proceedings of the Royal Society B: Biological Sciences* 288: 20202955.

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 B: Biological Sciences* 283: 20161387.

Morrison, T.H., Adger, W.N., Brown, K., Hettiarachchi, M., Huchery, C., Lemos, M.C. & Hughes, T.P. 2020. Political dynamics and governance of World Heritage ecosystems. *Nat Sustain* 3: 947–955.

Morton, R.D., Marston, C.G., O'Neil, A.W. & Rowland, C.S. 2021. Land Cover Map 2020 (land parcels, GB).

Murray, N.J., Clemens, R.S., Phinn, S.R., Possingham, H.P. & Fuller, R.A. 2014. Tracking the rapid loss of tidal wetlands in the Yellow Sea. *Frontiers in Ecology and the Environment* 12: 267–272.

Mustin, K., Arroyo, B., Beja, P., Newey, S., Irivine, R.J., Kestler, J. & Redpath, S.M. 2018. Consequences of game bird management for non-game species in Europe. *Journal of Applied Ecology* 55: 2285–2295.

Nagy, S. & Langendoen, T. 2020. Flyway trend analyses based on data from the African-Eurasian Waterbird Census from the period of 1967-2018. *Wetlands International, Wageningen*.

National Species Reintroduction Forum. 2014a. *The Scottish Code for Conservation Translocations. Scottish Natural Heritage, UK*.

National Species Reintroduction Forum. 2014b. *Best Practice Guidelines for Conservation Translocations in Scotland Version 1.1. Scottish Natural Heritage, UK*.

Navedo, J.G., Verdugo, C., Rodríguez-Jorquera, I.A., Abad-Gómez, J.M., Suazo, C.G., Castañeda, L.E., Araya, V., Ruiz, J. & Gutiérrez, J.S. 2019. Assessing the effects of human activities on the foraging opportunities of migratory shorebirds in Austral high-latitude bays. *PLoS One* 14: e0212441.

Newton, I. 2017. Invited commentary: fifty years of raptor research. *Journal of Raptor Research* 51: 95–106.

Newton, I. 2021. Killing of raptors on grouse moors: evidence and effects. *Ibis* 163: 1–19.

Nicholson, E., Fulton, E.A., Brooks, T.M., Blanchard, R., Leadley, P., Metzger, J.P., Mokany, K., Stevenson, S., Wintle, B.A., Woolley, S.N.C., Barnes, M., Watson, J.E.M. &

Ferrier, S. 2019. Scenarios and Models to Support Global Conservation Targets. *Trends in Ecology & Evolution* 34: 57–68.

Nicoll, M.A.C., Jones, C.G., Groombridge, J.G., Henshaw, S., Ruhomaun, K., Tatayah, V., Zuel, N. & Norris, K. 2021. Contrasting recovery trajectories of four reintroduced populations of the Endangered Mauritius Kestrel (Falco punctatus). *Ibis* 163: 1294–1309.

Niemczynowicz, A., Świętochowski, P., Brzeziński, M. & Zalewski, A. 2017. Non-native predator control increases the nesting success of birds: American mink preying on wader nests. *Biological Conservation* 212: 86–95.

Norbury, G. & van Overmeire, W. 2019. Low structural complexity of nonnative grassland habitat exposes prey to higher predation. *Ecological Applications* 29: e01830.

O'Donoghue, B.G. 2019. National survey of breeding Eurasian Curlew Numenius arquata in the Republic of Ireland, 2015–2017. *Wader Study* 126: 43–48.

Oppel, S., Beaven, B.M., Bolton, M., Vickery, J. & Bodey, T.W. 2011. Eradication of Invasive Mammals on Islands Inhabited by Humans and Domestic Animals. *Conservation Biology* 25: 232–240.

Owens, I.P. & Bennett, P.M. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences* 97: 12144–12148.

Owens, I.P., Burke, T. & Thompson, D.B. 1994. Extraordinary sex roles in the Eurasian dotterel: female mating arenas, female-female competition, and female mate choice. *The American Naturalist* 144: 76–100.

Pain, D., Hughes, B., Syroechkovskiy, E., Zöckler, C., Chowdhury, S., Anderson, G. & Clark, N. 2018. Saving the Spoon-billed Sandpiper: a conservation update. *British Birds* 111: 323–333.

Palacios, E., Vargas, J., Fernández, G. & Reiter, M.E. 2022. Impact of human disturbance on the abundance of non-breeding shorebirds in a subtropical wetland. *Biotropica* 54: 1160–1169.

Palmero, S., Belotti, E., Bufka, L., Gahbauer, M., Heibl, C., Premier, J., Weingarth-Dachs, K. & Heurich, M. 2021. Demography of a Eurasian lynx (Lynx lynx) population within a strictly protected area in Central Europe. *Sci Rep* 11: 19868.

