Managing wet grassland landscapes: impacts on predators and wader nest predation

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Abstract

Since the early twentieth century there has been widespread loss and degradation of wetlands resulting from land drainage and agricultural intensification. Many breeding wader populations in wetlands across Western Europe have declined severely as a consequence of this habitat loss, and their ranges are now increasingly restricted to nature reserves. The habitat requirements of these species, and management actions to achieve these conditions, are well-established but the recovery of many populations may be limited by high levels of predation of eggs and chicks. In this thesis, I assess the distribution of mammalian predators and their small mammal prey in a landscape managed for breeding waders within lowland wet grasslands, and use these findings to consider the potential for habitat management to reduce levels of nest predation for lapwing, *Vanellus vanellus*, and redshank, *Tringa totanus*. Within these wet grasslands, I show that small mammals are almost entirely restricted to tall vegetation, which is rare and typically occurs only in verges outside fields. Lapwing nest predation rates are lower when nests are closer to these verges and when there is more verge in the surrounding landscape. Lapwing nest predation is also lower when nests are closer to field edges in drier fields, and further from field edges in wetter fields. Red foxes are the primary nest predator, and nest predation rates of lapwing and redshank, and fox use of tracking plots, are lower when lapwing nest densities are higher. Modelled scenarios of potential influence of future changes in reserve management indicate that changes in surface flooding would have little impact on lapwing nest predation, but removal of verges could result in significant increases of ~10%. Combining environmental factors associated with nest predation with realistic habitat modifications can be a useful tool for assessing the potential scale of consequences of management actions.

Contents

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General Introduction

Current rates of species decline and extinction are substantially higher than would be expected from the fossil record (MEA 2005) and, unless efforts to mitigate these losses are implemented, the rate of extinction is likely to intensify in the future (Barnosky *et al.* 2011). Human influence now extends across all of the Earth's ecosystems, and much of the structure and functioning of these ecosystems cannot be understood without accounting for the dominant influence of humanity (Vitousek *et al.* 1997). The continued range of threats posed by climate change (Walther *et al.* 2002) and land use change (Foley *et al.* 2005) mean that many ecosystems and the species they support are under increasing threat (MEA 2005; Donald *et al.* 2006; Pereira *et al.* 2010).

A major problem for populations of declining species is that they are often constrained into relatively small areas (Jackson & Gaston 2008), and these fragments of natural and semi-natural habitats are often isolated within inhospitable surrounding landscapes. It has been suggested that mobile generalist predators may be attracted into these areas, as they are likely to support greater prey abundance than surrounding landscapes (Shears & Babcock 2002), and thus predation success may be higher in these areas (Batáry & Báldi 2004). Predation can therefore potentially have a disproportionately high impact on species of conservation concern, which are often concentrated in these habitat fragments. Management efforts to reduce fragmentation within the landscape have largely focussed upon improving the conditions within the surrounding landscape (Whittingham 2007; Wilson, Vickery, & Pendlebury 2007), and relatively little is typically known about any subsequent impacts on predation.

In this thesis I consider the issue of generalist predator impacts upon species of conservation concern within a fragmented wet grassland ecosystem, and the potential for habitat management within these landscapes to influence the impact of predation.

1. Environmental change influencing species interactions

Drivers of global environmental change, including climate change and land use change, are having substantial impacts on the distribution and extinction risk of the planet's flora and fauna (Walther *et al.* 2002; Thomas *et al.* 2004; MEA 2005). However, there is also a mounting body of evidence to suggest that changes in the environment are also influencing interactions among species (Tylianakis *et al.* 2008). Most food webs have many components with varying strengths of connections between them (Pimm, Lawton, & Cohen 1991), and altered interactions between species could represent a functionally important effect of habitat modification caused by anthropomorphic habitat changes. However, species interactions have often been overlooked in favour of diversity and richness measures in studies quantifying the influence of environmental change (Tylianakis, Tscharntke, & Lewis 2007).

Global climate changes are resulting in changing rates of warming and cooling, increased intensity of rainfall and changing storm frequencies (IPCC 2007), and these shifting conditions may also influence species interactions. For example, the breeding seasons of some amphibians in Britain have advanced in response to climate change, leading to altered temporal niche overlaps in which earlier breeding newts (*Triturus* spp.) exert a higher level of predation on frogs (*Rana temporaria*) that have not altered their reproductive phenology (Walther *et al.* 2002). The magnitude of species responses to climate change have been found to increase with trophic level (Byrnes *et al.* 2011), and different levels of response of species can disrupt trophic relationships, prompting trophic cascades as communities are destabilised in response to climate change (Voigt *et al.* 2003). For example, in microcosm experiments with aquatic microbes, the influence of environmental warming has been shown to disproportionately affect top predators and herbivores and lead to differences in ecosystem function (Petchey *et al.* 1999). Changing climatic conditions also have the potential to change the abundance and quality of prey species, which can disrupt predator-prey dynamics. For example, reductions in sea temperatures have been linked to smaller herring, *Clupea harengus,* which then reduces the breeding success of Atlantic puffins, *Fratercula arctica*, that prey on the herring (Durant, Anker-Nilssen, & Stenseth 2003). Long-term effects of altered environmental conditions can also disrupt community interactions and lead to simplifications of community structure (Suttle, Thomsen, & Power 2007).

While climate change poses a challenge for future management of ecosystems, land use change has been a long-term driver of environmental change, and habitat degradation continues to be a major threat to biodiversity conservation. The structure of food webs can alter top species' responses to habitat loss, with top predators more likely to persist in the face of habitat destruction when they are within a foodweb including high levels of omnivory (Melián & Bascompte 2002). Food web structure can be altered by habitat fragmentation, with habitat loss leading to contraction of foodwebs around a central core of highly-connected species (Valladares, Cagnolo, & Salvo 2012). In agricultural landscapes, increases in the intensity of management have been shown to lead to decreases in the evenness of interaction frequencies among cavity-nesting bees and wasps, even resulting in a single trophic interaction involving a pupal parasitoid dominating foodwebs (Tylianakis, Tscharntke, & Lewis 2007). Environmental destruction from processes such as eutrophication has also been shown to alter food web structures in Atlantic seagrass (Coll *et al.* 2011) and in Caribbean coastal habitats

(Piovia-Scott, Spiller, & Schoener 2011). Understanding the influence of environment change on ecological networks can improve the ability to predict and mitigate the impacts of these changes (Evans, Pocock, & Memmott 2013).

Predator-prey relationships are of considerable ecological interest and importance, and are frequently complex. The investigation of numerical (increase in predator density) and functional (change in predator intake rate with prey abundance) responses of predators can also be complicated by fluctuations in the abundance of alternative prey, such as seasonally available nests. Increases in prey abundance can increase predation such that competition no longer shapes communities (Roemer, Donlan, & Courchamp 2002; Henden *et al.* 2010). This is particularly the case where multiple predator species can prey on a single species, impacting on different life stages, and interacting with each other (Polis, Myers, & Holt 1989; Finke & Denno 2004), either through competition or through the existence of further predator-prey relationships at other trophic levels. Measures to address the impacts of particular predators are most likely to be successful if they are based on a good understanding of the intra-guild relationships of the potential predator species and the life stage at which impacts occur.

2. Determining the identity and impact of predators

The top-down regulation of prey by predators can be one of the main factors limiting prey population densities (Menge & Sutherland 1976). Knowledge of the identity of predators and their impact upon prey populations is important for understanding how alterations in their relationships could influence foodweb functioning. There are numerous methods for determining the identity and behaviours of predators (Stillman *et al.* 2006): predator scats, pellets or other field-signs can indicate presence within an area; prey remains identified within scats, pellets or stomachs of predators can provide evidence of the prey being consumed; and technologies such as dataloggers can provide information on the timing of predation events while cameras can link specific predator species to prey species, life stages and locations (Bolton *et al.* 2007a).

Predation is a natural process but perturbations to ecosystems can result in disproportionate impacts of predators which, when they involve rare or declining prey species, can become an issue of conservation concern. The huge impact that non-native mammalian predators can have on native endemic species with few or no native predators is well documented, for example in New Zealand (Dowding & Murphy 2001; Remeš, Matysioková, & Cockburn 2012) and on many island ecosystems (Blackburn *et al.* 2004; Sih *et al.* 2010). However, predation can also detrimentally impact species of conservation concern within their native foodwebs when processes or conditions change over time. For example, declines in the abundance of prey species resulting from habitat loss can mean that small, fragmented populations can be limited by predation, even from natural predators (Macdonald, Mace, & Barretto 1999).

Non-consumptive effects of predation that alter prey behaviour, morphology or life histories have been suggested to have fitness costs that can be equal to or stronger than direct effects of predation (Preisser, Bolnick, & Benard 2005). The indirect influence of predators on prey can act through behavioural changes in prey as a result of perceived predation risk, which can reduce key demographic parameters such as offspring production (Martin 2011). For example, pied flycatchers *Ficedula hypoleuca* have been shown to have fewer and smaller nestlings when nesting closer to sparrowhawk *Accipiter nisus* nests (Thomson *et al.* 2006). Female American mink *Mustela vison* have also been shown to modify their behaviour by reducing travel distances when the risk of predation by white-tailed sea eagles is higher, which may have consequences for species on which mink prey (Salo *et al.* 2008). Experimental manipulation of perceived predation risk using native predator call-playback has also shown that adult song sparrows *Melospiza melodia* lay and hatch fewer eggs, have lower brood mass and levels of parental provisioning, and parents are more prone to being flushed off nests, all of which contributes to fewer offspring being produced per year (Zanette *et al.* 2011). The costs of perceived predation risk can therefore be an important component of the impact of predators on populations of prey.

3. Management of landscapes to reduce predation

Predator species are typically larger than their prey, have higher metabolic requirements, and require larger home ranges (Gittleman & Harvey 1982) with sufficient resources for food and shelter (van Beest *et al.* 2011). Management aimed at reducing the impact of predation therefore needs to operate at appropriately large scales to influence predator behaviour and distribution. It has been suggested that more permanent reductions in predator populations could be achieved by reducing the carrying capacity of the landscape, by decreasing the availability of food and shelter resources (Frey & Conover 2007). Traditionally, predation has largely been managed through lethal control, which has been shown to be effective at maintaining post-breeding game-bird populations, but has variable success at increasing bird population sizes for the purpose of conservation (Côté & Sutherland 1997; Smith *et al.* 2010). In addition, control of individual predator species can potentially result in the compensatory effects of release of other predators, with no overall reduction in the impact of predation on the species of concern (e.g. Ellis-Felege *et al.* 2012). The spatial separation of predators and prey for conservation purposes has been carried out using fencing (Burns, Innes, & Day 2012) to protect small areas of high prey densities, and has been shown to be effective in increasing prey breeding success (Maslo & Lockwood 2009; Rickenbach *et al.* 2011; Malpas *et al.* 2013). Fencing of much larger areas has also been used to protect native endemic species from the impact of non-native prey in New Zealand (Ewen *et al.* 2011), but these areas require very substantial resources and ongoing maintenance (Gillies *et al.* 2003). Predator-free islands (Oppel *et al.* 2011) have also been critically important locations for translocations of vulnerable species, and have been very successful in removing the limiting impact of predation for highly endangered species (Armstrong *et al.* 2002). Less commonly used interventions such as diversionary feeding and conditioned taste aversion have also been used, with limited success (Gibbons *et al*. 2007).

Attempts to reduce the impact of predators on prey populations have also included increasing the complexity of habitat structure, in order to reduce prey accessibility. Greater complexity in habitat structure has been found to reduce predation rates in damselfish (Almany 2004), and creation of artificial refuges for fish has been found to reduce the foraging success of piscivorous cormorants, *Phalacrocorax carbo* (Russell *et al.* 2008). Landscapes can also be made less profitable to predators through changes in habitat structure that influence prey vulnerability to predators. For example, increases in vegetation height have been shown to increase levels of vigilance of grey partridges, *Perdix perdix*, for predators (Watson, Aebischer, & Cresswell 2007).

Model system: Predation of breeding waders on lowland wet grassland

Lowland wet grassland

Since the early twentieth century, and the rise of agricultural intensification, over 40% of wet grasslands within the UK have been lost to land drainage, with only 300,000 ha remaining at the turn of the twenty-first century (www.ukbap.org.uk). The ecosystem on which this thesis is focussed is lowland wet grassland, which is an internationally important habitat designated by the Ramsar Convention (1971). In Europe, this habitat is also afforded protection through Special Areas of Conservation under the EC Habitats Directive (92/43/EEC), and many sites are designated as Special Protection Areas under the EC Birds Directive (2009/147/EC) because of the important bird populations that they support. The habitat structure of lowland wet grasslands is typically maintained through management of water levels and flooding, and through regular cutting or grazing of grasses, rushes and sedges (Benstead *et al.* 1997; Fisher *et al.* 2011). Wet grassland can be restored in areas converted from arable production to fulfil the requirements of many species, particularly breeding waders (Eglington *et al.* 2008), and such restoration is an important focus of agri-environment initiatives in Europe (Wilson, Vickery, & Pendlebury 2007).

Breeding waders on lowland wet grassland

Many wader populations in wetlands across Western Europe have declined severely as a consequence of the widespread loss and degradation of wetlands resulting from land drainage and agricultural intensification (Wilson, Ausden, & Milsom 2004). Within England and Wales, declines in breeding populations of lapwing *Vanellus vanellus* (-36.8%)*,* redshank *Tringa totanus* (-28.7%)*,* snipe *Gallinago gallinago* (-61.8%) and curlew *Numenius arquata* (-38.9%) between 1982 and 2002 (Wilson, Ausden, & Milsom 2004) have contributed to these waders being designated as species of conservation concern in the UK (Eaton *et al.* 2009). The ranges of many breeding wader species in Western Europe are increasingly restricted to nature reserves and sites managed for birds within agri-environment schemes (Ausden & Hirons 2002; Smart *et al.* 2008; O'Brien & Wilson 2011). Management to provide appropriate habitat conditions for breeding waders includes maintaining sward heights suitable for nesting and water levels that ensure invertebrate prey are available for chicks (Smart *et al*. 2006; Eglington *et al*. 2008). However these interventions have not led to overall population recovery, and high levels of predation on nests and chicks have been identified as a key factor currently limiting population sizes of waders across Western Europe (Macdonald & Bolton 2008; Schekkerman, Teunissen, & Oosterveld 2009; Kentie *et al.* 2013; Malpas *et al.* 2013).

Identity and impact of predators of breeding waders within lowland wet grassland

Current declines in the populations of many grassland-breeding waders have been linked to decreases in reproductive success. Declining nest success and chick survival over the last four decades have been recorded in Eurasian oystercatcher *Haematopus ostralegus*, black-tailed godwit *Limosa limosa*, lapwing, redshank and curlew populations, and levels of predation of wader nests in Europe are estimated to have increased by ~40% (Roodbergen, van der Werf, & Hötker 2012). To maintain stable populations, it is estimated that lapwings require nest losses of under 50%, and fledging rates of ~0.6 – 0.8 chicks per pair, but few sites achieve these levels (Macdonald & Bolton 2008). Range contraction may also make the remaining wader breeding populations more vulnerable to the impacts of predation, and thus predation may contribute to future population declines and possibly local extinction through restricting breeding densities (Bolton *et al*. 2007b).

More research is required to determine the identity of key predators of breeding wading birds and their foraging behaviour, as this will inform both lethal and non-lethal solutions to reduce levels of predation (Gibbons *et al*. 2007). In particular, the impact of mammalian predators, including red foxes, *Vulpes vulpes*, and mustelids (stoat *Mustela ermine*, weasel *Mustela nivalis*), on breeding waders are not well understood, not least because of difficulties in accurately assessing their abundance and a lack of efficient and legal control methods for these species (Graham 2002; Bellebaum & Bock 2009).

Lowland wet grassland foodweb

There are many potential predators of ground-nesting waders in lowland wet grassland, both mammalian and avian, each of which could prey upon the different life stages of egg, chick and adult (Figure 1). As wader nests are only available within a restricted season between April and July, they are not a food source on which predators can specialise year-round. In the UK, all predators of wader nests are generalists, and thus their predation rates on waders can be dependent on the availability of other sources of prey. Given that breeding waders are now often restricted to protected areas, the impact of predation is likely to be influenced by the density and distribution of alternative prey, and in particular whether these prey are sufficiently abundant to attract predators to protected areas or scarce enough to result in prey switching by predators (Newton, 1998).

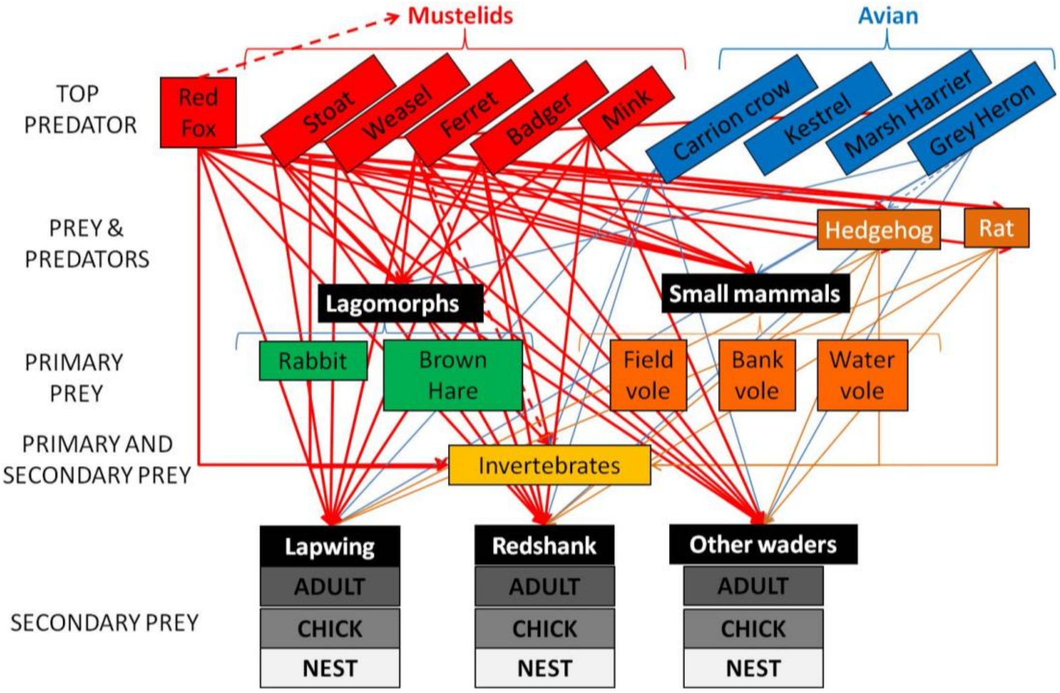

Figure 1 Food web of potential predators of ground-nesting wader species in the UK, including species not often found with lowland wetland habitats (e.g. hedgehog). Dotted red line represents one of many potential competitive relationships within the system.

The abundance and condition of alternative prey, primarily in the form of small mammals (voles, shrews and mice), may therefore influence predator impacts on wader breeding success. Nest predation rates can theoretically be affected by the abundance of alternative prey in several ways: increased abundance of alternative prey may either (i) increase the local density of predators and thus the likelihood of wader nests being encountered, or (ii) reduce the search area of individual predators and thus the likelihood of wader nests being encountered (especially if predator density is limited by e.g. territorial behaviour or breeding site availability). Alternatively, (iii) reductions in the density of alternative prey could increase the time that predators spend actively searching for wader nests (Stillman *et al*. 2006).

Studies have found that small mammal densities can be influenced by habitat connectivity and structure, and by habitat heterogeneity at the landscape scale (Gelling, Macdonald, & Mathews 2007; Moro & Gadal 2007). For example, the abundance of field voles, *Microtus agrestis*, has been found to be influenced by sward characteristics such as the amount of grass and dry vegetation litter (Tattersall *et al*. 2000), and small mammals are typically rare in open pastoral fields (Moro & Gadal 2007), especially in mid-field areas ((Tew, Macdonald, & Rands 1992). Within wet grasslands, the permeability of the landscape for small mammals and the influence of the differing sward conditions found within and outwith fields on small mammal abundance and distribution are not known. A key factor that is likely to influence small mammals within wet grassland habitats is the extent of surface flooding. High levels of flooding have been shown to adversely affect the demography of several small mammal species, with impacts on survival and delays in reproduction (Jacob 2003).

Even when small mammals are present within a habitat, their availability to predators may vary. Some rodents, for example *Peromyscus polionotus*, have been found to use indirect cues of predation risk (e.g. level of vegetation cover) in determining their foraging behaviour (Orrock, Danielson, & Brinkerhoff 2004), with foraging activity concentrated in areas sheltered by vegetation. Foxes forage largely using sound (Österholm 1964), and once potential prey have been located they typically leap on it in an attempt to capture it within their front paws (Macdonald 1987). This behaviour may be more effective in dense vegetation, as audio clues may be more apparent and predators may be more concealed from prey. Foxes have been shown, using radiotelemetry studies, to often show straight line movements between areas of dense planted cover and, within these areas, a high variability in turning angles indicates restricted-area foraging (Phillips *et al.* 2004). Foxes may be concentrating in these densely vegetated areas because of the increased foraging efficiency they can achieve through concentrating movement within a restricted area (Tinbergen, Impekoven, & Franck 1967). How the behaviour of both prey and predator are influenced by the structure of vegetation within lowland wet grassland are important considerations for how habitat management can be used to manipulate the foodweb within this landscape.