Pálsdóttir, A.E., Gill, J.A., Alves, J.A., Pálsson, S., Méndez, V., Ewing, H. & Gunnarsson, T.G. 2022. Subarctic afforestation: Effects of forest plantations on ground-nesting birds in lowland Iceland. *Journal of Applied Ecology* n/a.

Pearce-Higgins, J.W., Brown, D.J., Douglas, D.J., Alves, J.A., Bellio, M., Bocher, P., Buchanan, G.M., Clay, R.P., Conklin, J. & Crockford, N. 2017. A global threats overview for Numeniini populations: synthesising expert knowledge for a group of declining migratory birds. *Bird Conserv Int* 27: 6–34.

Pearce-Higgins, J.W., Dennis, P., Whittingham, M.J. & Yalden, D.W. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Global Change Biology* 16: 12–23.

Pearce-Higgins, J.W. & Grant, M.C. 2006. Relationships between bird abundance and the composition and structure of moorland vegetation. *Bird Study* 53: 112–125.

Pederson, R., Bocher, P., Garthe, S., Fort, J., Mercker, M., Auernhammer, V., Boschert, M., Delaporte, P., Elts, J., Fiedler, W., Korniluk, M., Krupiński, D., Marja, R., Rousseau, P., Thiess, L. & Schwemmer, P. 2022. Bird migration in space and time: chain migration by Eurasian curlew Numenius arquata arquata along the East Atlantic Flyway. *Journal of Avian Biology* 2022: e02924.

Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W.J., Turbé, A., Wulf, F. & Scott, A.V. 2014. EU agricultural reform fails on biodiversity. *Science* 344: 1090–1092.

Perkins, A.J., Maggs, H.E., Watson, A. & Wilson, J.D. 2011. Adaptive management and targeting of agri-environment schemes does benefit biodiversity: a case study of the corn bunting Emberiza calandra. *Journal of Applied Ecology* 48: 514–522.

Petermann, J.S. & Buzhdygan, O.Y. 2021. Grassland biodiversity. *Current Biology* 31: R1195–R1201.

Peterson, G.D., Cumming, G.S. & Carpenter, S.R. 2003. Scenario Planning: a Tool for Conservation in an Uncertain World. *Conservation Biology* 17: 358–366.

Pettorelli, N., Graham, N.A.J., Seddon, N., Maria da Cunha Bustamante, M., Lowton, M.J., Sutherland, W.J., Koldewey, H.J., Prentice, H.C. & Barlow, J. 2021. Time to integrate global climate change and biodiversity science-policy agendas. *Journal of Applied Ecology* 58: 2384–2393.

Pickett, S.R.A. & Siriwardena, G.M. 2011. The relationship between multi-scale habitat heterogeneity and farmland bird abundance. *Ecography* 34: 955–969.

Piersma, T., Baker, A., Gosling, L. & Sutherland, W. 2000. Behaviour and conservation.

Piersma, T., Lok, T., Chen, Y., Hassell, C.J., Yang, H.-Y., Boyle, A., Slaymaker, M., Chan, Y.-C., Melville, D.S., Zhang, Z.-W. & Ma, Z. 2016. Simultaneous declines in summer survival of three shorebird species signals a flyway at risk. *Journal of Applied Ecology* 53: 479–490.

Pimm, S.L., Jenkins, C.N. & Li, B.V. 2018. How to protect half of Earth to ensure it protects sufficient biodiversity. *Science Advances* 4: eaat2616.

Pisupati, B. & Prip, C. 2015. Interim assessment of revised national biodiversity strategies and action plans (NBSAPs).

Plard, F., Arlettaz, R., Jacot, A. & Schaub, M. 2020. Disentangling the spatial and temporal causes of decline in a bird population. *Ecology and Evolution* 10: 6906–6918.

Porteus, T.A., Reynolds, J.C. & McAllister, M.K. 2019. Population dynamics of Foxes during restricted-area culling in Britain: Advancing understanding through state-space modelling of culling records. *PloS ONE* 14: e0225201.

Potts, G.R. 1980. The effects of modern agriculture, nest predation and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). *Advances in Ecological Research* 11: 1–82.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25: 345–353.

Powell, A.N., Cuthbert, F.J., Wemmer, L.C., Doolittle, A.W. & Feirer, S.T. 1997. Captive-rearing Piping Plovers: Developing techniques to augment wild populations. *Zoo Biology* 16: 461–477.

Powers, R.P. & Jetz, W. 2019. Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nat. Clim. Chang.* 9: 323–329.