Management of lowland wet grassland landscapes to reduce wader nest predation

Within lowland wet grasslands, two distinct management strategies are commonly undertaken in an attempt to conserve breeding wader populations: habitat manipulation and predator control. These strategies are not mutually exclusive and can successfully complement one another (Eglington *et al*. 2008). For example, there are situations in which reducing mammalian predator (e.g. fox *Vulpes vulpes*) densities in wetlands can increase nest survival, but only in combination with additional habitat management (Bellebaum & Bock 2009). However, there are issues associated with lethal control of predators, as it is time-consuming, expensive, often controversial, and has the potential for unforeseen release of other predator or competitor species (Bodey, McDonald, & Bearhop 2009). The impact of predator control is also often dependent on initial predator densities (Bolton *et al.* 2007b). The contentious nature of lethal predator control has led to interest in identifying alternative non-lethal solutions (Smith *et al.* 2010).

The exclusion of mammalian predators with fences has been found to increase breeding wader success, with significantly more lapwing nests hatching and chicks fledging from within areas of lowland wet grassland surrounded by electrified fences (Malpas *et al.* 2013). However, these techniques are likely to be primarily appropriate for relatively small areas of high wader density in which mammalian predators are the main constraint on breeding success (Malpas *et al.* 2013). Previous studies have shown that lapwing nests are more vulnerable to predation close to field edges and in areas of low nesting densities (MacDonald & Bolton 2008), and these findings have stimulated recent attempts to reduce predation rates by manipulating habitat structure on wet grasslands. In 2008, a before-after-controlled experiment was conducted on a lowland wet grassland reserve in Eastern England to test whether two within-field habitat manipulations, designed to encourage lapwings to nest in field centres at higher densities (increased sward height in field edges and increased surface flooding in field centres), could improve nest survival (Bodey *et al.* 2010; Cole 2010). Taller vegetation in field edges was hypothesised to be avoided by lapwing because of their preference for nesting in open, short swards, and also to potentially provide suitable habitat for small mammals, which in turn may provide the mammalian and avian predators of breeding waders with an alternative prey source. Small mammals such as field voles (*Mictrotus agrestis*), a common prey item of foxes and mustelids (Battersby 2005), are known to avoid over-grazed areas with short swards (Evans *et al.* 2006). Although these manipulations did not result in any improvement in nest survival between years before (2008) and after (2009/10) the treatments were created, and there were no differences in nest survival between manipulated and control fields within the same year, there was a very high level of annual and between-species variation in nest success which may suggest that predation processes are operating over larger scales than individual fields. For example, if the distribution of small mammals influences predator distribution and activity, landscape-scale factors such as the size and connectivity of areas with differing vegetation structure and surface flooding, may be more relevant than field-scale vegetation structures.

There are a number of important differences between nature reserves and the wider countryside that could affect the wider applicability of models derived from studies on nature reserves. Densities of breeding waders will be much lower outside of reserves and this could affect how predation operates in the wider countryside. For example, waders nesting at low density may be a less profitable prey resource for foxes, but adult waders are also less likely to be able to use group defence to protect nests. This means that the relative importance of different nest predators may vary between reserves and the wider countryside. This is currently one of the key knowledge gaps which could have important implications for managing predation rates outside of reserves. Intensity of habitat management is also likely to vary, with consequences for the distribution of surface water and areas of taller vegetation in the landscape, and therefore the distribution of small mammals. Wider countryside sites are very unlikely to be as wet as nature reserves and the late and lighter grazing prescriptions in Higher Level Stewardship (HLS) breeding wader options could result in more in-field availability of taller, lightly-grazed swards suitable for small mammals.

Lowland wet grassland study sites

The research reported in this thesis aims to inform the potential for habitat manipulations to be used as a tool to influence patterns and rates of wader nest predation. To achieve this, field studies were carried out between 2010 and 2012, and longer-term data on wader demography and habitat structure recorded since 2003 were collated and added to the field data. These data were used to identify the predators responsible for wader nest losses, quantify the effects of habitat and landscape structure on the distribution and activity of mammalian predators and their small mammal prey, and identify the factors influencing patterns of wader nest predation. The study took place on wet grassland reserves throughout Eastern England (Figure 2), with the majority of fieldwork being carried out at Berney Marshes RSPB reserve (52°35’N 01°35’E, National Grid reference TG4605). Berney Marshes reserve, as with most examples of grasslands managed for breeding waders, is situated within a landscape of drier, commercially grazed grassland, but with the potential for reversion to breeding habitat through appropriately targeted agri-environmental schemes. Within the reserves, habitat management carried out is predominantly targeted at breeding waders, through maintaining short swards within fields and surface wet features (pools and footdrains) that are capable of containing water throughout the wader breeding season (Eglington *et al.* 2008; Fisher *et al.* 2011). Habitat management at all these sites has been successful at attracting high densities of nesting waders (e.g. Figure 3a), especially lapwing and redshank, but these populations all experience high predation levels (Bolton *et al.* 2007b) that are likely to be limiting local productivity (e.g. Figure 3b) and the capacity for these sites to act as source populations for wider population recovery. The availability of agri-environmental scheme funding targeted at improving lowland wet grassland for breeding waders provides a potential means for re-establishing these species in the wider countryside, however, this will require higher levels of productivity than are currently achieved.

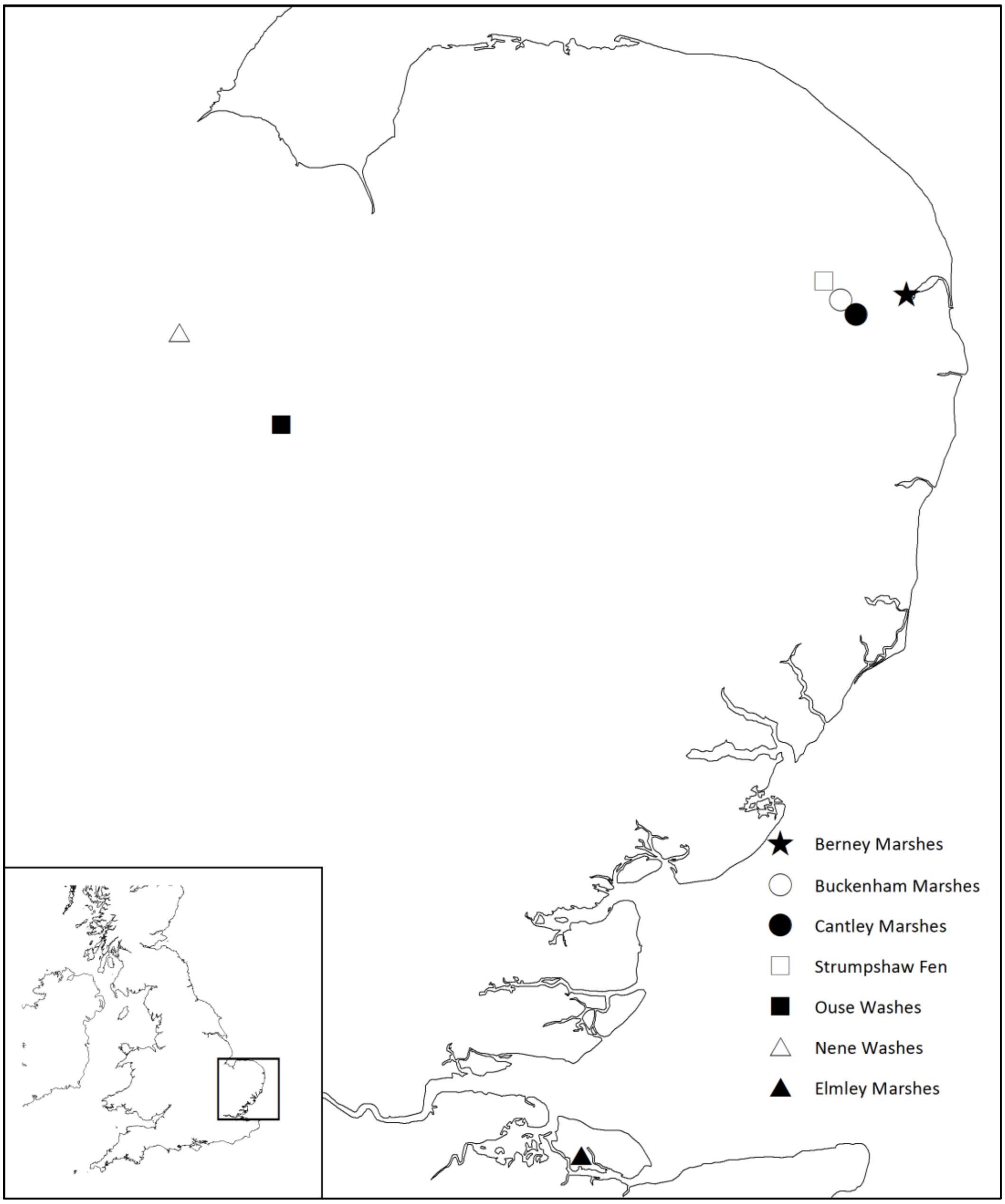

Figure 2 Locations of the seven RSPB-managed wet grassland nature reserves in the east of England (inset) used in the study, including the main study site at Berney Marshes.

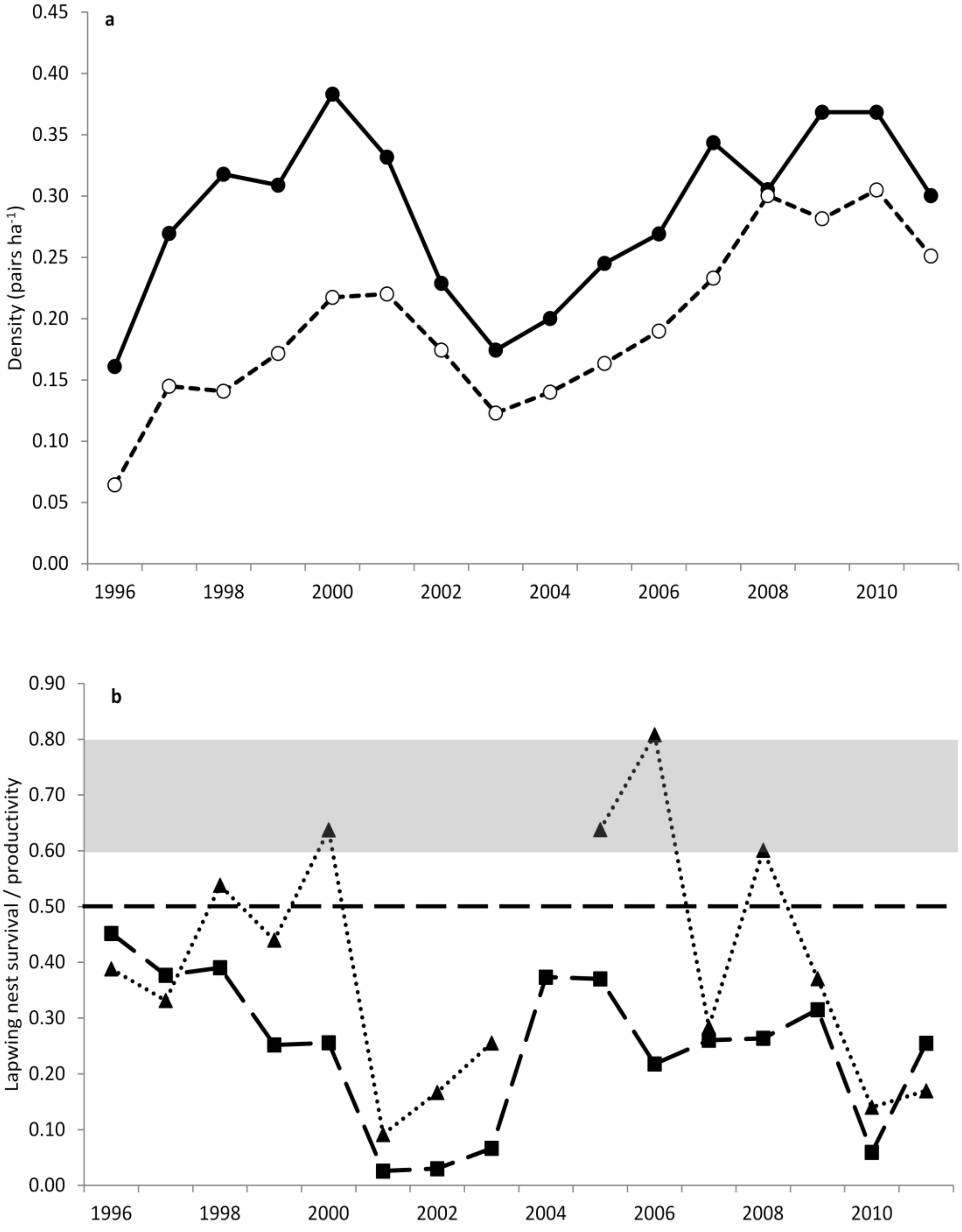

Figure 3 Annual variation in a) density of lapwing (●) and redshank (○) pairs and b) lapwing nest survival (■) and chicks fledged per pair (▲) within the 53 ha Old Arable area of Berney Marshes. Horizontal dashed line indicates nest losses of 50% and shaded grey area fledging rates of ~0.6 – 0.8 chicks per pair, which are estimated to be required for population stability (Macdonald & Bolton 2008). No predator control was carried out between 2000 and 2003 as part of Bolton *et al.* (2007b).

Outline of thesis

In **chapter one** I assess the consequences of conservation management for breeding waders for the distribution of alternative small mammal prey on lowland wet grasslands. In particular, I examine the variation in small mammal presence within fields and in adjacent verges of tall vegetation, and the extent to which this distribution is related to the sward structure found in these different parts of the wet grassland landscape. Small mammal activity was measured using a combinations of field signs, traps and ink tracking tunnels; a method developed in New Zealand for monitoring mustelids (Figure 4a; King & Edgar 1977), and which was primarily used here used to monitor small mammals (Figure 4b).

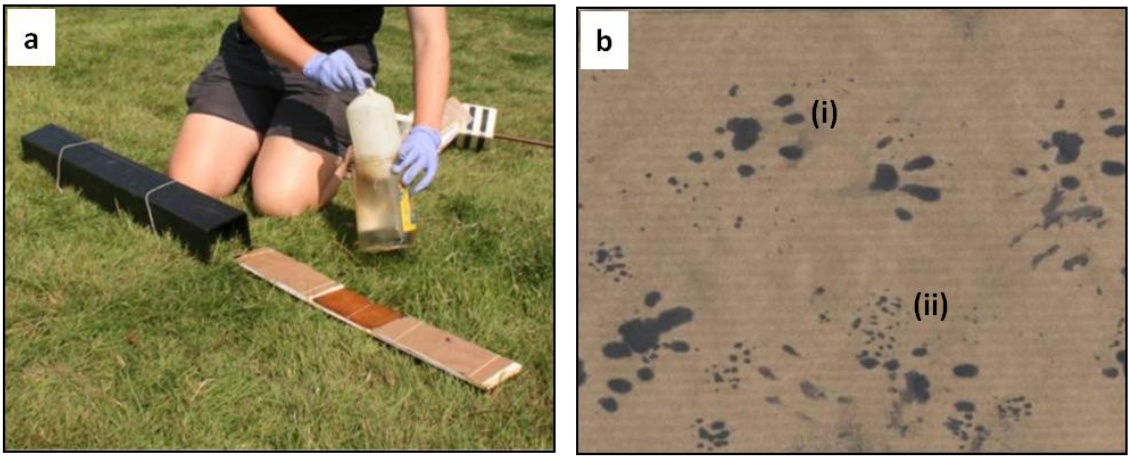

Figure 4 a) Tracking tunnel, showing internal paper and ink arrangement and b) example of tracking paper showing both (i) mustelid and (ii) small mammal prints.

Having determined that small mammals are predominantly found in areas of tall vegetation which, within lowland wet grassland, is typically rare and restricted to field verges; in **chapter two** I explore how the characteristics of verges influence small mammal activity. Specifically, I assess the influence of the size, quality and level of connectivity of patches of tall vegetation on small mammal activity within and adjacent to these patches, across seven RSPB-managed wet grasslands in Eastern England (Figure 2).

In **chapter three** I then consider whether the nest predation probability of lapwing and redshank is influenced by proximity to verges in the surrounding landscape at Berney Marshes, a site with high wader nesting densities (Figure 3a), but at which levels of nest survival and productivity are below the levels estimated to be required for population stability in most years since the mid-1990s (Figure 3b). I explore the variation in nest predation rates in fields that are or are not directly adjacent to verges, and how predation rates vary in areas with differing amounts of surrounding verge habitat, at different spatial scales.

As predation rates of wader nests do indeed vary in relation to surrounding verge habitat, in **chapter four** I explore the identity of predators of wader nests and the influence of verges on predator distribution and movement at Berney Marshes. I show that the main predator of wader nests at this site is the red fox and I then use fox track plots and trail cameras to explore fox movement across the wet grassland landscape. In particular, I quantify how fox activity is influenced by tall vegetation, and whether field wetness and high nesting densities of lapwing may act as barriers to predator movement.

The hatching success of lapwing and redshank has been monitored at Berney Marshes since 2003, and in **chapter five** I use these long-term data to quantify the impact on wader nest predation of landscape structure, field management and nesting lapwing densities. I then use the resulting models to estimate the potential impact of specific future habitat management scenarios, and to consider the magnitude of reduction in predation rates that could potentially result from proposed management actions.

In the **General Conclusion** section, the findings of the thesis are summarised, and the implications for future management of lowland wet grasslands for breeding waders, and future research directions, are considered.

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Chapter 1

Managing a foodweb: impacts on small mammals of managing grasslands for breeding waders

Animal Conservation, 2013, **16**, 207-215.

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Summary

1. Conservation management of landscapes often concentrates on the requirements of target species of conservation concern. However, such management may have repercussions for other components within the ecosystem's foodweb which may, in turn, indirectly influence the target species.
2. In Western Europe, many lowland wet grasslands are managed to encourage breeding wader populations, most of which have declined rapidly in recent decades. These species typically require short vegetation, high water levels and surface wet features but, even with provision of such habitat structure, many populations are limited by predation of eggs and chicks. As predator activity and impact on waders may be influenced by the availability of alternative prey sources, we investigate the influence of habitat management for waders on the distribution and activity of the main prey of mammalian predators; small mammals.
3. Livestock grazing to create the short sward structure that attracts breeding waders on wet grasslands means that areas of tall vegetation are largely restricted to verge areas outwith fields. The sward within these verges was significantly taller and denser, both in the lower and upper sections of the sward, than field centres and field edges, and these differences in sward height increased significantly over the wader breeding season. Although field edges were significantly taller and denser than field centres during the early season, by late season the sward structure of these areas did not differ significantly.
4. Activity rates of small mammals in ink tracking tunnels in the early season were low and similar across field centres, edges and verges but, by the late season, verges had significantly more activity. All monitoring methods found small mammal activity was largely restricted to verges and field edges with more than 80% density of cover in the lower sward and a sward height above ~ 20 cm.
5. The creation of extensive areas of short grass to attract breeding waders may be substantially reducing the abundance of alternative prey for the mammalian predators that are limiting wader productivity on many sites. Using this information to plan small mammal habitats within these landscapes may be a means of reducing the predation pressure on breeding waders, and there is an urgent need to establish whether predation rates on wader nests and chicks are lower when small mammals are abundant.

Introduction

Species-specific conservation management typically focuses on targeted conservation of a single species or group of species and the associated habitat requirements (Simberloff 1998). However, species of conservation concern are also constituents of wider communities and trophic foodwebs. The inherent complexities of manipulating such systems and communities means that the potential for management conflicts between species of conservation concern can be high (e.g. Vickery *et al.* 1997; Andelman & Fagan 2000). However, conservation management will also impact non-target species, which may be a key component of the foodwebs of target species.

Targeted species management often operates through 'bottom-up' procedures, in which habitat manipulations are carried out to create the small-scale habitat structure required by the target species (Smart *et al.* 2006; Eglington *et al.* 2008). However, providing specific habitat conditions for particular species may conflict with the requirements of other species within the system (e.g. Vickery *et al.* 1997). Alternatively, species management can operate through 'top-down' methods, such as the control of predators of target species (Smith *et al.* 2010). However, target species often fail to benefit from predator control (Bolton *et al.* 2007; Ausden *et al.* 2009), either because predation is not the limiting factor, ineffective control methods are employed or the impact of alternative predators within the foodweb increases, for example through mesopredator release as their natural predators are removed (Crooks & Soulé 1999; Ellis-Felege *et al.* 2012). In addition, management problems can arise when the predator species in a system is itself of conservation concern (e.g. Thirgood *et al.* 2000).

One of the most important breeding habitats for waders is lowland wet grassland (Wilson 2004), which is an internationally important habitat protected by the Ramsar Convention (1971) and, within Europe, through Special Areas of Conservation under the EC Habitats Directive (92/43/EEC). Globally, roughly half of wetland areas have been lost (Zedler & Kercher 2005), including the loss of over 40% of wet grasslands within the UK since the early twentieth century, due largely to agricultural intensification. By the turn of the last century, only 300,000 ha of wet grassland were estimated to remain within the UK (Benstead *et al.* 1997). In Western Europe, many of the breeding wader species of wet grasslands (e.g. lapwing (*Vanellus vanellus*), snipe (*Gallinago gallinago*), curlew (*Numenius arquata*), redshank (*Tringa totanus*) and black-tailed godwit (*Limosa limosa*) are increasingly restricted to nature reserves (Ausden & Hirons 2002), and management is therefore of increasing importance. The habitat structure of lowland wet grasslands is typically maintained through management of water levels and through regular cutting or grazing of grasses, rushes and sedges (Benstead *et al.* 1997; Fisher *et al.* 2011). Wet grassland can also be restored in areas converted from arable cropping, and such restoration is an important focus of agri-environment initiatives in Europe. However, the restoration process can be costly due to the reduction in agricultural profits and the practicalities of increasing field wetness, and is often therefore performed on relatively small scales (Eglington *et al.* 2009a).

As habitat management and restoration for breeding waders continues to develop it is important to ascertain the impacts on other species, and any consequent indirect influence on target species. One likely mechanism by which breeding waders may be indirectly influenced by habitat management is through changes in the numerical (increase in density) and functional responses (altered behaviour) of mammalian predators of nests and chicks (Bolton *et al.* 2007). In Europe, mammalian predators (primarily red fox (*Vulpes vulpes*) and stoat (*Mustela ermine*)) have been reported to be responsible for up to 70% of wader nest predation (Macdonald & Bolton 2008). The impact of predator species on breeding waders on wet grasslands is likely to depend upon whether overall prey abundance (primarily voles, shrews and mice) is sufficient to attract them to an area, but also not sufficiently abundant or available to prevent prey switching by predators (Newton 1998). Studies in the Netherlands have indicated that predation pressure on wader nests was higher during years with lower field vole (*Microtus agrestis*) densities, particularly for early nesting waders such as lapwing (Beintema & Muskens 1987).

The probability of nest or chick predation can theoretically be influenced by reduced abundance of small mammal prey in three main ways: (a) predator density may decline, which may reduce the likelihood of nests being predated; (b) the probability of predators actively searching for wader nests may increase (Stillman *et al.* 2006); or (c) predators may forage over larger areas, and thus encounter more wader nests. However, at the landscape scale, mammalian predators may be attracted to areas with relatively high food abundance (e.g. nature reserves situated within a less suitable agricultural matrix (Seymour, Harris, & White 2004)), and thus predator densities may be maintained despite a low abundance of alternative prey.

The management of breeding waders is an issue that incorporates both bottom-up approaches of habitat manipulation; through the creation of short swards and wet features to ensure there are appropriate nesting and chick rearing habitat (Eglington *et al.* 2008; Rhymer *et al.* 2010) and top-down control of predators. The main predator of wader nests on wet grasslands in Western Europe is the red fox (Macdonald & Bolton 2008; Fletcher *et al.* 2010; Eglington *et al.* 2009b). The diet of this generalist predator in the UK is dominated by small mammal species, such as field voles, particularly during the winter (Forman 2005). The abundance of small mammals may therefore influence the probability of seasonal prey-switching to secondary prey, such as wader nests and chicks (Sergio *et al.* 2008), but the consequences for small mammal abundance of habitat management for breeding waders are poorly understood (Bellebaum & Bock 2009). Here we assess the consequences of conservation management for breeding waders for the distribution of small mammal prey on lowland wet grassland, by quantifying (i) the extent of between-field and seasonal variation in sward structure within fields and adjacent verges, (ii) the variation in small mammal activity within fields and adjacent verges, and (iii) the extent to which small mammal distribution relates to spatial variation in sward structure resulting from management for breeding waders.

Methods

Study site

Studies of mammal distribution were carried out between March and early July within the Halvergate area of the Norfolk Broads, with the majority of the study area being within Berney Marshes RSPB reserve (52°35’N 01°35’E, National Grid reference TG4605). Habitat management carried out on this reserve is predominantly aimed at breeding waders, through maintaining short swards within fields and ensuring the presence of surface wet features (pools and footdrains) that are capable of containing water throughout the wader breeding season (Eglington *et al*. 2008; Bodey *et al.* 2010). As a result there are three distinct habitat structures found within the wet grassland landscape: short vegetation within the highly managed wet field centres, taller vegetation in the drier edges of fields and the tallest dry vegetation outwith fields (verges) that often follows roads and tracks (Table 1).

Scale of landscape structure and habitat assessment

Distribution of study fields across the reserve

Study fields were selected within the RSPB reserve (n = 21) and surrounding farmed grassland (n = 2; Figure 1), all of which were subject to similar management with comparable field wetness and grazing intensities.

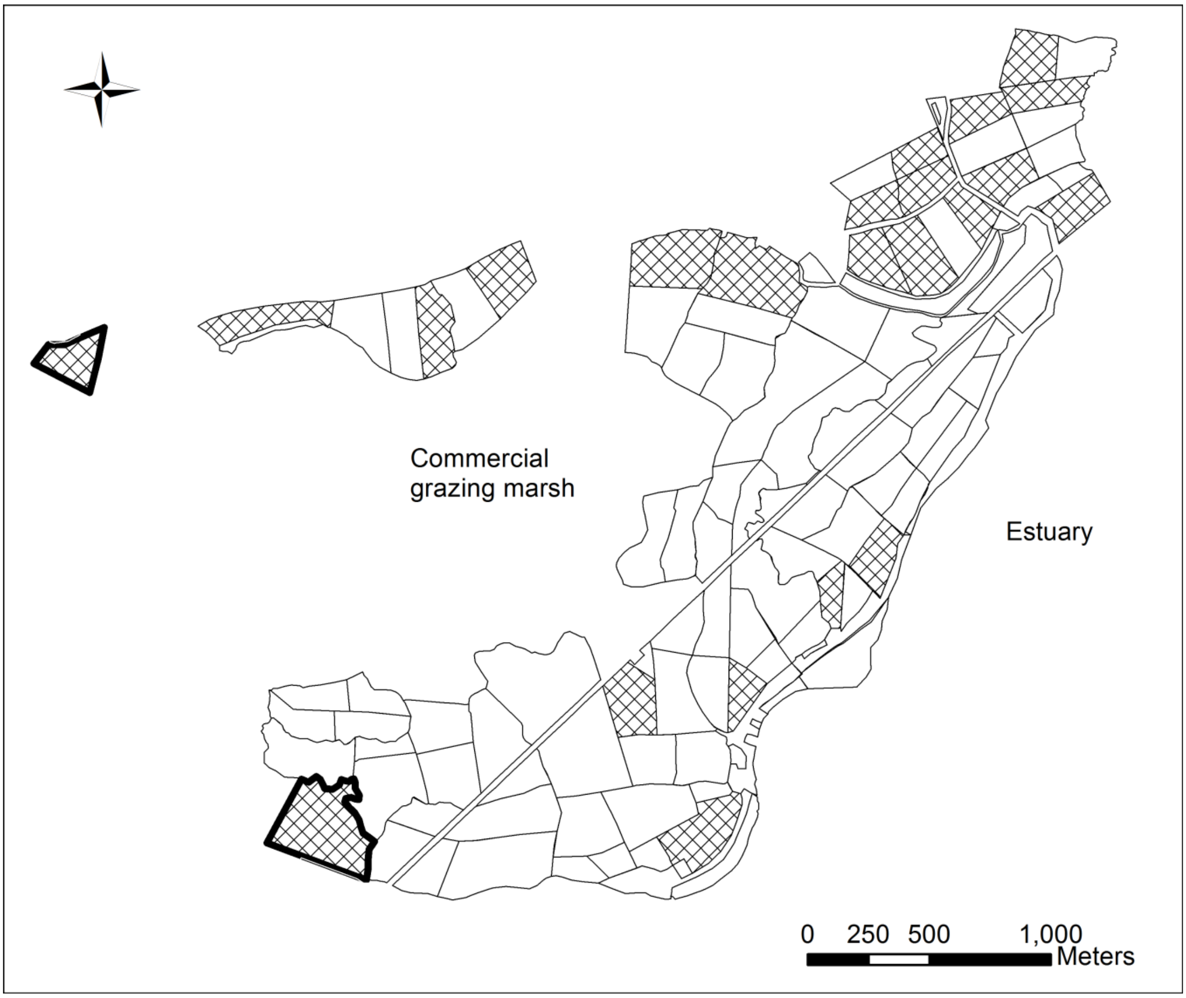

Figure 1 The distribution of the 23 study fields (hatched) within Berney RSPB reserve and adjacent farmland (bold outline) in Eastern England.

Sward characteristic variation between different areas of study fields

The sampling structure of the study was designed to capture the distinct habitat structures of field centres, field edges and verges (where present, see Table 1 for details). The sward characteristics of each of the habitat structures in each field were measured in March (during the lapwing pre-laying phase) and again in June (chick-rearing phase). Sampling of sward structure at each location was carried out along transects with 10 sampling locations at least 5 m apart (Figure 2). A zig- zag configuration was used to capture the variation in habitat structure (e.g. spoil banks in field edges).

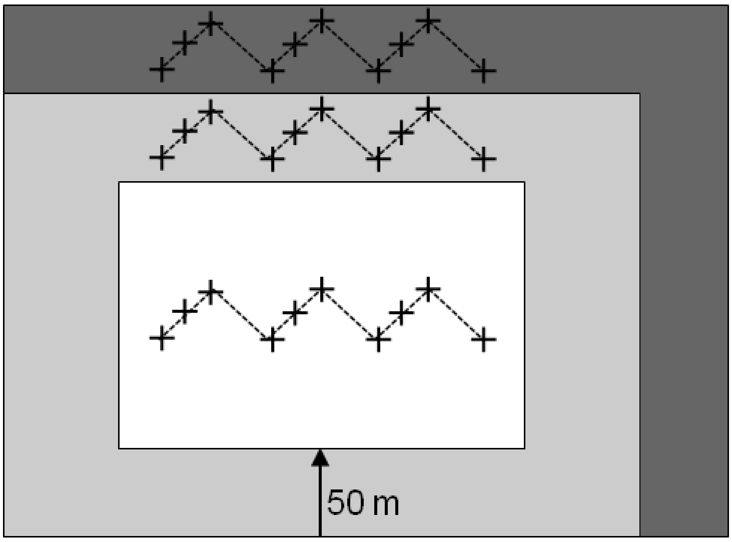

Figure 2 Configuration of sward structure sampling points (+) along transects of minimum length = 50 m (dashed lines) in field centres (white), field edges (light grey) and connected verges (dark grey).

At each sampling point, sward height and density measurements were recorded (for details see Table 1). Sward density was recorded both at ground level, to reflect the cover provided to small mammals within the sward (Glen, Sutherland, & Cruz 2010), and within the upper sward to reflect the cover and ease of movement for larger mammalian predators through the vegetation.

Table 1 The names, unit of measurement and description of variables recorded during surveys of sward structure on grazing marshes at Berney, Norfolk.

Variable	Unit	Description
Field centre		Area within the centre of fields (> 50 m from the ditch or field boundary) made up of short vegetation (< 10 cm).
Field edge		Boundary area (< 50 m from ditch or field boundary) of fields, typically comprised of taller vegetation (> 10 cm) along some or all of the field perimeter.
Verge		Long (~ 50 to > 500 m), narrow (~ 5 m) areas of predominantly tall vegetation (> 40 cm) of reeds and grasses, connected to adjacent fields by gateways or bridgeways across field boundary ditches.
Season		Early (March/April) and late (June/July) sampling periods.
Sward height	cm	Average of 10 vegetation height measures recorded with a sward stick (Stewart, Bourn, & Thomas 2001) along sampling transects (Figure 2).
Lower sward density	%	Percentage of a 10 cm^3 cube placed at ground level that was obscured by vegetation. Estimated visually from viewpoints 1 m away, at a height of 0.5 m in four horizontal directions (Glen, Sutherland, & Cruz 2010).
Upper sward density	%	Percentage of a 49 x 70 cm board obscured by vegetation assessed 11 cm above ground level. Estimated visually from a distance of 1 m and a height of 50 cm.

Surveys of mammal distribution and activity

Live trapping was used primarily to identify the small mammal species using field centres, field edges and attached verges (as this method was too time-consuming to be used in large-scale assessments of small mammal distribution throughout the season). Between mid April and late May, a grid of 25 Longworth small mammal traps 5 m apart was placed in the field centre, field edge and verge of seven separate fields. Traps were pre-baited for 24 hours with oats, apple, carrot and blowfly castors and then trapping was carried out for a further 72 hours, with checks at dawn and dusk. The species of all small mammals captured was recorded, and they were fur-clipped in order to identify re-trapped individuals.

Small mammal field signs

At each of the sward sampling points, the presence or absence of small mammal field signs were recorded through exhaustive searching (to reduce the problems arising from variation in sign detectability in different vegetation structures that can influence timed searches; Sibbald, Carter, & Simon 2006) of a 25 x 25 cm quadrat. The number of quadrats per transect in which small mammal signs were recorded was used as the response variable in subsequent analyses. Fresh field-signs of fresh droppings or latrines (primarily of field voles) and feeding signs (clippings of bitten-off grass stems and leaves often left in a criss-cross pattern) were recorded in the early and late seasons, but, due to their scarcity in the late season, analysis was only conducted on early season signs. Old field-signs of dry droppings or latrines (lacking the shine and brighter green colour of fresh samples) and runways (worn paths weaving through vegetation) can persist in the landscape (Redpath, Thirgood, & Redpath 1995) and so were only recorded during the early season.

Ink tracking tunnels

Ink tracking tunnels were centred along each sampling transect in 22 fields to track the distribution and activity levels of small mammals. Tunnels were a minimum of 20 m from any gateways or changes in habitat structure (e.g. transitions from field centre to edge), and field centre tunnels were a minimum of 50 m from the field boundary. Within field edges and verges, tunnels were placed within the tallest vegetation available, and tunnels were disguised with overhanging vegetation. A 9-night tracking period was carried out during both the early and late season (Table 1), with tunnels checked every three nights and papers in used tunnels replaced. The absence (no prints on any check) or presence (prints on 1, 2 or 3 checks) of mammals was used as the response variable in analyses.

Tunnels were constructed from black corrugated plastic (290 mm x 800 mm), bent to form the three sides of the tunnel and stapled to a wooden base (100 mm x 550 mm) onto which a tray made of corrugated plastic (99 mm x 550 mm) split into three sections was placed. A two-part ink tracking system, reliant on a chemical reaction to fix prints was used (following King & Edgar 1977). The centre section of the tray contained a well into which is placed a 4 mm thick sponge soaked in ink. On either side of the ink, a tracking paper that had previously been treated with a tannic acid and ethanol solution was fixed to the base with elastic bands.

Statistical analyses

Sward height (cm) and density of the lower and upper sward (% of cube or board, respectively, obscured by vegetation; see Table 1 for details) were log10 transformed to ensure the assumption of normality of residuals was met. Differences in sward characteristics between locations (field centre, edge and verge) in early and late season and the interaction between location and season were explored with a general linear model (glm with identity link function and a normal error distribution) in PASW v18 (PASW Inc., Chicago, IL.). In addition, separate models were constructed for early and late seasons to compare the sward characteristics of each location during each time period.

Variation in small mammal activity between field centres, edges and verges was explored using three response variables; (i) old field-signs (number of sample points per transect with a run or old droppings); (ii) fresh field-signs (number of sample points per transect with fresh droppings or feeding signs); and (iii) presence of small mammal footprints within a tunnel. Models of old and fresh field-signs were constructed with location alone, and models of tunnel use were constructed with season (early and late) and location, with the maximal model being reported. The data did not allow for exploration of interactions between location and season.

Due to strong collinearity between sward height and density (height-lower density: $r=0.97$, $p<0.001$; height-upper density: $r=0.93$, $p<0.001$; and lower-upper density: $r=0.95$, $p<0.001$; $N=138$), only a single representative variable was used in all analyses of sward characteristics: lower sward density was selected as the variable likely to have the greatest biological relevance for small mammals. Models of the effect of sward structure on old and fresh field-signs were constructed with lower sward density alone, and models of tunnel use were constructed with season (early and late) and lower sward density, and their interaction. Only significant interactions were retained within the models and are reported; non-significant ($p > 0.05$) interactions were removed by backwards deletion from full models. Field was initially included as a random factor in all models, but was then excluded as it explained virtually none of the variation in mammal distribution. All small mammal activity were analysed in PASW v18 (PASW Inc., Chicago, IL.) using generalised linear models, with a log link function and quasi-Poisson errors to correct for overdispersion in field-signs and a logit link function and a binomial error distribution for tunnel print presence data.

Results

Sward structure across wet grasslands

On grazing marshes managed primarily to attract breeding waders, grazing and high water levels result in sward structures within field centres and edges that are significantly shorter and less dense than verges (Figure 3). Swards on all three locations (centres, edges and verges) get significantly taller and denser over the season but sward height increases at different rates in different locations (Table 2), with verge sward height increasing significantly more than field centres and edges (Figure 3a).

Table 2 General linear models of the variation in sward characteristics between locations (field centres, edges and verges) and season (early and late) on grazing marshes (LSD and USD = lower and upper sward density, respectively, both log-transformed). (*p<0.05, **p<0.01, ***p<0.001).

Variable		Height		LSD		USD	
	df	*F*		*F*		*F*	
Location	2	89.83	***	53.62	***	94.14	***
Season	1	63.79	***	50.06	***	90.98	***
Location*season	2	3.09	*	2.03		1.94	
Error	132						

In the early season, verges were already significantly taller and denser than both field edges and field centres (Figure 3). Although the lower swards of field edges were taller and denser than field centres during the early season, by late season the sward structure of these areas did not differ significantly (Figure 3).

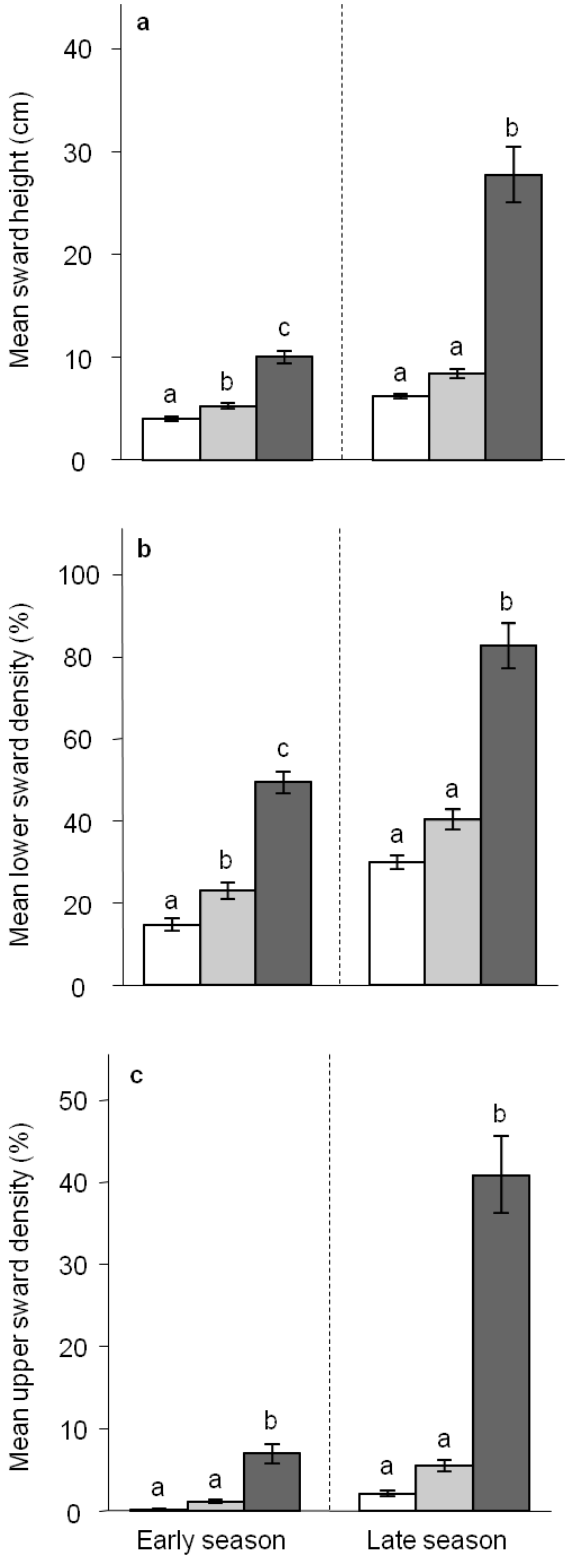

Figure 3 Variation between field centres (open), edges (light grey) and verges (dark grey) in mean (± SE) a) sward height (early season: $F_{2,66}$=47.84, p<0.001; late season: $F_{2,66}$=54.84, p<0.001), b) lower sward density (early: $F_{2,66}$=46.35, p<0.001; late: $F_{2,66}$=44.72, p<0.001) and c) upper sward density early: $F_{2,66}$=27.26, p<0.001; late: $F_{2,66}$=57.08, p<0.001). Within season, different letters denote significant differences (p<0.05) between locations from post-hoc tests.