Pringle, H., Wilson, M., Calladine, J. & Siriwardena, G. 2019. Associations between gamebird releases and generalist predators. *J Appl Ecol* 56: 2102–2113.

Ramírez-Albores, J.E., Prieto-Torres, D.A., Gordillo-Martínez, A., Sánchez-Ramos, L.E. & Navarro-Sigüenza, A.G. 2021. Insights for protection of high species richness areas for the conservation of Mesoamerican endemic birds. *Diversity and Distributions* 27: 18–33.

Ravetto Enri, S., Probo, M., Farruggia, A., Lanore, L., Blanchetete, A. & Dumont, B. 2017. A biodiversity-friendly rotational grazing system enhancing flower-visiting insect assemblages while maintaining animal and grassland productivity. *Agriculture, Ecosystems & Environment* 241: 1–10.

Rayner, M.J., Hauber, M.E., Imber, M.J., Stamp, R.K. & Clout, M.N. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy of Sciences* 104: 20862–20865.

Redford, K.H., Huntley, B.J., Roe, D., Hammond, T., Zimsky, M., Lovejoy, T.E., da Fonseca, G.A.B., Rodriguez, C.M. & Cowling, R.M. 2015. Mainstreaming Biodiversity: Conservation for the Twenty-First Century. *Frontiers in Ecology and Evolution* 3.

Redhead, J.W., Hinsley, S.A., Botham, M.S., Broughton, R.K., Freeman, S.N., Bellamy, P.E., Siriwardena, G., Randle, Z., Nowakowski, M., Heard, M.S. & Pywell, R.F. 2022. The effects of a decade of agri-environment intervention in a lowland farm landscape on population trends of birds and butterflies. *Journal of Applied Ecology* 59: 2486–2496.

Reif, J. & Hanzelka, J. 2020. Continent-wide gradients in open-habitat insectivorous bird declines track spatial patterns in agricultural intensity across Europe. *Global Ecology and Biogeography* 29: 1988–2013.

Reynolds, J.C., Short, M.J. & Leigh, R.J. 2004. Development of population control strategies for Mink *Mustela vison*, using floating rafts as monitors and trap sites. *Biological Conservation* 120: 533–543.

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.

Ridding, L.E., Redhead, J.W. & Pywell, R.F. 2015. Fate of semi-natural grassland in England between 1960 and 2013: A test of national conservation policy. *Global Ecology and Conservation* 4: 516–525.

Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G. & McDonald, R.A. 2012. Ecosystem restoration with teeth: what role for predators? *Trends in ecology & evolution* 27: 265–271.

Ritchie, E.G. & Johnson, C.N. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology letters* 12: 982–998.

Robertson, E.P., Tanner, E.P., Elmore, R.D., Fuhlendorf, S.D., Mays, J.D., Knutson, J., Weir, J.R. & Loss, S.R. 2022. Fire management alters the thermal landscape and provides multi-scale thermal options for a terrestrial turtle facing a changing climate. *Global Change Biology* 28: 782–796.

Robinson, R.A., Balmer, D.E. & Marchant, J.H. 2008. Survival rates of hirundines in relation to British and African rainfall. *Ringing & Migration* 24: 1–6.

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.

Robinson, R.A., Sanders, J.D. & Rees, E.C. 2020. Survival of Eurasian Curlew Numenius arquata differs by season but not breeding origin. *Wader Study* 127.

Roilo, S., Engler, J.O., Václavík, T. & Cord, A.F. 2023. Landscape-level heterogeneity of agri-environment measures improves habitat suitability for farmland birds. *Ecological Applications* 33: e2720.

Roodbergen, M., van der Werf, B. & Hotker, 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.

Roos, S., Smart, J., Gibbons, D.W. & Wilson, J.D. 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. *Biological Reviews* 93: 1915–1937.

Rosenberg, K.V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A., Stanton, J.C., Panjabi, A., Helft, L., Parr, M. & Marra, P.P. 2019. Decline of the North American avifauna. *Science* 366: 120–124.

Ross, A.K., Lawes, J.C., Elphinstone, A., Stutsel, S. & Letnic, M. 2021. Headstarting as a cost-effective conservation strategy for an endangered mammal. *Current Biology* 31: R465–R466.

Russell, J.C., Jones, H.P., Armstrong, D.P., Courchamp, F., Kappes, P.J., Seddon, P.J., Oppel, S., Rauzon, M.J., Cowan, P.E., Rocamora, G., Genovesi, P., Bonnaud, E., Keitt, B.S., Holmes, N.D. & Tershy, B.R. 2016. Importance of lethal control of invasive predators for island conservation. *Conservation Biology* 30: 670–672.