Small mammal distribution across wet grasslands

During live trapping on seven fields, three species were captured in field verges: field vole (8 individuals); common shrew *Sorex araneus* (20 individuals) and bank vole *Clethrionomys glareolus* (6 individuals). Only one species (common shrew, 2 individuals) was captured in the field edge and no small mammals were captured in field centres. Consistent with the patterns in the sward characteristics, small mammal old field-signs in the early season were significantly more frequent in verges and field edges than in field centres, with verges having the highest frequency (Table 3a, Figure 4a). Verges also had the highest frequency of fresh field-signs during the early season (Table 3a, Figure 4b). Use of ink tunnels by small mammals did not differ significantly between early and late season and was low across field centres and edges and higher in verges (Table 3a, Figure 4c).

Table 3 Results of generalised linear models investigating the influence of a) location and season and b) lower sward density and season on levels of small mammal activity (measured as old (n=69) and fresh (n=69) field-signs and tunnel use (n=132)) in different locations (field centres, edges and verges). (*p<0.05, **p<0.01, ***p<0.001).

Variable		Old field-signs		Fresh field-signs		Tunnel usage	
a	*df*	X^2		X^2		X^2	
Location	2	44.55	***	17.35	***	11.52	***
Season	1					1.45	
b							
LSD	1	106.69	***	15.61	***	11.67	***
Season	1					4.62	*
LSD*Season	1					4.18	*

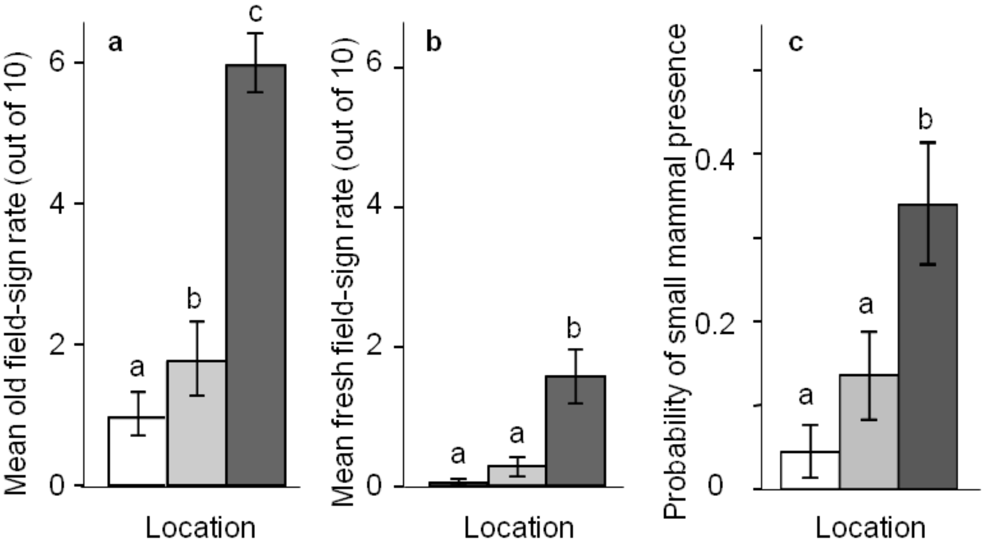

Figure 4 Variation between field centres (open), edges (light grey) and verges (dark grey) in mean (± SE) small mammal a) old field-signs, b) fresh field-signs and c) probability of ink tracking tunnel use. See Table 3a for statistical analyses. Different letters denote significant differences ($p<0.05$) between locations from post-hoc tests.

Influence of sward structure on small mammal activity

Old and fresh field-signs and tunnel use by small mammals all increased significantly with increasing lower sward density (Figure 5a and 5b; Table 3b). The relationship between tunnel use and lower sward density also differed significantly between early and late season (Figure 5c; Table 3b, significant interaction), as the tall and dense sward with the highest levels of small mammal activity was only available in the late season (Figure 3).

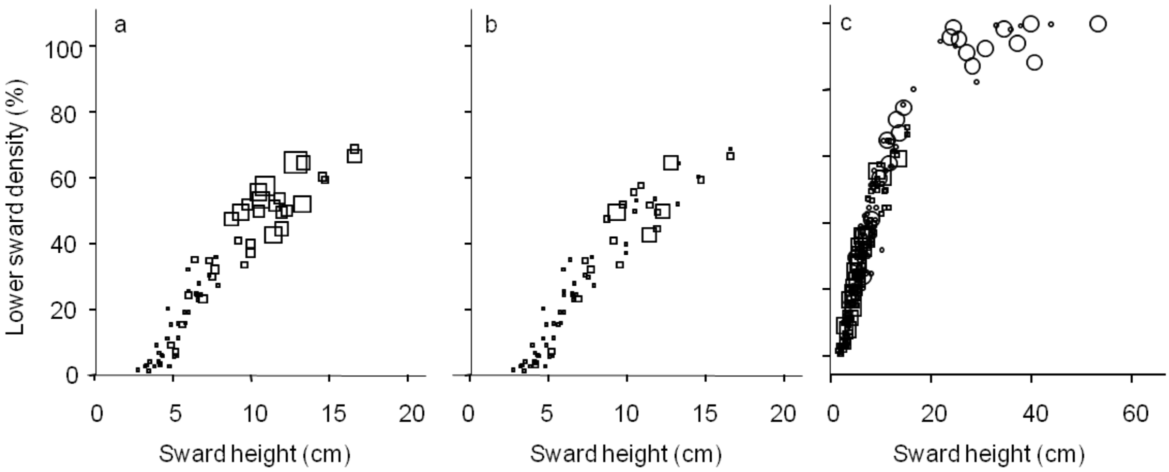

Figure 5 The variation in sward height and lower sward density at locations with differing levels of small mammal activity measured as a) old field-signs; b) fresh field-signs and c) ink-tracking tunnels in early (squares) and late season (circles). Increasing point size represents increasing level of activity (from 0 – 10) for field-signs and absence to presence for tunnel use. See Table 3b for statistical analyses.

Discussion

Habitat management for breeding waders on lowland wet grassland is predominantly concerned with maintaining short swards within fields, particularly in field centres to provide suitable nesting and chick rearing habitat. Consequently, tall vegetation is limited to the verges around fields, and field edges can have slightly taller swards than field centres, possibly as a result of lower levels of flooding in field edges resulting in less suppression of vegetation growth. In this landscape, the highest rates of small mammal activity were consistently found in verges, with old and fresh field signs and tunnel use all being 2-3 times more frequent in verges than field centres and edges, and small mammals being very rarely recorded in field centres. This difference was largely due to higher levels of small mammal activity in tall and dense swards, which are found almost exclusively in verges.

Sward structure on managed wet grassland

Lowland wet grasslands managed to attract breeding waders are predominantly open landscapes of short vegetation with only small areas of taller vegetation in boundary verge features (ADAS 1996). This relatively homogenous landscape structure is maintained through grazing or mowing regimes and high water tables to create surface water and suppress vegetation growth (Fisher *et al.* 2011). Field edges are often slightly elevated compared to the centre of fields (due to build up of spoil from clearing of ditches) and have fewer wet features (Eglington *et al.* 2009a), and can thus have slightly taller vegetation, which is appropriate nesting habitat for species such as redshank. By contrast, field verges rarely receive any direct management, and are thus typically taller and denser than the vast majority of the landscape.

Small mammal activity on managed wet grassland

Maintaining a largely homogenous open and wet landscape for breeding waders has clear consequences for other components of the foodweb. Levels of small mammal activity within fields was extremely low, as has been reported elsewhere (Moro & Gadal 2007; Tew, Macdonald, & Rands 1992). In addition to the lack of vegetation cover within fields, flooding has been shown to adversely affect the survival of some small mammal species (Jacob 2003) and has even been suggested as a management option to reduce the small mammal prey of mammalian predators of breeding waders (Thorup 1998; Bellebaum & Bock 2009). As field edges are typically less prone to flooding and surface water compared to field centres, this could be responsible for the slightly higher small mammal activity found in edge areas, supporting results from other studies in pastoral farmland (Montgomery & Dowie 1993). However, as surface water often dries out quickly (depending on the weather conditions) during the wader breeding season (Eglington *et al*. 2008), the longer-lasting effects of flooding on vegetation may be of greater relevance to small mammal abundance and distribution. As verge habitats are rarely subject to the flooding that occurs within fields, they may provide a more predictable environment, encouraging both vegetation growth and the associated higher small mammal activity.

Over the course of the season, increases in small mammal activity are likely to reflect juvenile dispersal, and this may increase use of lower quality habitats (e.g. Collins & Barrett 1997). However, the lack of any seasonal increase in activity within field centres suggests that the sward structure of these areas may be too short to support any substantial small mammal activity, even for dispersing juveniles. If within field areas are acting as barriers for small mammals, then their dispersal within the landscape may be influenced by the connectivity of the taller vegetation around fields (Gelling, Macdonald, & Mathews 2007). However, density of the sward, particularly at ground-level, is also important for small mammals (Tattersall *et al.* 2000), and denser swards may provide a medium through which runs can be created and which provides sufficient cover from predators.

Old field-signs represent small mammal activity before the wader breeding season, and may thus reflect the distribution of the small mammal prey of mammalian predators in their pre-breeding period. The pattern of small mammal activity detected in the early season by old field-signs is consistent with the recent activity detected using fresh field-signs and tracking tunnels. Detectability of runs, which make up the majority of old field-signs, is relatively constant across different sward conditions, while old droppings are easier to detect in taller vegetation where they are often protected from weathering. Fresh feeding and dropping field-signs have similar detectability issues to old field-signs, as they are often also found within runs in taller vegetation where they are likely to have been more protected from weather conditions than field signs in more open vegetation. However, the consistency of the patterns in small mammal activity identified with field signs and with tracking tunnels (which do not vary in detectability), suggests that variation in detectability of mammal signs in different sward structures did not greatly influence the findings.

The indirect methods for quantifying small mammal presence and activity used in this study can identify patterns of distribution and habitat use of small mammals, but not their abundance or population structure. However, given the almost complete absence of small mammal signs within fields, and the lack of any within-field captures of small mammals during live trapping, it is likely that sign presence captures the overall distribution of small mammals in the landscape. The abundance of small mammals within the verge habitats is unknown, and may well vary in response to verge size and connectivity, given the apparent effectiveness of the fields as barriers to dispersal.

Implications for wet grassland management

As mammalian predation of breeding waders is currently a major factor limiting their productivity on lowland wet grassland (Macdonald & Bolton 2008), effective management of predator distribution and behaviour is urgently needed. Traditional, top-down direct control of predators alone, which often does not reduce predation of nests and chicks sufficiently (Bolton *et al.* 2007), is time-consuming and nature conservation organisations tend to resort to predator control as a last resort (Ausden *et al.* 2009). Habitat manipulations to influence the structure of the foodweb and the availability of differing prey sources may provide an alternative method of reducing predation on the breeding wader species that are often the primary target of conservation action in these landscapes. While large areas of short vegetation that are being maintained in wet grassland have been effective in attracting waders, they may also have inadvertently altered the foodweb in these landscapes by adversely influencing small mammal populations.

The findings reported here suggest that small mammals on lowland wet grassland are currently highly restricted, but efforts to increase their abundance and distribution are likely to be relatively straightforward. Designing areas of tall dense swards into these landscapes will increase the area of available small mammal habitat, and may also facilitate their dispersal through the landscape. However, further work is needed to determine the influence of these management practices on predation of breeding waders. If predation of the productivity stages of breeding waders occurs irrespective of the alternative food sources in the environment then increasing small mammal populations may have no effect on wader productivity. Determining the impact of proximity to alternative food sources on breeding wader predation levels needs to be the focus of future work in this area.

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Chapter 2

Influence of habitat structure and connectivity on small mammals in grasslands managed for breeding waders

Summary

1. In recent years, many studies have considered the influence of habitat connectivity on population persistence and colonisation rates, with implications for landscape-scale management. These studies have highlighted that landscape-scale management, which considers the area, connectivity and quality of habitat features, can influence the persistence of local populations and community structure.
2. In lowland wet grasslands that are being managed to conserve declining populations of breeding waders, small mammals are largely restricted to patches of tall vegetation in landscapes of otherwise unsuitably short vegetation. Improving the management of tall vegetation could potentially increase small mammal distribution, which may also influence the distribution and activity of predators that consume both small mammals and the nests of declining waders. In particular, if small mammal activity is influenced by the size, shape and connectivity of tall vegetation patches, landscape-scale management of tall vegetation could be an important conservation tool.
3. On six lowland wet grassland sites in Eastern England, small mammal activity was measured with ink tracking tunnels, between April and July 2011. On all sites, small mammal activity increased significantly over the season but, despite tall vegetation patch sizes ranging from ~0.05 to 5 ha, small mammal activity did not vary significantly among patches.
4. At an additional wet grassland site, the distribution of tall vegetation was mapped to explore the influence of patch connectivity and structure on small mammal activity. Patches with greater connectivity had significantly higher levels of small mammal activity, and patches with denser swards (>90% cover) had around three times more small mammal activity than the least dense swards (<10% cover). However, small mammal activity was lower in tall vegetation patches within fields than in field verges, and within-field patches had lower connectivity and sward density than verges.
5. These findings suggest that small mammal populations in lowland wet grassland landscapes can be encouraged by the provision of tall vegetation patches of any size, as long as sward structures are sufficiently dense and the value of patches can be increased by increasing connectivity. Currently the taller dense vegetation required by small mammals is only found outside fields, but whole fields or corridors within fields provide potential for increasing small mammal habitat if managed specifically for that purpose. Within lowland wet grasslands managed for breeding waders, management of the amount, location and connectivity of tall vegetation suitable for small mammals may therefore have a role to play in influencing the behaviour of predators that prey on small mammals and breeding waders.

Introduction

The size and quality of habitat patches, and the levels of connectivity between them, are considered the cornerstones of metapopulation dynamics, influencing local rates of colonisation and extinction (Hanski 1994). Larger habitat patches typically support larger populations that are at lower risk of extinction through demographic stochasticity, and greater connectivity among patches can increase the likelihood of colonisation. As well as size and connectivity, studies of a range of taxa have highlighted the need to consider habitat quality when investigating patch occupancy (Franken & Hik 2004; Holland & Bennett 2007), because population persistence can be influenced by, for example, the amount of habitat that provides suitable foraging conditions, microclimatic conditions and protection from predation (Franken & Hik 2004).

Landscapes managed specifically for single species, or groups of species, of conservation interest often have management activities designed to deliver the specific habitat types required by the target species. This method of management may overlook the impact that such practices could have on other key components of the ecosystem. Single species management can potentially be adapted to achieve its aims while also encouraging a wider range of taxa, particularly if keystone species are the focus (Simberloff 1998). There is also growing interest in landscape-scale management which provides conditions suitable for a wide range of taxa and communities (RSPB 2011), including the possibility of re-wilding large areas (Vera 2009). Landscape-scale management should consider the identity, position and connectivity of features in the landscape that affect the persistence of local populations.

One habitat that is frequently subject to specific conservation management is lowland wet grassland which, in Western Europe, is often managed to benefit populations of breeding waders (Verhulst, Kleijn, & Berendse 2007) that are declining. Within England and Wales declines in breeding populations of lapwing *Vanellus vanellus* (-36.8%), redshank *Tringa totanus* (-28.7%), snipe *Gallinago gallinago* (-61.8%) and curlew *Numenius arquata* (-38.9%) between 1982 and 2002 (Wilson, Ausden, & Milsom 2004) have contributed to these waders being designated as species of conservation concern in the UK (Eaton *et al.* 2009). Provision of appropriate breeding habitat (Smart *et al.* 2006) has been able to successfully attract waders into a few relatively small areas, typically nature reserves, that are specifically managed for them, however this has not led to overall population recovery. Predation is a key issue limiting the breeding success of these waders, because studies that have reduced the impact of predators either through lethal control (Fletcher *et al.* 2010) or exclusion using fences (Malpas *et al.* 2013) have demonstrated significant improvements in breeding success. In this latter study, the number of lapwing chicks fledged per pair increased from 0.23 to 0.79 after the construction of fences, a value above the threshold necessary for population stability (Macdonald & Bolton 2008).

In Western Europe, one of the main predators of wader eggs and chicks are red foxes *Vulpes vulpes,* a generalist predator species whose varied diet can include not only birds, but also invertebrates, and predominantly, mammals (Dell'Arte *et al.* 2007). Foxes have been identified as prolific predators of wader nests using nest camera evidence, accounting for 61.1% of recorded predation events across a range of predominantly wet grassland studies (Macdonald & Bolton 2008). However, wader eggs and chicks are only available for a small proportion of the year and the diet of foxes in the UK is generally dominated by small mammal species, such as field voles *Microtus agrestis*, particularly during the winter (Forman 2005). The abundance, distribution and availability of small mammals could therefore influence the probability of seasonal prey-switching to secondary prey, such as wader nests and chicks (Sergio *et al.* 2008).

Habitat management for breeding waders is mainly concentrated within fields, and generally involves the creation of wet features and the maintenance of short swards through grazing and mowing (Fisher *et al.* 2011). Previous studies have shown that this management can restrict the occurrence of small mammals to patches of taller denser swards which typically occur in verges outside fields, and occasionally in field edges (Laidlaw *et al.* 2013). The abundance and distribution of small mammal prey for generalist predators within these landscapes can therefore be limited by the availability of suitable patches of tall vegetation.

Patches of tall vegetation in lowland wet grasslands that support small mammals may therefore provide many predators with access to their small mammal prey. In addition, these patches may provide cover for mammalian predators, such as foxes, and perching or nesting locations for avian predators, such as corvids, when these patches also contain trees. The location and structure of areas of tall vegetation are therefore likely to have an influence on predator activity and distribution, and may therefore also influence the impact of these predators on nesting waders. Tall vegetation patches suitable for small mammals typically have a patchy distribution within lowland wet grasslands, and can vary in size, shape and connectivity to other suitable habitat. How this variation influences both prey and predator activity is fundamental to understanding the implications of landscape-scale management of habitat structure. For example, tall vegetation patches can occur as small areas of verge along tracks, reedbeds along ditches, isolated copses or whole fields excluded from grazing and cutting activities. Altering the size of these patches or the connectivity between them, by creating linear, connecting corridors of verge vegetation, could potentially influence both the activity of predators within these habitats and their routes of movement through the landscape. Ultimately this could provide a means of manipulating landscape structure to reduce predator activity around areas with high breeding wader densities.

Here we assess the influence of the size, quality and level of connectivity of patches of tall vegetation on small mammal activity within and adjacent to these patches, within lowland wet grassland. Across seven wet grasslands sites in Eastern England managed for breeding wader and throughout the wader breeding season, we assess (i) levels of small mammal activity in tall vegetation patches varying in size and structure, (ii) the influence of connectivity between patches on small mammal activity, (iii) differences in small mammal activity in tall vegetation patches within and outwith fields and (iv) the influence of adjacent tall vegetation patches on small mammal presence within fields.

Methods

Study sites

The variation in small mammal activity among patches of tall vegetation varying in size and connectivity was assessed on seven areas of wet grassland in Eastern England (General Introduction, Figure 2), all of which are managed as nature reserves by the RSPB: Strumpshaw Fen (52°61’N 01°46’E, National Grid reference TG3406), Buckenham Marshes (52°60’N 01°47’E, TG3505), Cantley Marshes (52°58’N 01°51’E, TG3804), Ouse Washes (52°45’N 00°16’E, TL4786), Nene Washes (52°57’N -00°06’E, TL3299), Elmley Marshes (51°40’N 00°77’E, TQ9270) and Berney Marshes RSPB reserve (52°35’N 01°35’E, TG4605). Habitat management on these reserves is predominantly aimed at providing suitable habitat conditions for breeding waders, through maintenance of short swards (primarily with livestock grazing) and surface wet features (with water level management) that are capable of containing water throughout the wader breeding season (Eglington *et al.* 2008; Fisher *et al.* 2011). As a result there are three distinct habitat structures typically found within these wet grassland landscapes: short (i.e. <10 cm in the early season) vegetation within the highly managed and often wet field centres, taller vegetation (> 10 cm height) in the drier edges of fields and outwith fields (> 40 cm height by late season), on the verges that often follow roads, tracks, railways and rivers (Laidlaw *et al.* 2013).

Small mammal monitoring

Mammal activity and presence was quantified using ink tracking tunnels constructed from corrugated plastic and containing an ink-soaked sponge adjacent to paper treated with tannic acid on which mammal footprints are recorded, following a chemical reaction between the ink and treated paper (for details see Laidlaw *et al. 2013*). Two 90 x 240 mm pieces of treated paper are used within each tunnel, one on each side of the sponge. The relative activity level of small mammals for each tunnel was assessed by overlaying each paper with an acetate grid (split into 30 x 30 mm squares) and the number of squares that contained at least one whole or partial small mammal print was counted; a maximum score of 48 was therefore possible from the two papers in each tunnel. Small mammals were considered to be present at a tunnel site if their footprints were recorded on any one of the sampling occasions during each time period (i.e. late or early season).

Is small mammal activity influenced by the size and sward density of patches?

To assess the variability in small mammal activity across wet grassland sites subject to similar management criteria, ink tracking tunnels were deployed in patches of tall vegetation (i.e. >10 cm in the early season) on six wet grassland sites (five patches each on Strumpshaw, Buckenham, Ouse Washes, Nene Washes and Elmley; four patches on Cantley), between April and July 2011. The majority of sampling locations were in verges outside fields (n = 26), with three in patches of tall vegetation within fields (Table 1). Within each reserve, sampled patches were spread across the site, with a mean distance between patches of 47.4 m ± 89.6 SD. On these six reserves, each of the 29 patches of tall vegetation had four ink tracking tunnels, placed a minimum of 5 m apart and at least 20 m away from gateways. Tunnels were run for a 9-night tracking period, with papers collected once at the end of this period; this was repeated in the early (April), mid (mid to late May) and late season (mid June to early July) in 2011.

Patch size

The area of tall vegetation patches in all reserves was measured from aerial photographs in ArcGIS (ArcMap Version 9.3). Patch area was used in preference to patch perimeter, as patches predominantly had straight edges.

Table 1 Number of patches or fields within each site used in analyses of the influence of patch area, sward density, connected patch area, patch type and attachment to verges on small mammal activity and presence across seven RSPB reserves.

			Patches	
Analyses	Sites	Year	Field edge	Verges
1	Strumpshaw	2011	1	4
	Buckenham	2011	0	5
	Cantley	2011	0	4
	Nene	2011	2	3
	Ouse	2011	0	5
	Elmley	2011	0	5
2, 3	Berney Marshes	2011	11	14
			Fields	
			Verge attached	No verge attached
4	Berney Marshes	2010	24	22

Sward structure

Sward structure of the tall vegetation patches was measured during June and July 2011. Sward structure was measured along transects with 10 sampling locations at least 5 m apart, and following a zig- zag configuration to capture the variance in vegetation structure (see Laidlaw *et al.,* 2013 for details). Sward density at ground level was measured at each sampling location as the amount of a 10 cm^3 cube obscured by vegetation, estimated by eye. Sward height (cm) was measured with a sward stick and calculated from the average of three sward height measures at each sample location (Stewart, Bourn, & Thomas 2001).

Is small mammal activity influenced by the connectivity between patches?

On Berney Marshes RSPB reserve, the variability in small mammal activity in patches of tall vegetation varying in size, structure and degree of connectivity was quantified in 25 patches spread throughout the reserve, between April and July 2011. Patch size and sward structure was measured as described above. In addition, for each study patch, all other areas of tall vegetation that had a contact point within 15 m of the study patch (termed connected patches) and for which the intervening substrate was considered suitable for small mammals (e.g. grass covered tracks) were identified. The total area of connected patches for each study patch was then calculated from aerial photographs. Seven patches, all field edges, were over 40 m from the nearest verge and therefore were considered to have no connected verge. The same tunnel sampling design was used in the 25 tall vegetation patches at Berney Marshes (Figure 1), but the 9-night tracking periods were repeated 10 times throughout the wader breeding season, from April to July 2011.

Is small mammal activity similar within and outwith fields?

As the 25 patches of tall vegetation at Berney Marshes were located in both field edges (n=11) and in verges outside fields (n=14), the activity levels of small mammals in these two locations were compared.

Figure 1 The distribution of tall habitat patches outwith fields (black), and within fields (solid light grey) in which small mammal activity was recorded. The locations of non-surveyed verge habitat (green) and the fields with (double hatched) and without (single hatched) verge attached across Berney Marshes and surrounding farmed grassland are also indicated.

Is small mammal presence within fields influenced by the presence of an adjacent verge?

The influence of attachment to a verge with tall vegetation on within-field small mammal presence was assessed in 46 fields between April and July 2010. Small mammal presence was compared on fields with (n=24) and without (n=22) a verge attached, on Berney Marshes and surrounding farmed grassland (Figure 1). All fields were subject to similar management, with comparable field wetness and grazing intensities. A single ink tracking tunnel was placed along the field edge, a minimum of 20 m from gateways, and a second tunnel was placed in the field centre, a minimum of 50 m from the field boundary. Tunnels were run for 9-night tracking periods, repeated in the early (late March to early April), mid (May) and late (June) season, with tunnels checked every three nights and papers in used tunnels replaced.

Statistical analysis

The influence on small mammal activity (proportion of tracking paper with prints in each tunnel) of patch size and sward density across six reserves, and of patch size, sward density and connectivity at Berney Marshes, was determined using general linear mixed models (Table 2: Analyses 1 & 2). Due to strong collinearity between sward height and density at Berney Marshes in both the early (March and April: r=0.90, n=1000, p<0.001) and late (June: r=0.76, n=1000, p<0.001) season, only late season sward density was used in all analyses of sward characteristics, as this variable was considered likely to have the greatest biological relevance for small mammals. Field identity was initially included as an additional random factor, but was then excluded as it explained virtually none of the variation in mammal distribution. Site was also included initially as a random factor within Analysis 2 and then as a fixed factor to explore specific differences across sites. As the same parameters were retained in both of these models, the fixed factor model is reported.

To explore the influence of location on small mammal activity, a general linear mixed model was used that included a seasonal component and its interaction with location (Table 2: Analysis 3). To avoid pseudoreplication arising from four tunnels being deployed in each sampling location, these three models included a random factor of tunnel identity nested within sampled habitat patch. Sward density measurements were arcsine square root transformed, while patch area and area connected were log10 transformed to ensure the assumptions of the models were met (Table 2).

The influence of verge connectivity, location within field, season and the two-way interactions on small mammal absence (no prints recorded during any survey period) or presence (prints on any of the three survey periods) was explored using generalised linear models (Table 2:

Analysis 4). Non-significant ($p > 0.05$) interactions were removed by backwards deletion from the full model, with verge connectivity retained. All models were carried out in PASW v18 (PASW Inc., Chicago, IL.).

Table 2 Descriptions of small mammal (SM) response variables and all explanatory variables used in models of their distribution and activity. Maximal models are shown for each analysis.

ANALYTICAL APPROACH

Analysis	Response		Explanatory variable (random terms in parentheses)
Analysis 1: Is small mammal activity influenced by the size and sward density of patches?			
	SM activity		Site, time period, patch area, lower sward density, (tunnel within patch)
Analysis 2: Is small mammal activity influenced by the connectivity between patches?			
	SM activity		Time, patch area, lower sward density, connected patch area, (tunnel within patch)
Analysis 3: Is small mammal activity similar within and outwith fields?			
	SM activity		Time, location, time*location (tunnel within patch)
Analysis 4: Is small mammal presence within fields influenced by the presence of an adjacent verge?			
	SM presence		Attachment, time period, location in field, location in field*attachment, location in field*season

RESPONSE VARIABLE DESCRIPTIONS

Analysis	Variable	Distribution (link)	Explanation
1,2,3	SM activity	Normal (identity)	Prop. Of the 48 grid squares with SM prints (√ arcsine transformed)
4	SM presence	Binomial (logit)	Presence/absence of SM prints during tunnel check

EXPLANATORY VARIABLE DESCRIPTIONS

Analysis	Variable	Factor levels	
1	Site	6 sites	Six lowland wet grassland reserves in the East of England
1,4	Time period	Early:middle:late	Early (late March to early April); middle (May); or late (June) for 9 nights each
2,3	Time	10 periods	Consecutive time periods of 9 nights each, from April - July
3	Location	Field:verge	Patch location, either within fields or verges outwith fields
1,2	Patch area	Continuous	Area (log 10 transformed) of tall vegetation patches
1,2	Lower sward density	Continuous	Sward density in late season (√ arcsine transformed)
2	Connected patch area	Continuous	Area (log 10 transformed) of accessible tall vegetation < 15 m from patch
4	Attachment	Attached or not	Whether or not study field was connected to a verge
4	Location in field	Edge:middle	Tunnel locations < 50 m (edge) or > 50 m (middle) from the field boundary

Results

Is small mammal activity influenced by the size and sward density of patches?

Across all six wet grassland reserves, small mammal activity increased significantly over the course of the season and, although activity varied between sites, there were consistent increases in the level of activity across the season (Table 3 Analysis 1, Figure 2a). However, despite patch size ranging from ~0.05 to 5 ha, small mammal activity was not significantly related to either patch area ($F_{1,339}$= 0.51, p=0.48) or sward density ($F_{1,339}$=0.45,p=0.50; sward density only varied between 90 and 100%) on these sites (Table 3 Analysis 1, Figure 2b and c).

Table 3 Results of general linear mixed models exploring the influence on small mammal activity of Analysis 1: patch size and sward density (controlling for site and seasonal (time) variation); Analysis 2: patch size, sward density and area of connected patch (controlling for seasonal variation); and Analysis 3: patch location (controlling for seasonal variation). Maximal models are shown in Table 2.

Analysis	Variable	Estimate	SE	*df*	*F*	*p*
1	(Intercept)	-0.497	0.076	1	34.483	**<0.001**
	Time	0.444	0.027	1	271.500	**<0.001**
	Site			5	14.636	**<0.001**
2	(Intercept)	-0.478	0.067	1	51.086	**<0.001**
	Time	0.064	0.004	1	231.751	**<0.001**
	Area connected	0.050	0.004	1	19.668	**<0.001**
	Lower sward density	0.253	0.057	1	19.428	**<0.001**
3	(Intercept)	0.097	0.040	1	1.266	0.261
	Time	0.005	0.006	1	224.076	**<0.001**
	Location	-0.255	0.054	1	22.286	**<0.001**
	Time*Location	0.106	0.008	1	189.066	**<0.001**

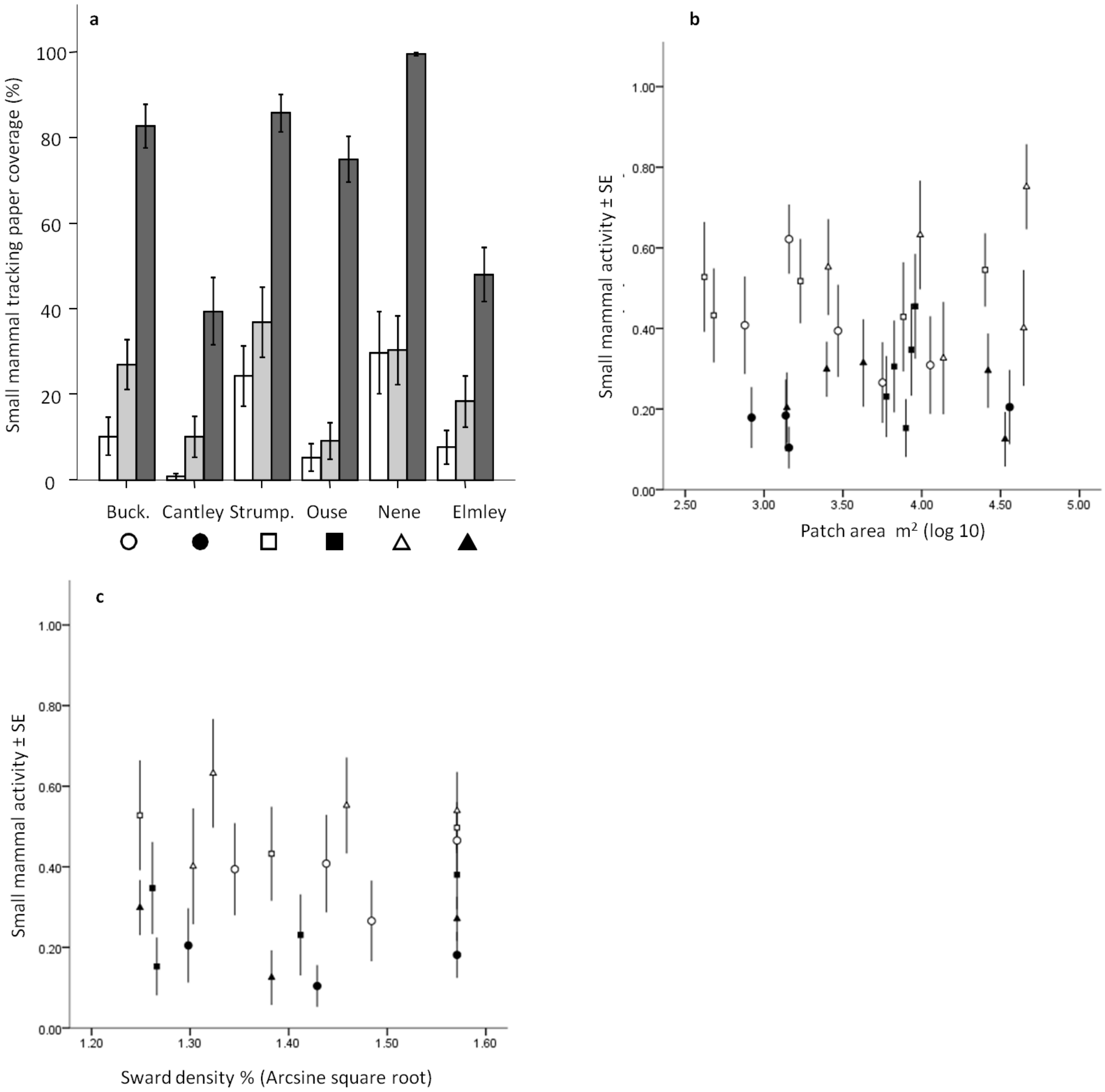

Figure 2 Small mammal activity (percentage cover of tracking papers with small mammal prints) a) on six wet grassland nature reserves (mean ± SE) during early (open bars), mid (light grey bars) and late season (dark grey bars) and, on patches across these six reserves that vary in b) area and c) ground-level sward density. See Table 3 Analysis 1 for statistics.

Is small mammal activity influenced by the connectivity between patches?

The activity of small mammals was not significantly influenced by patch size (Table 3 Analysis 2, Figure 3a). However, patches with a denser sward had significantly more small mammal activity, with the denser swards of verges (> 90% cover) having roughly three times the small mammal activity of the least dense sward measured (< 10% cover) (Table 3 Analysis 2, Figure 3b). Patches with a greater area of connected tall vegetation had significantly more small mammal activity, with unconnected patches having roughly half the activity found in verge patches that were connected (Table 3 Analysis 2, Figure 3c).

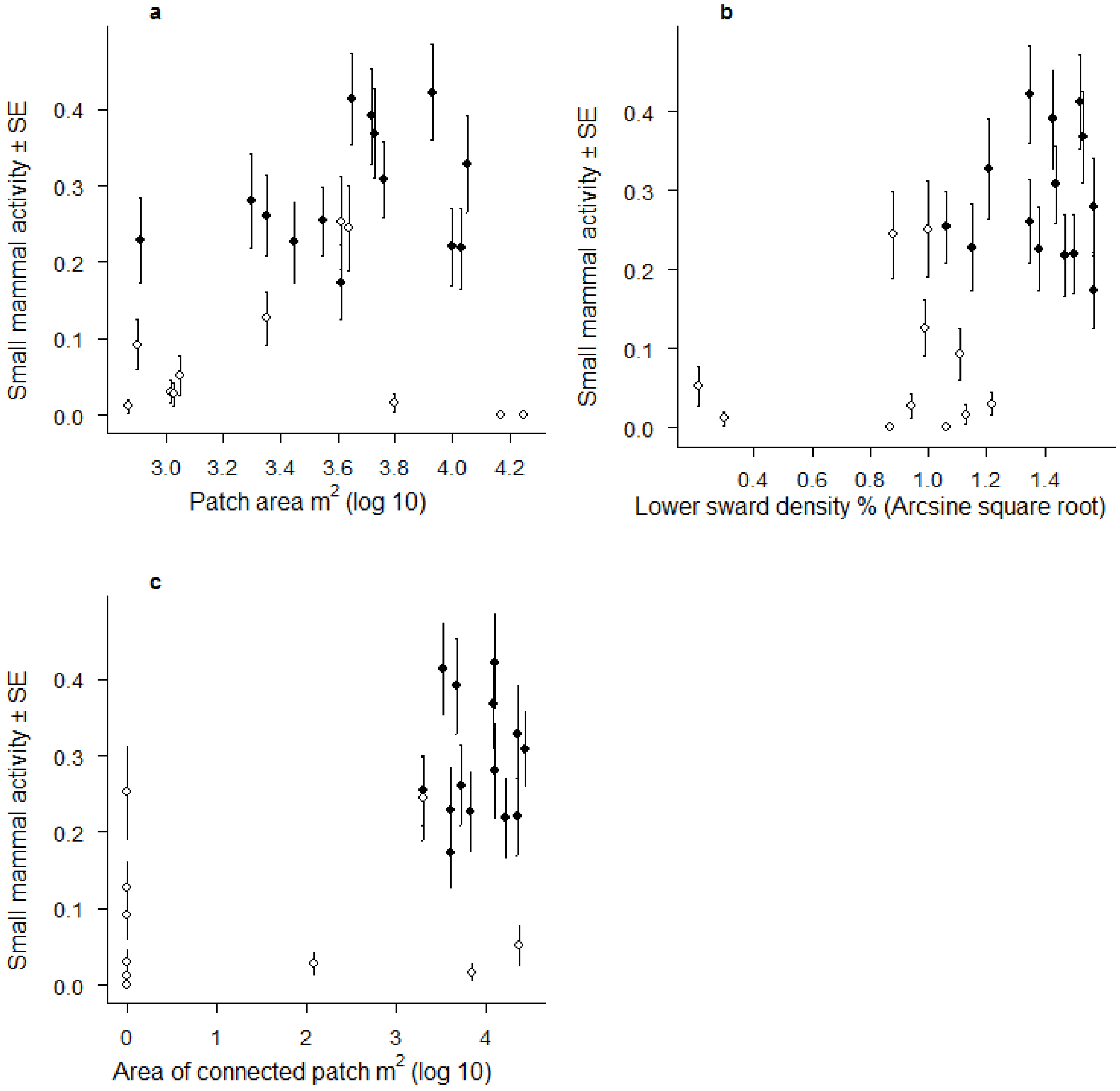

Figure 3 The variation in small mammal activity (mean proportion cover of tracking papers with small mammal footprints) across 25 tall vegetation patches varying in a) area, b) ground-level sward density, and c) area of connected tall vegetation, located either within fields (open circles) or in field verges (closed circles) at Berney Marshes. See Table 3 Analysis 2 for statistics.

Is small mammal activity similar within and outwith fields?

Small mammal activity increased significantly over the course of the wader breeding season at Berney, but only in the patches of tall vegetation that were in field verges, and not in tall vegetation patches in field edges (Table 3 Analysis 3, Figure 4).

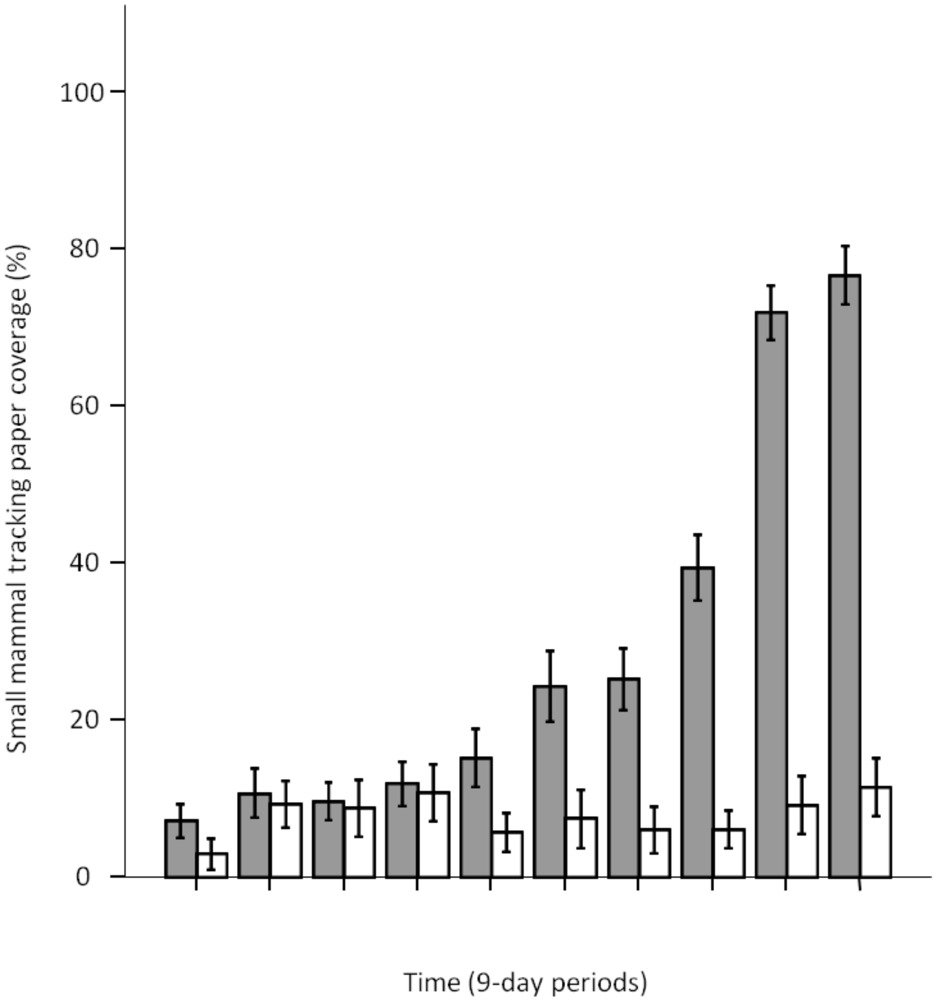

Figure 4 Seasonal variation in the mean (± SE) percentage cover of tracking papers with small mammal prints in tall vegetation patches in verges (closed bars) and within fields (open bars) at Berney Marshes, between 27 March and 25 Jun 2011. See Table 3 Analysis 3 for statistics.