Saalfeld, S.T., McEwen, D.C., Kesler, D.C., Butler, M.G., Cunningham, J.A., Doll, A.C., English, W.B., Gerik, D.E., Grond, K. & Herzog, P. 2019. Phenological mismatch in Arctic-breeding shorebirds: Impact of snowmelt and unpredictable weather conditions on food availability and chick growth. *Ecology and Evolution* 9: 6693–6707.

Sæther, B.-E. & Bakke, Ø. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81: 642–653.

Sala, E., Costello, C., De Bourbon Parme, J., Fiorese, M., Heal, G., Kelleher, K., Moffitt, R., Morgan, L., Plunkett, J., Rechberger, K.D., Rosenberg, A.A. & Sumaila, R. 2016. Fish banks: An economic model to scale marine conservation. *Marine Policy* 73: 154–161.

Salafsky, N., Boshoven, J., Burivalova, Z., Dubois, N.S., Gomez, A., Johnson, A., Lee, A., Margoluis, R., Morrison, J., Muir, M., Pratt, S.C., Pullin, A.S., Salzer, D., Stewart, A., Sutherland, W.J. & Wordley, C.F.R. 2019. Defining and using evidence in conservation practice. *Conservation Science and Practice* 1: e27.

Sales, L.P., Galetti, M., Carnaval, A., Monsarrat, S., Svenning, J.-C. & Pires, M.M. 2022. The effect of past defaunation on ranges, niches, and future biodiversity forecasts. *Global Change Biology* 28: 3683–3693.

Salzman, J., Bennett, G., Carroll, N., Goldstein, A. & Jenkins, M. 2018. The global status and trends of Payments for Ecosystem Services. *Nat Sustain* 1: 136–144.

Sandercock, B.K., Alfaro-Barrios, M., Casey, A.E., Johnson, T.N., Mong, T.W., Odom, K.J., Strum, K.M. & Winder, V.L. 2015. Effects of grazing and prescribed fire on resource selection and nest survival of upland sandpipers in an experimental landscape. *Landscape Ecol* 30: 325–337.

Sandercock, B.K. & Gratto-Trevor, C.L. 2023. Breeding populations of Marbled Godwits and Willets have high annual survival and strong site fidelity to managed wetlands. *Ecology and Evolution* 13: e9667.

Sanderson, F.J., Wilson, J.D., Franks, S.E. & Buchanan, G.M. n.d. Benefits of protected area networks for breeding bird populations and communities. *Animal Conservation* n/a.

Sanz-Pérez, A., Giralt, D., Robleño, I., Bota, G., Milleret, C., Mañosa, S. & Sardà-Palomera, F. 2019. Fallow management increases habitat suitability for endangered steppe bird species through changes in vegetation structure. *Journal of Applied Ecology* 56: 2166–2175.

Schamel, D., Tracy, D.M., Lank, D.B. & Westneat, D.F. 2004. Mate guarding, copulation strategies and paternity in the sex-role reversed, socially polyandrous red-necked phalarope Phalaropus lobatus. *Behavioral Ecology and Sociobiology* 57: 110–118.

Schils, R.L.M., Bufe, C., Rhymer, C.M., Francksen, R.M., Klaus, V.H., Abdalla, M., Milazzo, F., Lellei-Kovács, E., Berge, H. ten, Bertora, C., Chodkiewicz, A., Dămătîrcă, C., Feigenwinter, I., Fernández-Rebollo, P., Ghiasi, S., Hejduk, S., Hiron, M., Janicka, M., Pellaton, R., Smith, K.E., Thorman, R., Vanwalleghem, T., Williams, J., Zavattaro, L., Kampen, J., Derkx, R., Smith, P., Whittingham, M.J., Buchmann, N. & Price, J.P.N. 2022. Permanent grasslands in Europe: Land use change and intensification decrease their multifunctionality. *Agriculture, Ecosystems & Environment* 330: 107891.

Schnell, J.K., Harris, G.M., Pimm, S.L. & Russell, G.J. 2013. Estimating extinction risk with metapopulation models of large-scale fragmentation. *Conservation Biology* 27: 520–530.

Schorger, A.W. 1955. The passenger pigeon, its natural history and extinction.

Schroeder, J., Piersma, T., Groen, N.M., Hooijmeijer, J.C., Kentie, R., Lourenço, P.M., Schekkerman, H. & Both, C. 2012. Reproductive timing and investment in relation to spring warming and advancing agricultural schedules. *J Ornithol* 153: 327–336.

Seddon, P.J., Armstrong, D.P. & Maloney, R.F. 2007. Developing the science of reintroduction biology. *Conservation biology* 21: 303–312.

Seidl, A., Mulungu, K., Arlaud, M., van den Heuvel, O. & Riva, M. 2020. Finance for nature: A global estimate of public biodiversity investments. *Ecosystem Services* 46: 101216.

Sekercioglu, C.H. 2011. Functional extinctions of bird pollinators cause plant declines. *Science* 331: 1019–1020.

Sergio, F., Tavecchia, G., Blas, J., Tanferna, A. & Hiraldo, F. 2021. Demographic modeling to fine-tune conservation targets: importance of pre-adults for the decline of an endangered raptor. *Ecological Applications* 31: e2266.

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.

Silva, J.P., Correia, R., Alonso, H., Martins, R.C., D’Amico, M., Delgado, A., Sampaio, H., Godinho, C. & Moreira, F. 2018. EU protected area network did not prevent a country wide population decline in a threatened grassland bird. *PeerJ* 6: e4284.

Silva-Monteiro, M., Pehlak, H., Fokker, C., Kingma, D. & Kleijn, D. 2021. Habitats supporting wader communities in Europe and relations between agricultural land use and breeding densities: A review. *Global Ecology and Conservation* 28: e01657.

Simón, M.A., Gil-Sánchez, J.M., Ruiz, G., Garrote, G., Mccain, E.B., Fernández, L., López-Parra, M., Rojas, E., Arenas-Rojas, R., Rey, T.D., García-Tardío, M. & López, G. 2012. Reverse of the Decline of the Endangered Iberian Lynx. *Conservation Biology* 26: 731–736.

Siriwardena, G.M., Calbrade, N.A. & Vickery, J.A. 2008. Farmland birds and late winter food: does seed supply fail to meet demand? *Ibis* 150: 585–595.

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. *BULLETIN-WADER STUDY GROUP* 100: 80–85.

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.

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, P.A., McKinnon, L., Meltofte, H., Lanctot, R.B., Fox, A.D., Leafloor, J.O., Soloviev, M., Franke, A., Falk, K., Golovatin, M., Sokolov, V., Sokolov, A. & Smith, A.C. 2020. Status and trends of tundra birds across the circumpolar Arctic. *Ambio* 49: 732–748.

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.

Staggenborg, J. & Anthes, N. 2022. Long-term fallows rate best among agri-environment scheme effects on farmland birds—A meta-analysis. *Conservation Letters* 15: e12904.

Stanbury, A., Eaton, M., Aebischer, N., Balmer, D., Brown, A., Douse, A., Lindley, P., McCulloch, N., Noble, D. & Win, I. 2021. The status of our bird. *British Birds* 114: 723–747.

Stevens, M., Murn, C. & Hennessey, R. 2020. Population change of red kites milvus milvus in central southern england between 2011 and 2016 derived from line transect surveys and multiple covariate distance sampling. *Acta Ornithologica* 54: 243–254.

Storm, G.L., Andrews, R.D., Phillips, R.L., Bishop, R.A., Siniff, D.B. & Tester, J.R. 1976. Morphology, reproduction, dispersal, and mortality of midwestern Red Fox populations. *Wildlife Monographs* 49: 3–82.

Strassburg, B.B.N., Iribarrem, A., Beyer, H.L., Cordeiro, C.L., Crouzeilles, R., Jakovac, C.C., Braga Junqueira, A., Lacerda, E., Latawiec, A.E., Balmford, A., Brooks, T.M., Butchart, S.H.M., Chazdon, R.L., Erb, K.-H., Brancalion, P., Buchanan, G., Cooper, D., Díaz, S., Donald, P.F., Kapos, V., Leclère, D., Miles, L., Obersteiner, M., Plutzar, C., de M. Scaramuzza, C.A., Scarano, F.R. & Visconti, P. 2020. Global priority areas for ecosystem restoration. *Nature* 586: 724–729.

Studds, C.E., Kendall, B.E., Murray, N.J., Wilson, H.B., Rogers, D.I., Clemens, R.S., Gosbell, K., Hassell, C.J., Jessop, R. & Melville, D.S. 2017. Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. *Nature communications* 8: 1–7.

Sullivan, M.J., Newson, S.E. & Pearce-Higgins, J.W. 2015. Using habitat-specific population trends to evaluate the consistency of the effect of species traits on bird population change. *Biological Conservation* 192: 343–352.

Sutherland, W.J., Alvarez-Castañeda, S.T., Amano, T., Ambrosini, R., Atkinson, P., Baxter, J.M., Bond, A.L., Boon, P.J., Buchanan, K.L., Barlow, J., Bogliani, G., Bragg, O.M., Burgman, M., Cadotte, M.W., Calver, M., Cooke, S.J., Corlett, R.T., Devictor, V., Ewen, J.G., Fisher, M., Freeman, G., Game, E., Godley, B.J., Gortázar, C., Hartley, I.R., Hawksworth, D.L., Hobson, K.A., Lu, M.-L., Martín-López, B., Ma, K., Machado, A., Maes, D., Mangiacotti, M., McCafferty, D.J., Melfi, V., Molur, S., Moore, A.J., Murphy, S.D., Norris, D., van Oudenhoven, A.P.E., Powers, J., Rees, E.C., Schwartz, M.W., Storch, I. & Wordley, C. 2020. Ensuring tests of conservation interventions build on existing literature. *Conservation Biology* 34: 781–783.