Is small mammal presence within fields influenced by the presence of an adjacent verge?

Small mammals were present in field edges significantly more than in field centres (mean ± SE proportion of small mammal print presence: field centres 0.022 ± 0.007; field edges 0.048 ± 0.010, Figure 5, Table 4) but there was no significant influence of whether or not fields were connected to a verge (connected: 0.023 ± 0.007; not connected: 0.046 ± 0.001 Figure 5, Table 4). The presence of a verge also did not influence the difference in small mammal presence between the centre and edge of fields (Table 4: NS location*verge interaction).

Table 4 Results of generalised linear model to determine the influence of adjacent verges on small mammal presence within fields, recorded in ink-tracking tunnels on 46 fields on Berney Marshes (Table 2: Analysis 4). Minimum models are shown above the dashed lines, and non-significant variables (with estimates from the full model) are shown below the dashed lines.

Variable	*df*	X^2	*p*
(Intercept)	1	108.332	**<0.001**
Verge presence	1	2.614	0.106
Location	1	4.486	**0.034**
Season	1	1.955	0.162
Location*Verge presence	1	1.352	0.245
Location*Season	1	1.955	0.162

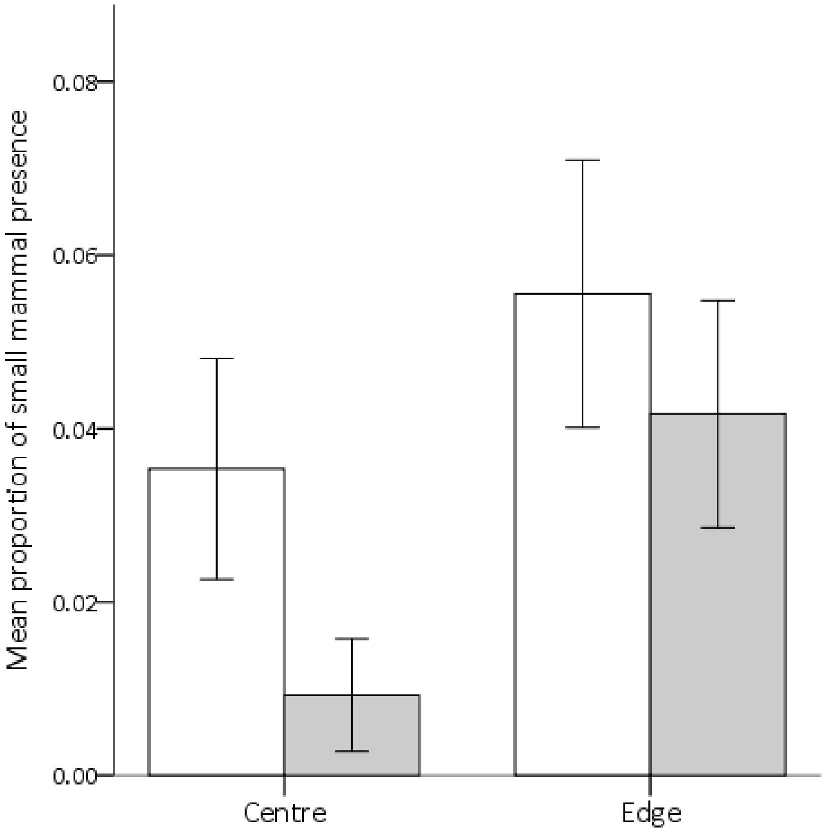

Figure 5 Variation in the mean (± SE) proportion of tracking tunnels with small mammal prints in field centres and edges in fields connected (open bars) and not connected (closed bars) to a verge, at Berney Marshes during March-July 2010.

Discussion

Across these wet grassland reserves that are managed primarily for breeding waders, small mammal activity was significantly greater in patches of tall vegetation that had denser swards, and those with larger areas of connected verge. However, the positive effect of connectivity on small mammal activity resulted in part from differences between areas of tall vegetation within fields and verges. Verge patches varied little in the degree of connectivity and had denser vegetation by the end of the season, while within field areas were typically less connected and with less dense swards, probably because of the grazing pressure they experience. By contrast, patch size had no clear effect on levels of small mammal activity, and fields that were adjacent to verges had similar levels of within-field small mammal activity to fields without adjacent verges. These results suggest that patches of tall vegetation of any size (> 0.05 ha, the minimum recorded in the study) are capable of supporting small mammals in these landscapes, but that activity levels will be greater in patches with dense ground-level sward structure.

Vegetation structure outside fields is often denser and taller due to fewer constraints imposed by grazing or water management, and because the species composition of verges differs to that within fields. As both sward height and density have been found to increase over the season in these habitats (Laidlaw *et al.* 2013), it is likely that the seasonal changes in vegetation structure will influence the distribution and activity of small mammals. While small mammal activity increased throughout the wader breeding season at all seven wet grassland sites, there was no increase in small mammal activity in patches within fields that had less dense vegetation. The use of vegetation structure variables, such as sward density, as a surrogate of patch quality for individuals or populations have been challenged due to the lack of consensus on how to measure these variables (Mortelliti, Amori, & Boitani 2010). However, during this study our consistent use of a simple, rapid and objective method of assessing the microhabitat (Glen, Sutherland, & Cruz 2010), to link conditions to small mammal activity, has demonstrated that this method could be widely utilised within future management of lowland wet grasslands, providing methodological consistency across this habitat.

Small mammal activity in patches of tall vegetation increased significantly with the area of connected tall vegetation. The verge areas outwith fields are often linear, running along tracks which link different areas of the reserve, giving verges the potential to act as habitat corridors. Landscape structure has been found to influence landscape connectivity for beetle populations, based on movements of individual beetles, where as the distance between patches increased, the connectivity decreased (Goodwin & Fahrig 2002). The level of connectivity of verge patches within the lowland wet grassland was constrained by the existing landscape structure. In our study, patches of vegetation within fields were often isolated from other areas of tall vegetation, and all the patches that had no connected area of verge were found within fields. Previous studies have found that small mammal presence is influenced by both habitat connectivity (positive predictor of wood mice *Apodemus sylvaticus*) and structure (hedgerow gappiness is a negative predictor of bank voles *Clethrionomys glareolus*; Gelling, Macdonald, & Mathews 2007) and that habitat heterogeneity at the landscape scale can increase small mammal diversity and density (Moro & Gadal 2007). The low level of use of patches within lowland wet grassland fields by small mammals is likely to be due to a combination of the lack of connectivity to other suitable areas as well as the lower density of vegetation. Even when fields were adjacent to verges, potentially improving their connectivity to source populations of small mammals, there was no significant increase in small mammal presence within those fields.

Across all seven wet grassland sites, levels of small mammal activity in tall vegetation patches varied little in relation to patch size (Figures 2b & 3a). Although without a large range of patch sizes it may be hard to determine whether this habitat characteristic is influencing small mammals in wet grassland, as metastudies of the relationship between patch size and mammal density failed to find an association between these variables if patch size range was small (Bowers & Matter 1997). Consistently high late season small mammal activity of tracking papers with ~80% print coverage across the majority of sites, suggests that the same processes influencing activity were operating across the sites.

During this study, we considered small mammals as a single group to focus on their function as an important prey source within the food web in this managed landscape. However, different small mammal species may have specific responses to habitat structure, for example through differences in spacing behaviour and the impact of factors such as territoriality, sex differences in home range, sex-biased dispersal, formation of kin groups and mating systems (Wolff, Schauber, & Edge 1997). The activity measures used in this study (frequency of prints within tracking tunnels) is a relative, rather than absolute, measure of activity and may not reflect variation in abundance. For the purpose of identifying potential habitat management activities that could change current small mammal activity the species identity or the number of individuals is not required. This study has determined that small mammals within lowland wet grassland, where they are the main prey of the generalist predators of breeding waders, are supported within patches of tall vegetation (>0.05 ha), but that their activity will be greater in patches with dense ground-level structures.

Implications for wet grassland management

In wet grassland landscapes managed for breeding waders, small mammals are primarily found in the tall, dense vegetation in verges and rarely within fields. The findings from this study suggest that configuration of tall habitat patches is relatively unimportant in terms of supporting small mammal populations within these wet grassland environments. Verges may provide a supply of the main small mammal prey of mammalian predators, but there does not appear to be any spillover of small mammals into adjacent fields, the influence of verges on small mammal distribution appears to operate at larger scales than the field-scale.

The creation of verges should provide habitat for small mammals and potentially increase the prey available for generalist predators within lowland wet grassland. In turn, this could alter predator behaviour in a way that could reduce predation on breeding waders. Verge creation could be a flexible management tool as only relatively small areas of verge appear necessary to provide suitable conditions for small mammals, even where connectivity between patches is limited. The tall vegetation patches selected for this study were selected as being representative of those currently available in the landscape, and were predominantly narrow verges that bordered tracks, paths or embankments (rail/river). There is however scope for altering the present configuration of verge habitats in wet grassland landscapes through the addition of tall habitat areas for example, copses with tall grass understory, or tall grasses and reeds along ditches. The size of these created patches is not necessarily important, as long as they provide dense vegetation and some level of connection to other patches. Within wet grasslands there could also be potential for small mammal habitat creation within fields that are either not appropriate or likely to be poorer quality breeding wader fields. Potentially whole fields, particularly those lacking wet features or short vegetation, could be devoted to providing small mammal habitats. However, in this study tall vegetation within fields was not as good at providing high small mammal activity compared with verges outside fields. Further work would be needed to identify the best infield management to promote high small mammal activity (e.g. through exclusion of grazing). As a first step to determining whether provision of tall vegetation has potential as a tool for breeding wader conservation we need to determine the influence of tall vegetation areas on predator behaviour and rates of wader nest predation. To ensure future management is sympathetic to the requirements of these species of conservation concern, the influence of positioning of tall vegetation habitats within the landscape needs to be elucidated. The design and creation of tall habitat patches for small mammals within lowland wet grassland landscapes could then potentially become a tool in the management to reduce the predation of breeding waders.

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Chapter 3

Influence of landscape structure on nest predation rates of grassland-breeding waders

Summary

1. Human activities such as agricultural intensification have greatly reduced the area of natural and semi-natural habitats throughout the developed world. Small amounts of remaining habitat can experience increased rates and intensity of predation, particularly when the surrounding landscape is likely to be inhospitable to prey and predators. High levels of predation can potentially have implications for the sustainability of populations that may have commercial or conservation value.
2. Excluding predators to reduce impacts of predation can be effective but is often not feasible or desirable. Consequently, there is a growing interest in identifying landscape-scale habitat management techniques that could be used to reduce rates of predation on species of concern. For example, management tools which influence the amount or diversity of resources for predatory species could influence their distribution and behaviour, which may then influence their impact on species of concern.
3. Widespread drainage of wetland habitats in Europe have resulted in remaining lowland wet grassland being fragmented, with the existing populations of waders in these fragments being subject to unsustainably high levels of predation. The habitat structure on lowland wet grassland is primarily short vegetation. Within this, the provision of tall vegetation could influence predation rates by providing habitat for the small mammal prey of the generalist predators that also prey on waders, as well as areas of shelter for these predators.
4. On an area of wet grassland in the East of England that is primarily managed for breeding waders, the nest distribution and hatching success of nesting lapwing, *Vanellus vanellus*, and redshank, *Tringa totanus*, has been measured annually since 2003. Here those data are used to quantify the influence on nest predation rates of proximity to areas of tall vegetation.
5. Lapwing nests were significantly less likely to be predated in fields adjacent to areas of tall vegetation, and their likelihood of being predated increased significantly with distance from these tall vegetation patches, and decreased with increasing amounts of tall vegetation within both 0.5 km and 1 km of the nest. For redshank nests, predation probability varied annually, but was not significantly influenced by proximity to, or area of, nearby tall vegetation.
6. These findings suggest that the distribution and activity of predators in lowland wet grassland landscapes may be influenced by the presence of areas of tall vegetation, and thus that there may be scope for landscape-scale management of vegetation structure to influence levels of predation on breeding waders in these habitats. However, the

effectiveness of such techniques is likely to depend on the extent to which predator activity is focussed around areas of tall vegetation, and whether these effects are consistent across the range of environmental conditions present on wet grasslands.

Introduction

The vulnerability of populations of prey species to the impacts of predation can vary depending on the complexity of local predator-prey interactions, with dramatic effects of predation on local populations possible, an example being predator mediated population cycles of small mammals (Korpimäki & Krebs 1996). At the other end of the spectrum, an example of a simpler system is when predators are introduced to previously predator-free islands where prey have few evolved predator defences (Blackburn *et al.* 2004; Sih *et al.* 2010). The impacts of predators on the sustainability of prey populations can be of particular concern in relation to species of economic value (e.g. farmed or managed animals such as gamebirds; Tapper, Potts, & Brockless 1996) or species of conservation concern. With many species of conservation concern now being constricted to small fragments of appropriate habitat (Wilson *et al.* 2005), there may be disproportionate impacts of predators on vulnerable populations (Fischer & Lindenmayer 2007), with predators being more abundant, active and species rich within fragments, especially within the context of agricultural landscapes (Chalfoun, Thompson, & Ratnaswamy 2002).

A reduction of the impacts of predation on local prey populations can sometimes be achieved through control of predator numbers in areas surrounding populations of conservation concern (Fletcher *et al.* 2010), or complete predator eradication (Oppel *et al.* 2011). However, these methods are time consuming, expensive and often controversial, with the potential for unforeseen release of other predator or competitor species (Bodey, McDonald, & Bearhop 2009). In addition, the impact of predator control is often dependent on initial predator densities (Bolton *et al.* 2007a), which can be difficult to assess. Predator exclusion can also be effective in some circumstances. For example, electrified exclosures to protect ground-nesting species have been found to significantly increase hatching success of piping plovers *Charadrius melodus* (Maslo & Lockwood 2009), and survival and fledging success of lapwing chicks have also been found to be higher within fenced plots that exclude mammalian predators (Rickenbach *et al.* 2011; Malpas *et al.* 2013). However, as fencing of sufficiently large areas is not likely to be a practical option in the wider countryisde, there is growing interest in developing managment techniques that can influence predator distribution and activity through changes in habitat structure that may influence the abundance, diversity and behaviour of prey species. Management of habitat composition can also be used to separate areas supporting different types of prey, or to alter the availability of cover vegetation, and thus to divert predators away from areas with species of conservation concern (Seymour, Harris, & White 2004). Finally, removal of suitable breeding habitats for predators, such as nesting trees or raised ground that is appropriate as dens or diurnal resting sites, have been suggested as means of decreasing predator densities (Bellebaum 2002).

Many ground-nesting wader populations in North West Europe have been in sharp decline in recent decades (Wilson, Ausden, & Milsom 2004; Roodbergen, van der Werf, & Hötker 2012), and several species are increasingly constrained to protected areas (Ausden & Hirons 2002; Smart *et al.* 2008). Impacts of predators within these landscapes have been identified as the key issue constraining the recovery and sustainability of several of these wader populations (Malpas *et al.* 2013). The predators of both chicks and nests of ground-nesting waders comprise a range of generalist predators, including foxes *Vulpes vulpes*, stoats *Mustela erminea*, weasels *Mustela nivalis*, marsh harriers *Circus aeruginosus* and corvids, all of which consume a range of small mammal species, lagomorphs and birds (Holyoak 1968; Underhill-Day 1985; McDonald, Webbon, & Harris 2000; Kidawa & Kowalczyk 2011). Small mammals, such as field voles (Forman 2005), are often a key part of the diet of these generalist predators, and therefore the distribution of small mammals within the landscape could influence predation rates on other components of the diet. In lowland wet grasslands managed to encourage breeding wader populations, grazing is typically used to maintain short swards that are attractive to waders, and taller vegetation is often limited to areas outside fields that provide appropriate feeding habitat and shelter for small mammals (Laidlaw *et al.* 2013) and generalist predators. Management for breeding waders limits the distribution of patches of tall vegetation that could provide small mammal prey and/or shelter for generalist predators, and could therefore alter predator behaviour and patterns of nest predation. Here we assess the influence of patches of tall vegetation on nest predation rates of breeding waders. We use a nine-year dataset of wader breeding distribution and demography at one of the east of England’s largest remaining wader populations to quantify the probability of nest predation for lapwing and redshank in (i) fields with and without adjacent tall vegetation patches and (ii) areas with differing amounts of, and distances to, tall vegetation, at different spatial scales.

Methods

Study site

The influence of the area and distribution of tall vegetation on patterns of nest predation in lapwing *Vanellus vanellus* and redshank *Tringa totanus* in a grassland landscape was explored at Berney Marshes RSPB reserve (52°35'N 01°35'E, National Grid reference TG4605). Habitat management carried out on this reserve is predominantly aimed at providing suitable nesting conditions for breeding waders, through maintaining short swards within fields and ensuring the presence of surface wet features throughout the wader breeding season (Eglington *et al*. 2008). Grazing pressure from commercial livestock on the reserve is typically ~1 Lu (livestock units) ha^{-1} (Bodey *et al.* 2010), which results in within field sward heights of ~5-15 cm across most of the reserve. However, ~5% of the reserve is comprised of patches of taller vegetation, which ranges from verges with vegetation >~15 cm bordering roads, tracks, riverbanks and railways, to copses with trees and dense undergrowth (Figure 1).

Wader nest monitoring and survival

The nesting success of breeding waders has been monitored intensively at Berney Marshes since 2003 (Smart *et al.* 2006; Eglington *et al.* 2009; Bodey *et al.* 2010). In each year, between 33 and 52 fields were studied intensively, with surveys being carried out every 4-5 days to locate as many nesting attempts as possible. Lapwing (n = 937 nests) nest in short, open grassland and their nests are visible and these are primarily located through observation of incubating adults from a vehicle. In contrast, redshanks (n = 417 nests), which nest in taller vegetation, are not visible when incubating eggs and a late flushing response to disturbance in this species means that nests are located by systematic searching and incidental flushing of adults from concealed nests. Nest locations have been spatially referenced using GPS since 2007 for redshank, and 2005 for lapwing (Figure 1).

The wader breeding season at these latitudes typically ranges from March to July, with pairs capable of renesting following losses at the egg stage, although the probability of doing so decreases later in the season (Beintema & Muskens 1987). The date on which each nest was first located (termed FIND DAY in analyses) provides an indication of the period during the season in which nests were active (the majority of nests are found within 10 days of laying). All nests were marked and visited a minimum of every five days, and more regularly near their estimated hatch date to determine their fate. Nests were considered successful if one or more eggs hatched and predated nests were defined as those that were empty without any eggshell fragments in the nest to indicate successful hatching (Green, Hawell, & Johnson 1987).

To determine the time and date of nest failures, Ibutton dataloggers (Maxim Integrated Products Ltd, CA, USA) have been placed in a random selection of nests (between 40 – 85% of all nests monitored) since 2007. These loggers record a temperature trace at specified intervals (every seven minutes in this study), with a sharp and permanent decline in nest temperature below the incubation temperature indicating a nest has been predated (Bolton *et al.* 2007b), or the gradual cooling associated with a hatched nest allowing for the date, time and type of nest fate to be recorded. For predated nests in which the exact date of predation was not known (e.g. dataloggers not deployed), the failure day was taken as the midpoint between the final two visits. Nests that were deserted (n = 33), flooded (n = 11) or trampled (n = 54) without any evidence of prior predation were excluded from the analyses of hatched (n = 594) and predated (n = 760) nests.