Sutherland, W.J., Alves, J.A., Amano, T., Chang, C.H., Davidson, N.C., Max Finlayson, C., Gill, J.A., Gill Jr, R.E., González, P.M. & Gunnarsson, T.G. 2012. A horizon scanning assessment of current and potential future threats to migratory shorebirds. *Ibis* 154: 663–679.

Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. 2004. The need for evidence-based conservation. *Trends in ecology & evolution* 19: 305–308.

Sutherland, W.J., Taylor, N.G., MacFarlane, D., Amano, T., Christie, A.P., Dicks, L.V., Lemasson, A.J., Littlewood, N.A., Martin, P.A. & Ockendon, N. 2019. Building a tool to overcome barriers in research-implementation spaces: The Conservation Evidence database. *Biological conservation* 238: 108199.

Swan, G., Naidoo, V., Cuthbert, R., Green, R.E., Pain, D.J., Swarup, D., Prakash, V., Taggart, M., Bekker, L. & Das, D. 2006. Removing the threat of diclofenac to critically endangered Asian vultures. *PLoS biology* 4: e66.

Syroechkovski, E., Tomkovich, P., Kashiwagi, M., Taldenkov, I., Buzin, V., Lappo, E. & Zöckler, C. 2010. Population decline in the spoon-billed sandpiper (Eurynorhynchus pygmeus) in northern Chukotka based on monitoring on breeding grounds. *Biology bulletin* 37: 941–951.

Taylor, R.C. & Dodd, S.G. 2013. Negative impacts of hunting and suction-dredging on otherwise high and stable survival rates in Curlew Numenius arquata. *Bird Study* 60: 221–228.

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.

Thaxter, C.B., Joys, A.C., Gregory, R.D., Baillie, S.R. & Noble, D.G. 2010. Hypotheses to explain patterns of population change among breeding bird species in England. *Biological Conservation* 143: 2006–2019.

Thomas, S.M., Soka, G.E. & Mulungu, L.S. 2022. Influence of vegetation structure, seasonality, and soil properties on rodent diversity and community assemblages in west Mount Kilimanjaro, Tanzania. *Ecology and Evolution* 12: e9211.

Thorup, O. 2006. Breeding waders in Europe 2000. International Wader Studies 14. *International wader study group, UK*.

Tittensor, D.P., Walpole, M., Hill, S.L., Boyce, D.G., Britten, G.L., Burgess, N.D., Butchart, S.H., Leadley, P.W., Regan, E.C. & Alkemade, R. 2014. A mid-term analysis of progress toward international biodiversity targets. *Science* 346: 241–244.

Török, P., Brudvig, L.A., Kollmann, J., N. Price, J. & Tóthmérész, B. 2021. The present and future of grassland restoration. *Restoration Ecology* 29: e13378.

Trewby, I.D., Wilson, G.J., Delahay, R.J., Walker, N., Young, R., Davison, J., Cheeseman, C., Robertson, P.A., Gorman, M.L. & McDonald, R.A. 2008. Experimental evidence of competitive release in sympatric carnivores. *Biology Letters* 4: 170–172.

Tuyttens, F.A.M., Delahay, R.J., Macdonald, D.W., Cheeseman, C.L., Long, B. & Donnelly, C.A. 2000. Spatial perturbation caused by a Badger (Meles meles) culling operation: implications for the function of territoriality and the control of bovine tuberculosis (Mycobacterium bovis). *Journal of Animal Ecology* 69: 815–828.

Unep-Wcmc, I. 2021. Protected Planet Report 2020. *Gland: Cambridge, UK*.

Urban, M.C. 2015. Accelerating extinction risk from climate change. *Science* 348: 571–573.

Valkama, J. & Currie, D. 1999. Low productivity of curlews Numenius arquata on farmland in southern Finland: causes and consequences. *Ornis Fennica* 76: 65–70.

Valkama, J., Robertson, P. & Currie, D. 1998. Habitat selection by breeding curlews (Numenius arquata) on farmland: the importance of grassland. pp. 141–148. JSTOR.

Valkó, O., Török, P., Deák, B. & Tóthmérész, B. 2014. Review: Prospects and limitations of prescribed burning as a management tool in European grasslands. *Basic and Applied Ecology* 15: 26–33.

van der Kolk, H., Allen, A.M., Ens, B.J., Oosterbeek, K., Jongejans, E. & van de Pol, M. 2020. Spatiotemporal variation in disturbance impacts derived from simultaneous tracking of aircraft and shorebirds. *Journal of Applied Ecology* 57: 2406–2418.

Van der Kolk, H., Krijgsveld, K., Linssen, H., Diertens, R., Dolman, D., Jans, M., Frauendorf, M., Ens, B. & Van de Pol, M. 2020. Cumulative energetic costs of military aircraft, recreational and natural disturbance in roosting shorebirds. *Animal Conservation* 23: 359–372.

Verhoeven, J.T. 2014. Wetlands in Europe: perspectives for restoration of a lost paradise. *Ecological engineering* 66: 6–9.

Verhoeven, M.A., Jelle Loonstra, A.H., Pringle, T., Kaspersma, W., Whiffin, M., McBride, A.D., Sjoerdsma, P., Roodhart, C., Burgess, M.D., Piersma, T. & Smart, J. 2022. Do ditch-side electric fences improve the breeding productivity of ground-nesting waders? *Ecological Solutions and Evidence* 3: e12143.

Verhoeven, M.A., Loonstra, A.H.J., McBride, A.D., Macias, P., Kaspersma, W., Hooijmeijer, J.C.E.W., van der Velde, E., Both, C., Senner, N.R. & Piersma, T. 2020. Geolocators lead to better measures of timing and renesting in black-tailed godwits and reveal the bias of traditional observational methods. *Journal of Avian Biology* 51.

Verhulst, J., Kleijn, D. & Berendse, F. 2007. Direct and indirect effects of the most widely implemented Dutch agri-environment schemes on breeding waders. *J Appl Ecol* 44: 70–80.

Verhulst, S., Oosterbeek, K., Rutten, A. & Ens, B. 2004. Shellfish Fishery Severely Reduces Condition and Survival of Oystercatchers Despite Creation of Large Marine Protected Areas. *Ecology and Society* 9.

Vervoort, R. & Kempenaers, B. 2020. Variation in lek attendance and copulation success of independent and satellite male ruffs Calidris pugnax. *Ardea* 107: 303–320.

Viana, D.S., Santoro, S., Soriguer, R.C. & Figuerola, J. 2023 A synthesis of Eurasian Curlew (Numenius arquata arquata) demography and population viability to inform its management. *Ibis*.

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.

Vickery, J.A., Bradbury, R.B., Henderson, I.G., Eaton, M.A. & Grice, P.V. 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. *Biological Conservation* 119: 19–39.

Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R. & Stopak, D. 2021. Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences* 118: e2023989118.

Waldron, A., Miller, D.C., Redding, D., Mooers, A., Kuhn, T.S., Nibbelink, N., Roberts, J.T., Tobias, J.A. & Gittleman, J.L. 2017. Reductions in global biodiversity loss predicted from conservation spending. *Nature* 551: 364–367.

Walmsley, D.C., Delory, B.M., Alonso, I., Temperton, V.M. & Härdtle, W. 2021. Ensuring the Long-Term Provision of Heathland Ecosystem Services—The Importance of a Functional Perspective in Management Decision Frameworks. *Frontiers in Ecology and Evolution* 9.

Warren, M.S., Maes, D., van Swaay, C.A.M., Goffart, P., Van Dyck, H., Bourn, N.A.D., Wynhoff, I., Hoare, D. & Ellis, S. 2021. The decline of butterflies in Europe: Problems, significance, and possible solutions. *Proceedings of the National Academy of Sciences* 118: e2002551117.

Waterhouse, L., Heppell, S.A., Pattengill-Semmens, C.V., McCoy, C., Bush, P., Johnson, B.C. & Semmens, B.X. 2020. Recovery of critically endangered Nassau grouper (Epinephelus striatus) in the Cayman Islands following targeted conservation actions. *PNAS* 117: 1587–1595.

Watson, J.E.M., Dudley, N., Segan, D.B. & Hockings, M. 2014. The performance and potential of protected areas. *Nature* 515: 67–73.

Watson, R.T., Sebunya, K., Levin, L.A., Eisenhauer, N., Lavorel, S., Hickler, T., Lundquist, C., Gasalla, M. & Reyers, B. 2021. Post-2020 aspirations for biodiversity. *One Earth* 4: 893–896.

Watt, A. 1936. Studies in the ecology of Breckland: I. Climate, soil and vegetation. *Journal of Ecology* 24: 117–138.

Watts, B.D. & Turrin, C. 2016. Assessing hunting policies for migratory shorebirds throughout the Western Hemisphere. *Wader Study* 123: 1–10.