To determine the daily nest predation rate (DPR) for each species, the Mayfield method (Mayfield 1961, 1975) was used, in which the number of exposure days represents the period over which each nest was monitored from discovery to predation or hatching. This method accounts for the increased likelihood of locating nests that survived for longer periods:

$$DPR = \frac{\text{Total number of monitored nests predated}}{\text{Total number of days nests were under observation}}$$

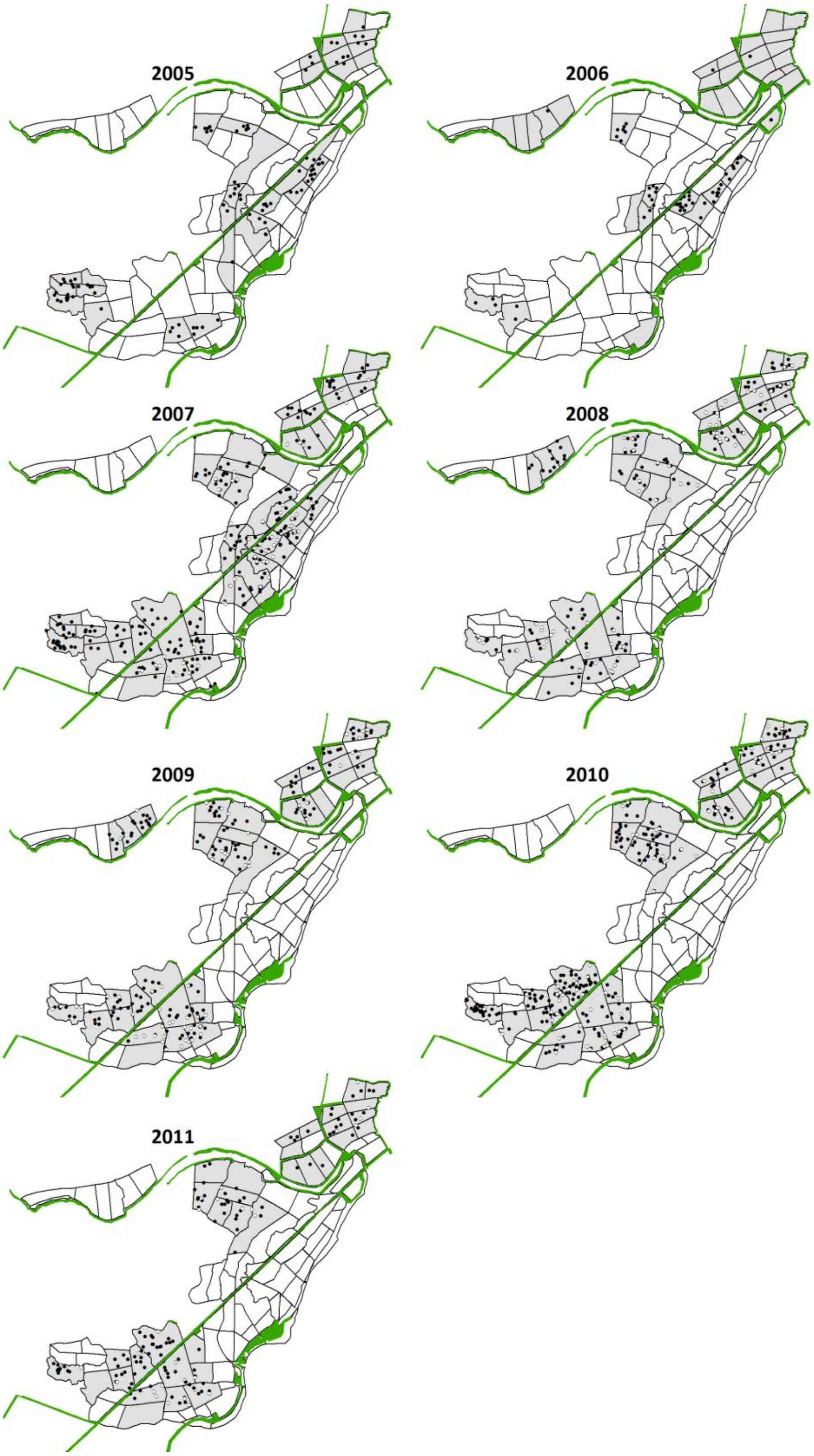

Figure 1 The distribution of monitored fields (grey) and lapwing (●) and redshank (○) nests at Berney Marshes between 2005 and 2011, and of tall vegetation outside fields (green).

Scale of landscape structure and habitat assessment

Patches of tall vegetation, which are generally found as verges outside fields, provide the only suitable habitat for small mammals in this landscape (Laidlaw *et al.* 2013). These patches may therefore be a source of prey or shelter for predators. The area and distribution of all patches of tall vegetation (> 15 cm) within the reserve landscape were mapped in ArcGIS v.9.3, by digitising outlines from aerial photographs (Millennium Map 2000; Figure 1). Ground-truthing confirmed which fields were CONNECTED to a tall vegetation patch (e.g. via gateways or earth bridges). The DIRECT DISTANCE from each wader nest to the nearest tall vegetation patch was measured as the shortest straight line distance in ArcGIS. To investigate the influence on hatching success of the amount of tall vegetation within the vicinity, the AREA of tall vegetation within circular buffers of radius 0.2 (0.13 km^2), 0.5 (0.79 km^2) and 1.0 km (3.14 km^2) around each nest was calculated in ArcGIS. The different sized buffers represent different scales at which tall vegetation could influence wader hatching success: from potential local-scale effects on predator movement within wet grassland up to larger landscape-scale effects on predator presence and abundance.

Statistical analysis

Variation in daily nest predation rates were explored with Generalized Linear Models (GLMs) in R (v 2.13.1), using a formulation of Mayfield's (1961, 1975) method as a logistic model with a binomial error term, in which success or failure (hatched or predated) was modelled with exposure days as the binomial denominator (Aebischer 2009).

To assess whether nest predation probabilities differed on fields that were and were not connected to a verge, the daily predation rates for lapwing and redshank were modelled in GLMs, with CONNECTED or not to a verge and YEAR as fixed factors, for all nests between 2003 and 2011 (Table 1). Subsequently, for spatially referenced nests only, these daily nest failure rate models were extended to incorporate seasonal variation in predation risk by including FIND DATE, and to explore the effects of nest location relative to verges by including DIRECT DISTANCE to verge and AREA of verge within a buffer (Table 1). Separate models were constructed for each species and with each buffer distance (0.2, 0.5 and 1.0 km; all three spatial-scales could not be incorporated in a single model due to collinearity; Table 1). Non-significant variables were removed from these models (although their estimates and associated probabilities in maximal models are also reported, for completeness). All models were carried out in R (v 2.13.1)

DPRs predicted from these models were then transformed to predation probabilities by estimating nest survival rates over the incubation period (S) by raising the daily survival rate (1-DPR) to the power of the species incubation periods (from first egg laid: redshank = 30 days; lapwings = 32 days; Crick, Baillie, & Leech 2003; Kragten & De Snoo 2007). Nest predation probability over the incubation period was then calculated as 1-S.

Table 1 Descriptions of response and explanatory variables and model structures used in analyses of nest predation probabilities of lapwing and redshank. The numbers of wader nests used in each analysis are shown separately for fields with (V) or without (NV) a verge connected. GPS = spatially referenced nests.

Model response	Data used	Lapwing		Redshank		Model structure
		V	NV	V	NV	
Nest predation rate	All nests	290	647	98	319	Year+ Verge connection
	GPS nests	281	632	90	165	Year+ Find day+ Verge connection + Distance to verge + Verge within 0.2 km
						Year+ Find day+ Verge connection + Distance to verge + Verge within 0.5 km
						Year+ Find day+ Verge connection + Distance to verge + Verge within 1 km

Type	Variable	Distribution (link)	Explanation
Response	Nest predation rate	Binomial (logit)	Nest outcome (Predated or Hatched) accounting for exposure days ; (cbind(predated outcome, exposure days)
Explanatory	Year		Lapwing: 2005-2011; Redshank 2007-2011
	Find date		Day after March 1st when nest was found
	Verge connection		Nest field connected or not to a verge (e.g. gateway or other entrance).
	Distance to verge	m	Straight line distance between nest and nearest verge (measured in ArcGIS v10)
	Verge within 0.2 km	m^2	Area of verge within a buffer of 0.2 km radius centred on each nest
	Verge within 0.5 km	m^2	Area of verge within a buffer of 0.5 km radius centred on each nest
	Verge within 1 km	m^2	Area of verge within a buffer of 1 km radius centred on each nest

Results

The number of nests monitored each year ranged from ~50 – 200 for lapwing and ~25 – 70 for redshank (Figures 2a and 3a). The nesting period for lapwing spanned late March to mid July, and peaked in the first week of April (Figure 2b), with redshank nesting starting later and peaking in the last week of April (Figure 3b). Both wader species nested in fields that were and were not connected to a verge. In unconnected fields, around half the nests of both species were predated, while approximately two-thirds of redshank nests and half of lapwing nests in fields with verges connected were predated (Figures 2c and 3c). Both lapwing and redshank nested at a range of distances from the nearest verge up to a distance of ~500 m (Figure 2d and 3d). Most nests had less than ~4% (<5000 m^2) of the surrounding land made up of verge habitat, at all three scales (Figures 2e-g and 3e-g). The largest scale (1 km) encompassed a large proportion of the reserve, and so no nests had small amounts of surrounding verge (Figures 2g and 3g).

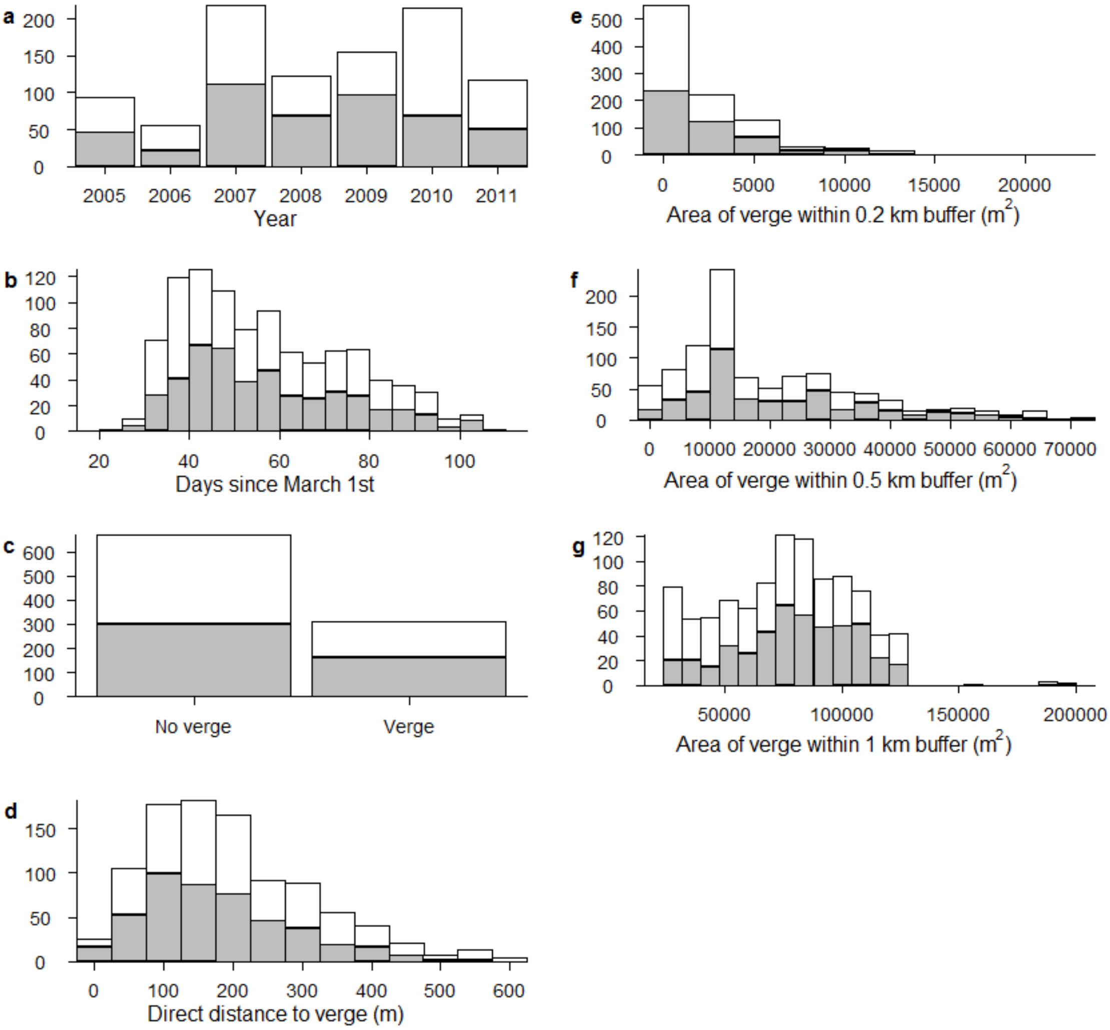

Figure 2 Number of lapwing nests that were predated (white) and hatched (grey) for different a) years, b) days since the 1st March, c) presence of an attached verge, d) direct distance from nest to verge, e) area of verge within 0.2 km of nest, f) area of verge within 0.5 km of nest, and g) area of verge within 1 km of nest.

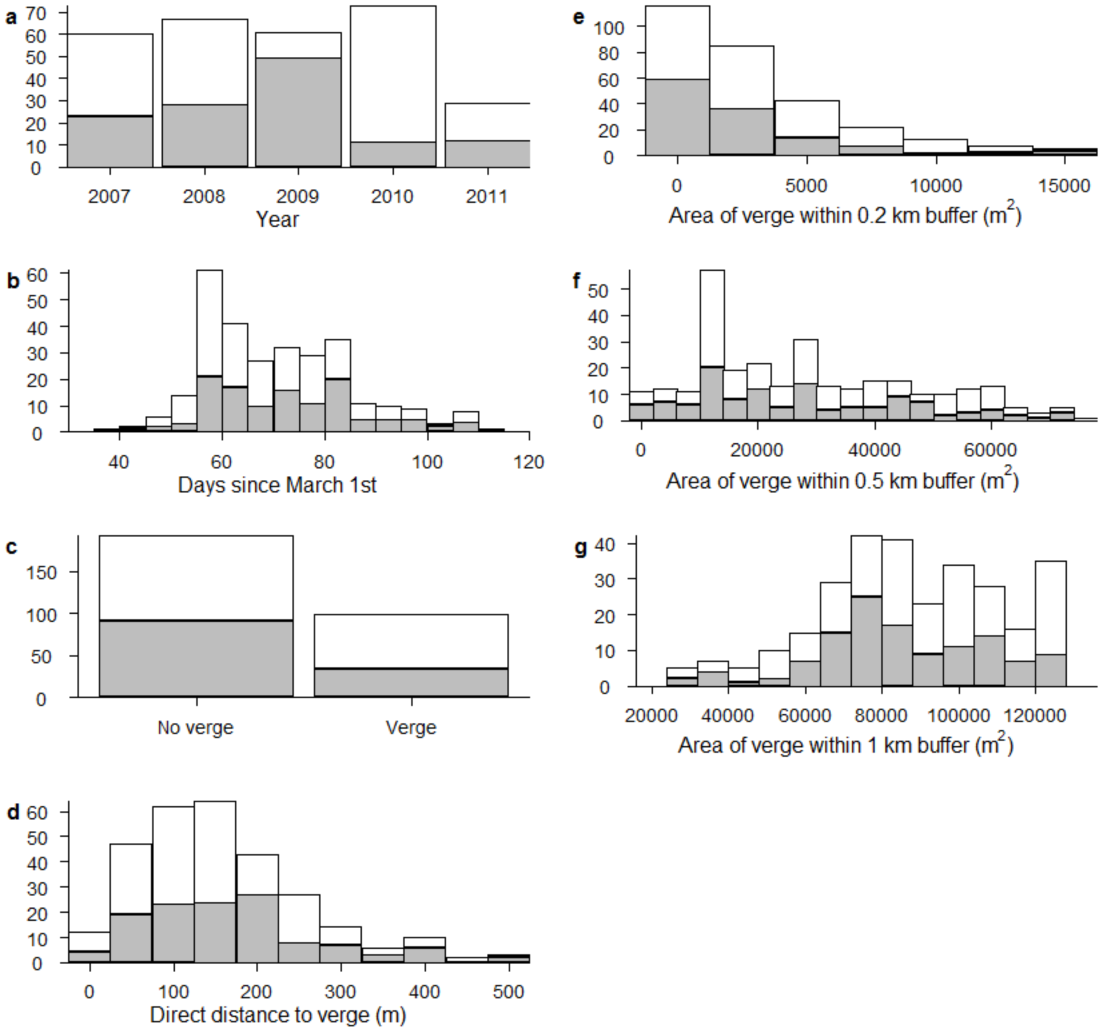

Figure 3 Number of redshank nests that were predated (white) and hatched (grey) for different a) years, b) days since the 1st March, c) presence of an attached verge, d) direct distance from nest to verge, e) area of verge within 0.2 km of nest, f) area of verge within 0.5 km of nest, and g) area of verge within 1 km of nest.

Effect of verge connectivity on nest predation rates

Over the nine years during which wader nesting success was monitored, lapwing nest predation probability varied significantly between years (Figure 4a; year: z = 2.42, df = 958, p = 0.016) and was significantly lower in fields that were connected to a verge (mean probability of predation over the incubation period: 0.67 ± 0.08 SE) compared with fields without a verge connected (0.76 ± 0.06; verge presence: z = -2.51, df = 958, p = 0.012). Redshank predation probability did not vary significantly between years (Figure 4b; year: z = 1.66, df = 287, p = 0.097). Although the annual sample size of redshank nests that were predated (n = 9 – 41) or hatched (n = 12 – 62) was small, excluding year from the analysis did not alter the lack of any significant difference in predation probability between fields connected (0.88 ± 0.07) or not to a verge (0.75 ± 0.07; verge presence: z = 1.694, df = 288, p = 0.090).

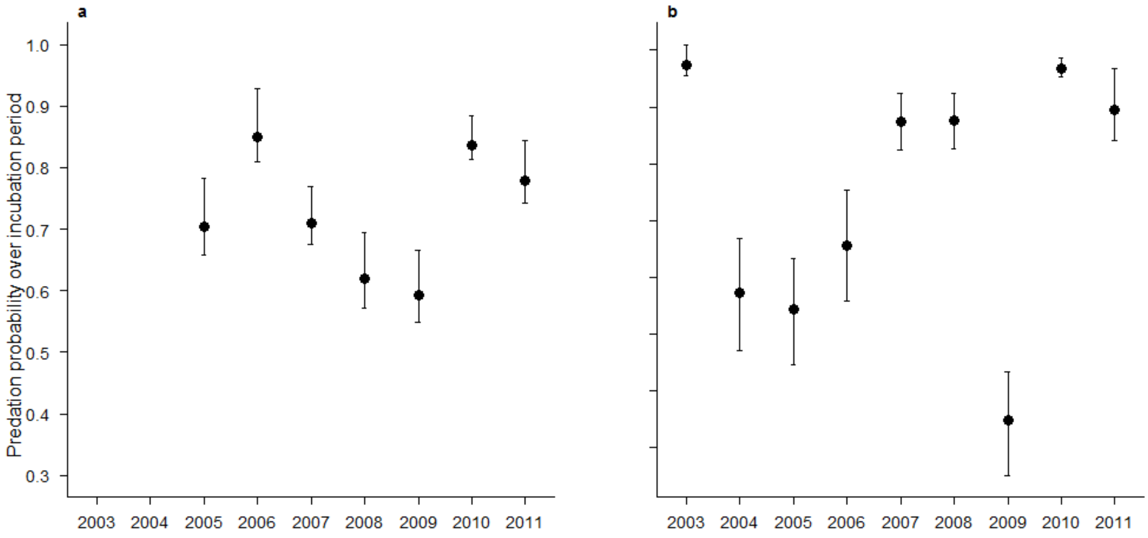

Figure 4 Annual variation in nest predation probability (± SE) of a) lapwing and b) redshank at Berney Marshes.

Effect of verge connectivity, proximity and extent on predation rates of nests

Of the 913 spatially referenced lapwing nests, those that were more distant from the nearest verge had significantly higher predation probabilities (Table 2a, Figure 5a,b). The area of verge within 0.2 km did not significantly influence predation probabilities of lapwing nests but nests with larger areas of verge within the surrounding 0.5 km (Figure 5c) and 1 km (Figure 5d) had significantly lower predation probabilities (Table 2b,c). Distance to verge was not a significant predictor of predation probability in the model that included area of verge within 1 km (Table 2c), suggesting that the relative effect of area of verge at this large scale (when all nests have some verge habitat in the surrounding buffer area) is greater than distance to the nearest verge.

For nesting redshank, in the years during which nests were spatially referenced (2007 onwards) there was significant annual variation in predation probability of the 255 nests, but none of the environmental or seasonal variables significantly influenced nest predation probability (Table 3).