Wauchope, H.S., Jones, J.P.G., Geldmann, J., Simmons, B.I., Amano, T., Blanco, D.E., Fuller, R.A., Johnston, A., Langendoen, T., Mundkur, T., Nagy, S. & Sutherland, W.J. 2022. Protected areas have a mixed impact on waterbirds, but management helps. *Nature* 605: 103–107.

Wauchope, H.S., Shaw, J.D., Varpe, Ø., Lappo, E.G., Boertmann, D., Lanctot, R.B. & Fuller, R.A. 2017. Rapid climate-driven loss of breeding habitat for Arctic migratory birds. *Global Change Biology* 23: 1085–1094.

Weiser, E.L., Brown, S.C., Lanctot, R.B., Gates, H.R., Abraham, K.F., Bentzen, R.L., Bêty, J., Boldenow, M.L., Brook, R.W., Donnelly, T.F., English, W.B., Flemming, S.A., Franks, S.E., Gilchrist, H.G., Giroux, M.-A., Johnson, A., Kennedy, L.V., Koloski, L., Kwon, E., Lamarre, J.-F., Lank, D.B., Lecomte, N., Liebezeit, J.R., McKinnon, L., Nol, E., Perz, J., Rausch, J., Robards, M., Saalfeld, S.T., Senner, N.R., Smith, P.A., Soloviev, M., Solovyeva, D., Ward, D.H., Woodard, P.F. & Sandercock, B.K. 2018. Life-history tradeoffs revealed by seasonal declines in reproductive traits of Arctic-breeding shorebirds. *Journal of Avian Biology* 49: jav-01531.

White, G. & Hirons, G. 2019. The predator exclusion fence manual. Guidance on the use of predator exclusion fences to reduce mammalian predation on ground-nesting birds on RSPB reserves.

Whitehorn, P.R., Navarro, L.M., Schröter, M., Fernandez, M., Rotllan-Puig, X. & Marques, A. 2019. Mainstreaming biodiversity: A review of national strategies. *Biological Conservation* 235: 157–163.

Whittingham, M.J. & Evans, K.L. 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis* 146: 210–220.

Wijewardena, T., Keevil, M.G., Mandrak, N.E., Lentini, A.M. & Litzgus, J.D. 2023. Evaluation of headstarting as a conservation tool to recover Blanding's Turtles (Emydoidea blandingii) in a highly fragmented urban landscape. *Plos one* 18: e0279833.

Williamson, D. & Williamson, J. 1984. Botswana's fences and the depletion of Kalahari wildlife. *Oryx* 18: 218–222.

Wilson, L.J., Rendell-Read, S., Lock, L., Drewitt, A.L. & Bolton, M. 2020. Effectiveness of a five-year project of intensive, regional-scale, coordinated management for little terns Sternula albifrons across the major UK colonies. *Journal for Nature Conservation* 53: 125779.

Wong, D.T.Y., Gruber, B., Sarre, S.D. & Osborne, W.S. 2021. Agricultural modification to vegetation drives presence and abundance of a threatened fossorial legless lizard. *Austral Ecology* 46: 437–448.

Woodward, I., Aebischer, N., Burnell, D., Eaton, M., Frost, T., Hall, C., Stroud, D. & Noble, D. 2020. Population estimates of birds in Great Britain and the United Kingdom. *Br. Birds* 113: 69–104.

Wright, H.L., Lake, I.R. & Dolman, P.M. 2012. Agriculture—a key element for conservation in the developing world. *Conservation Letters* 5: 11–19.

Xu, H., Cao, Y., Yu, D., Cao, M., He, Y., Gill, M. & Pereira, H.M. 2021. Ensuring effective implementation of the post-2020 global biodiversity targets. *Nat Ecol Evol* 5: 411–418.

Ylimaunu, O., Ylimaunu, J., Hemminki, O. & Liehu, H. 1987. Breeding ecology and size of the breeding Curlew (Numenius arquata) population in Finland. *Lintumies* 22: 98–103.

Young, H.S., McCauley, D.J., Galetti, M. & Dirzo, R. 2016. Patterns, Causes, and Consequences of Anthropocene Defaunation. *Annual Review of Ecology, Evolution, and Systematics* 47: 333–358.

Zhao, X., Zhou, D. & Fang, J. 2012. Satellite-based Studies on Large-Scale Vegetation Changes in ChinaF. *Journal of Integrative Plant Biology* 54: 713–728.

Zielonka, N.B., Hawkes, R.W., Jones, H., Burnside, R.J. & Dolman, P.M. 2020. Placement, survival and predator identity of Eurasian Curlew Numenius arquata nests on lowland grass-heath. *Bird Study* 1–13.