Table 2 Results of binomial models of nest survival for lapwing with differing areas of verge habitat in the surrounding (0.2 km, 0.5 km and 1 km buffer models). Minimum models are shown above the dashed lines, and non-significant variables (with estimates from the full model) are shown below the dashed lines. Estimates and SE are logits, with 2005 acting as a reference year

Variable	Estimate	Std. Error	z value	Pr(>|z|)
0.2 km buffer model				
(Intercept)	-3.711	0.177	-20.975	<0.001
Year (2006)	0.584	0.231	2.525	0.012
Year (2007)	0.149	0.178	0.839	0.401
Year (2008)	-0.198	0.203	-0.978	0.328
Year (2009)	-0.208	0.199	-1.043	0.297
Year (2010)	0.548	0.171	3.197	0.001
Year (2011)	0.332	0.194	1.714	0.087
Distance to verge	0.001	0.000	3.935	<0.001
Find date	0.005	0.003	1.893	0.058
Verge connected	-0.099	0.115	-0.855	0.392
Verge in 0.2 km buffer	0.000002	0.00002	0.116	0.907
0.5 km buffer model				
(Intercept)	-3.512	0.199	-17.616	<0.001
Year (2006)	0.550	0.232	2.369	0.018
Year (2007)	0.155	0.178	0.870	0.384
Year (2008)	-0.192	0.203	-0.945	0.345
Year (2009)	-0.200	0.200	-1.001	0.317
Year (2010)	0.547	0.171	3.189	0.001
Year (2011)	0.331	0.194	1.707	0.088
Distance to verge	0.001	0.0004	2.918	0.004
Verge in 0.5 km buffer	-0.00001	0.000003	-2.073	0.038
Find date	0.005	0.003	1.756	0.079
Verge connected	-0.065	0.112	-0.583	0.560
1 km buffer model				
(Intercept)	-2.749	0.191	-14.375	<0.001
Year (2006)	0.560	0.230	2.433	0.015
Year (2007)	0.109	0.177	0.617	0.538
Year (2008)	-0.274	0.203	-1.351	0.177
Year (2009)	-0.318	0.198	-1.608	0.108
Year (2010)	0.431	0.170	2.531	0.011
Year (2011)	0.237	0.193	1.227	0.220
Verge in 1 km buffer	-0.00001	0.000002	-4.710	<0.001
Find date	0.004	0.003	1.623	0.105
Verge connected	-0.081	0.111	-0.735	0.463
Distance to verge	0.001	0.0005	1.413	0.158

Table 3 Results of binomial models of nest survival for redshank with differing areas of verge habitat in the surrounding (0.2 km, 0.5 km and 1 km buffer models). Minimum models are shown above the dashed lines, and non-significant variables (with estimates from the full model) are shown below the dashed lines. Estimates and SE are logits, with 2007 acting as a reference year

Variable	Estimate	Std. Error	z value	Pr(>|z|)
0.2 km buffer model				
(Intercept)	-2.840	0.169	-16.789	<0.001
Year (2008)	0.008	0.236	0.033	0.973
Year (2009)	-1.480	0.336	-4.403	0.000
Year (2010)	0.592	0.215	2.746	0.006
Year (2011)	0.143	0.302	0.474	0.635
Find date	-0.003	0.006	-0.527	0.598
Verge connected	0.283	0.196	1.446	0.148
Distance to verge	0.001	0.001	0.961	0.337
Verge in 0.2 km buffer	0.00004	0.00003	1.446	0.148
0.5 km buffer model				
(Intercept)	-2.840	0.169	-16.789	<0.001
Year (2008)	0.008	0.236	0.033	0.973
Year (2009)	-1.480	0.336	-4.403	<0.001
Year (2010)	0.592	0.215	2.746	0.006
Year (2011)	0.143	0.302	0.474	0.635
Find date	-0.002	0.006	-0.360	0.719
Verge connected	0.300	0.195	1.536	0.125
Distance to verge	0.0004	0.001	0.425	0.671
Verge in 0.5 km buffer	0.000001	0.000005	0.237	0.812
1 km buffer model				
(Intercept)	-2.840	0.169	-16.789	<0.001
Year (2008)	0.008	0.236	0.033	0.973
Year (2009)	-1.480	0.336	-4.403	<0.001
Year (2010)	0.592	0.215	2.746	0.006
Year (2011)	0.143	0.302	0.474	0.635
Find date	-0.002	0.006	-0.417	0.677
Verge connected	0.312	0.196	1.593	0.111
Distance to verge	0.001	0.001	0.519	0.604
Verge in 1 km buffer	0.000003	0.000004	0.701	0.483

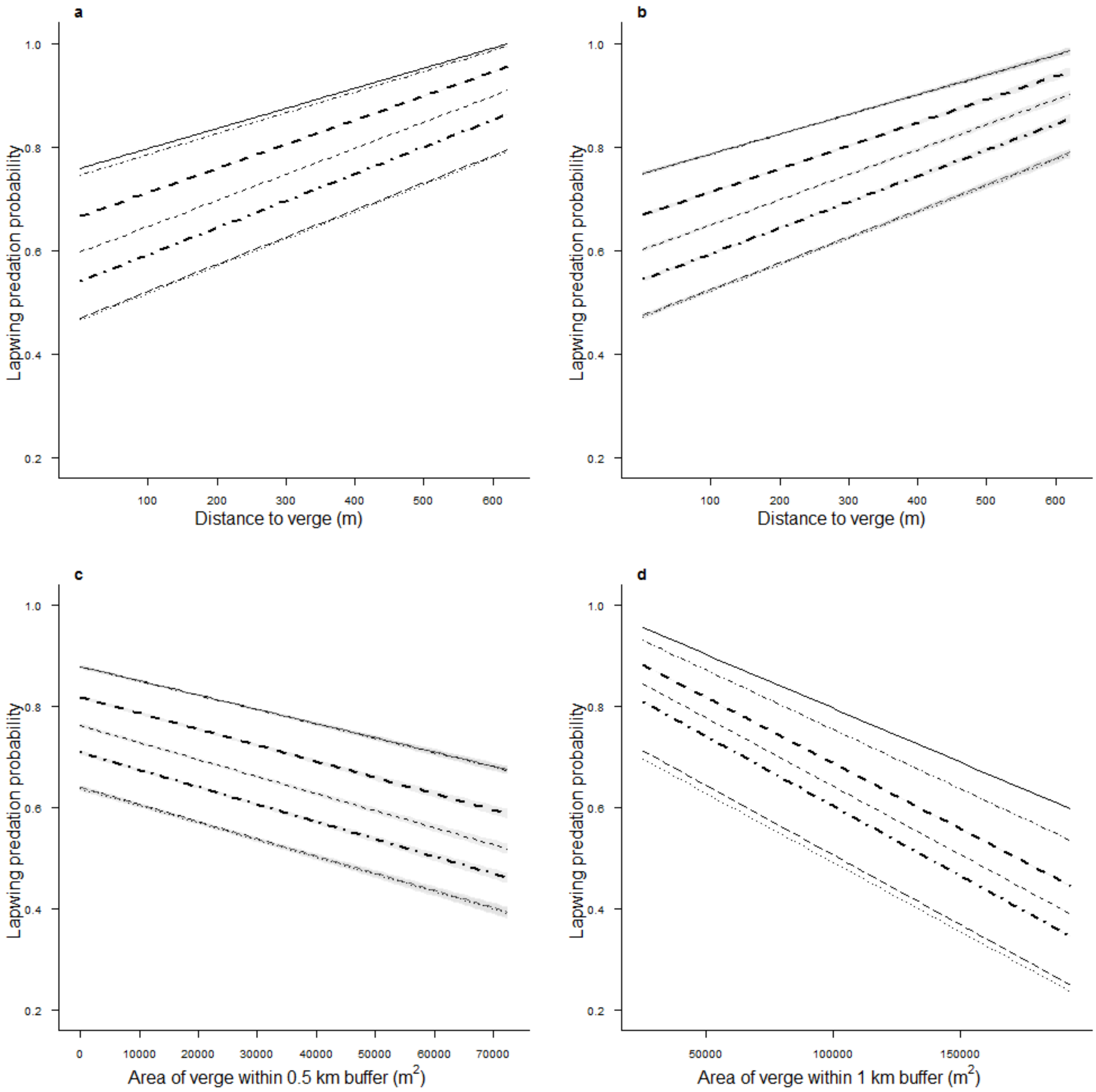

Figure 5 Predicted predation probability (shading indicates 95% confidence intervals) for lapwing nests in different years (2005: thick dot-dash line; 2006: solid line; 2007: dashed line; 2008: long-dashed line; 2009: dotted line; 2010: dot-dashed line; 2011: thick dashed line) in relation to a) distance to the nearest verge (Table 2: 0.2 km buffer); b) distance to nearest verge (Table 2: 0.5 km buffer) and c) area of verge within 0.5 km (Table 2: 0.5 km buffer); and d) area of verge within 1 km buffer of each a nest (Table 2: 1 km buffer).

Discussion

Landscape structure has potential to influence rates and patterns of predation, which could be an important management tool if predation is limiting the success of populations. Within lowland wet grasslands, areas of tall vegetation are typically rare and patchily distributed within the landscape, but evidence from this study suggests their presence may influence nest predation levels in breeding waders. Lapwings nesting in fields directly connected to patches of tall vegetation had higher survival rates (Figure 4) and the closeness and extent of these patches positively influenced nest survival from field-scales to landscape-scales (Figure 5). These effects of the presence of tall vegetation were not apparent for redshank, as there was no evidence for connectivity, proximity or extent of tall patches influencing nest predation patterns in this species.

The location and extent of areas of tall vegetation in relation to fields that support nesting breeding waders has not previously been considered in terms of predator management, but could influence the vulnerability of proximate nests to predation. There was no influence of the area of verge at the local-scale (0.2 km buffer) on the predation likelihood of lapwing nests, with distance to verge being the most important factor at this scale. However, lapwing nests were significantly more likely to be predated when there was less tall vegetation in the area surrounding the nest field (0.5 km buffer). This pattern was also sustained when the buffer size was increased to 1 km, which is representative of landscape-scale effects working across large sections of the reserve. Potentially, an increase in the amount of tall vegetation in the landscape could alter the predation pressure on breeding waders, but these effects may not be apparent for all species, as predation of redshank nests was not influenced by tall vegetation at any scale. A greater understanding of the impact on landscape structure on breeding waders would therefore be required to ensure management is appropriate for the range of wader species breeding in these habitats.

Potential mechanisms influencing verge effects on nest predation

The possible mechanisms through which patches of tall vegetation could influence predation rates include altering prey density, predator behaviour or carrying capacity of landscape for predators. However, further elucidation of how tall vegetation may be influencing predation rates does not necessarily improve our understanding of the potential impacts of manipulating this habitat, as predicting how populations will respond to novel environmental changes from past patterns is unreliable (Norris 2004). The effects of tall vegetation could be non-linear, such that increasing the amount of tall vegetation beyond current levels may not alter predation rates.

Influence of prey type and abundance

Within areas managed for breeding waders, the tall vegetation areas outside fields provide the only source of the main prey (small mammals e.g. voles) for the predators of breeding waders (Laidlaw *et al.* 2013). The probability of predation of lapwing nests was lower when there was a verge connected to the nest field, or the distance to verge decreased. This lower predation probability near tall vegetation could result from the increased level of prey available to predators within these tall habitats, reducing predator need to search for wader nests. Tall verge habitats have been found to support several small mammals, with those bordering roads in Britain providing habitat that supports small mammals (e.g. for bank vole *Clethrionomys glareolus*, wood mice *Apodemus sylvaticus* and field vole *Microtus agrestis*) at summer densities similar to those found in hedgerows (Bellamy *et al.* 2000).

Higher lapwing nest predation levels were recorded at greater distances from the tall vegetation of verges. As tall vegetation patches are not available continuously through the landscape, searching for wader nests may be relatively more profitable for predators when far from tall vegetation and the small mammal prey it supports. Such predator switching in response to prey density has been explored conceptually (van Baalen *et al.* 2001) and identified empirically (Kjellander & Nordström 2003). Alternatively, individual predators may specialise on the wader nest stage to fulfil their energetic requirements, and these specialist individuals may therefore be less likely to focus their activities around tall vegetation. Generalist predators could have specialised hunting behaviours to locate and predate wader nests, for example there are anecdotal records of individual crows specialising in predating lapwing eggs (Ausden *et al.* 2009). Predators have been found to specialise on specific nests types to the extent of failing to recognise nests of abnormal appearance (Martin 1988). Individuals specialising on wader nests may also favour large, open areas of grassland without tall vegetation obscuring their view, to allow better location of areas with likely wader nests through the observation of adult waders. For example, open areas within hunting grounds have been found to provide favourable hunting conditions for wolves, where they are able to better view their elk prey (Kauffman *et al.* 2007).

Edge use in fragmented landscapes

Areas of tall vegetation within lowland wet grasslands provide spatial heterogeneity, which has been found to alter prey availability, leading to modified encounter, kill and consumption rates within predator-prey interactions (see Gorini *et al.* 2011 for review). Predation rates are often observed to increase along habitat edges, with more fragmented habitats being more heavily predated (Batáry & Báldi 2004). In fragmented agricultural landscapes, carnivores (especially mustelids) have been found to use narrow strips of shrubby vegetation and dense long-stemmed grasses more often than the hayfield matrix (Sálek *et al.* 2009). Where there is tall vegetation within the landscape, the intersection between this and shorter, within-field habitats may provide predators using these areas with more prey options, as species found in both habitats types will be in close proximity to one another, which is a commonly observed edge effect (Odum 1971). For lapwings, however, there was no increased rate of predation at the habitat interface between the taller verge habitats and wet grassland fields connected to them, compared to fields that were not on the edge of habitats. However, there was no clear evidence that either lapwing or redshank avoided nesting close to verges, although this was not explicitly addressed within this study.

Influence of shelter

Tall vegetation areas may also provide shelter for predator species, which is likely to be a contributing factor to the importance of these areas for predators. Foxes operating in and around the study site may have only small patches of tall vegetation within their home range, as red fox territories can vary from < 0.5 km^2 to ~20 – 30 km^2 (Goszczyński 2002). With small mammal prey clumped in these scarce tall vegetation areas, it may be expected that wader nests closer to tall vegetation may experience higher predation rates as a result of increased predator activity in these areas. In open habitats, nesting waders have been found to electively nest further from raised structures that avian predators frequently used for searching for prey (Wallander, Isaksson, & Lenberg 2006), suggesting an increased vulnerability to predation in these areas.

Implications for wet grassland management

This study provides evidence that the presence of tall vegetation in wet grassland landscapes may influence the predation pressure on breeding wader nests, and thus suggests that management of tall vegetation could potentially be used as a tool to alter nest predation rates which are currently unsustainably high. Outside of fields, tall vegetation areas within the landscape are currently present along roads, railways or riverbanks with no specific management being undertaken in association with breeding waders. Tall vegetation could be provided within the landscape by increasing the area of verge outside of fields, or ensuring that mowing of existing verges occurs after the wader breeding season (late July), so that the tall vegetation is available to predators for as long as possible in the landscape. Future work could determine the feasibility and effectiveness of providing tall vegetation within whole fields that are not appropriate for breeding waders (e.g. too dry). As the position of tall vegetation within the landscape appears to be important in influencing predation on wader nests, there may also be potential to consider this habitat type within agri-environment schemes targeted at improving conditions for breeding waders. At present, these schemes target conditions within fields only, such as wetness and sward condition, and landscape-scale issues such as proximity to tall vegetation are not considered. Before specific management prescriptions can be determine though, the impact of proximity to tall vegetation on predation rates of wader nests needs to be explored more fully, paying particular attention to whether these effects are consistent across the range of environmental conditions present in wet grassland and not just those present within nature reserves.

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Chapter 4

Factors influencing the distribution and movement of Red Foxes, *Vulpes vulpes*, on lowland wet grasslands

Summary

1. Landscape structure can influence the distribution and movement patterns of predators, and can potentially influence their impact on their prey. In cases where prey species are of conservation concern, understanding the factors that influence predator movements can potentially inform the development of landscape-scale management to reduce the impacts of predators.
2. Many wader populations across Western Europe have declined severely as a result of wetland degradation, and impacts of predators, particularly red foxes *Vulpes vulpes*, have been identified as a constraint to population recovery. Identifying landscape structures that influence movement patterns of these predators may allow their impact on waders to be reduced through appropriate habitat management.
3. On a large area of lowland wet grassland in the east of England, we use nest temperature loggers and nest-camera data to explore the contribution of red foxes to wader nest predation. We then investigate whether the use of track plots by foxes is influenced by (i) extent of surface flooding (which may act as a barrier to movement), (ii) proximity to tall vegetation (which can provide shelter and access to small mammal prey) and (iii) wader nesting density (as wader group mobbing defences may deter predators).
4. Between 2007 and 2011, 85% of 364 wader nests were predated at night, indicating predation by mammalian predators. Cameras deployed on a subset of nests found foxes to be the only species observed to predate wader nests, and all these predation events occurred at night.
5. Fox track plot use did not vary with distance to tall vegetation, distance to field edge, extent of surface water within fields or field area, but there were significant seasonal declines (from ~60% probability of use in April to ~20% in June) and annual variation (between 32 and 95% of track plots used each year). Track plots were also ~20% less likely to be used in areas with higher densities of lapwing nests (> six lapwing nests within 100 m) than areas with no nearby nesting lapwing. Trail camera images also indicated that fox activity along field verges was significantly higher than within fields.
6. These data suggest that the distribution and activity of foxes in lowland wet grasslands can be influenced by the distribution of nesting waders and by managed features such as the presence of tall vegetation. Management of landscape structure may therefore have potential as a tool to reduce wader nest predation.

Introduction

Natural variation within landscapes in the quality, seasonality, area, isolation, or fragmentation of food resources and protective cover can influence the distribution and movement patterns of individuals (Bascompte & Vilà 1997). Many habitats, features or substrates, , such as roads (Shepard *et al.* 2008), wind turbines (Hötker, Thomsen, & Jeromin 2006) and field boundaries (Wratten *et al.* 2003), although not necessarily impermeable, can act as barriers to movement for species. Previous studies have indirectly quantified the ease of movement of individual animals through landscapes, for example by measuring their speed, with faster speeds reflecting greater ease of movement. For example, wolves, *Canis lupus*, have been found to travel twice as fast along linear habitats compared with the interior of forests (James 1999).

Anthropogenic changes to landscape quality and configuration can also have direct and indirect consequences for species at different trophic levels. Barriers to movement may directly influence the distribution of species at higher trophic levels such as predators, and the consequent changes in predator activities may indirectly influence the distribution, abundance or success of their prey. For example, predation rates on passerine nests have been shown to decrease with increasing depth of water in marshes, as fewer predator species are able to access these nests (Picman, Milks, & Leptich 1993). Similarly, mammalian predation of greylag goose eggs is lower in reedbed sites in which water channels and higher vegetation densities act as natural barriers to predator movement (Kristiansen 1998).

Scaling-up from the impact of differences in habitat structure to the influence of habitat configurations at landscape-scales, can also have important consequences for predator distribution. Protected areas are the cornerstone of conservation, with many populations of species of conservation concern now constrained into relatively small managed areas (Jackson & Gaston 2008). The small size of many nature reserves, coupled with surrounding landscapes that are often inhospitable to species within protected areas, may act as honeypots, attracting more mobile predatory species into areas with greater prey abundance (Shears & Babcock 2002; Eglington *et al.* 2009). The problem of attraction of predators to protected areas can also be exacerbated by general increases in the abundance of predatory species in the wider countryside, resulting from changes in levels of human activities such as game-keeping (Tapper 1992; Whitfield, Fielding, & Whitehead 2008; Smart *et al.* 2010). However, underlying these recent changes in management are historical manipulation of ecosystems and foodwebs, with extirpation of many of the apex predators that predate red foxes, such as wolves (Palomares & Caro 1999) from most of their former Western European range. This reduction in abundance of top predators may also have resulted in mesopredator release of species such as the medium-sized predatory red foxes (Elmhagen & Rushton 2007), potentially resulting in 'unnaturally' high levels of predation pressure on species within protected areas (Macdonald & Bolton 2008).

Many wader populations in wetlands across Western Europe have declined severely as a consequence of the widespread loss and degradation of wetlands resulting from land drainage and agricultural intensification (Wilson, Ausden, & Milsom 2004). Consequently, populations of many bird species that breed in wetland habitats have become increasingly restricted to managed reserves and areas within agri-environment schemes (Ausden & Hirons 2002; Wilson 2007; Smart *et al.* 2008; O'Brien & Wilson 2011). Efforts to improve wetland management within these areas have been effective at attracting breeding waders (Smart *et al.* 2006; Eglington *et al.* 2008, 2010), but impacts of predators of nests and chicks are constraining the recovery of wader populations (Malpas *et al.* 2013). On wet grasslands in Western Europe, evidence from nest cameras shows red foxes to be the main predator of wader nests (Macdonald & Bolton 2008). In the UK, the diet of this generalist predator is dominated by small mammal species (Forman 2005) which, within wet grassland landscapes, are largely restricted to tall areas of vegetation outside fields (Laidlaw *et al.* 2013).

There are a variety of management practices undertaken on lowland wet grassland to reduce the impact of predators on breeding waders on grasslands, including lethal control (Bolton *et al.* 2007b), exclusion using fenced areas (Malpas *et al.* 2013) and habitat manipulation to reduce availability of predator breeding sites (Gibbons *et al.* 2007; Bodey *et al.* 2010). Predator removal or exclusion methods can be effective but can also be controversial, time- and resource-consuming and often only have a temporary influence on predator activity (Smith *et al.* 2010). In addition, while reducing mammalian predator abundance or access to nesting areas can increase nest survival, additional habitat management to facilitate chick survival may also be needed (Bellebaum & Bock 2009). However, if manipulation of habitat structure can be effective at reducing the impact of predators on breeding waders, such methods may be more practical and feasible, both in intensively managed reserves and across the wider countryside.

In wet grassland landscapes, water is one of the most prolific natural barriers to movement of terrestrial species, and could potentially be used to influence the behaviour of predatory species. Levels of surface water in wet grasslands are managed through drainage into ditches that separate fields, and in managed wet features within fields such as pools and footdrains (Eglington *et al.* 2008). Although foxes are capable of crossing water bodies by swimming (Trewhella & Harris 1988), crossing deep and wide (~5 m) ditches may be avoided by mammalian predators when moving through the landscape if alternative dry routes via gateways or other similar crossing points are available. Within-field wet features may also limit the ease with which they can hunt in all parts of the field. While ditches are a permanent structure in the landscape, the surface water on the ground varies with rainfall and evapotranspiration, leading to seasonal reductions in the amount of surface water within fields (Eglington *et al.* 2008), and variation between years driven by spring rainfall can also be apparent. In fields with extensive surface water, the slightly raised field edges are typically drier and are therefore likely to remain accessible. These narrow edges may also be more easily searched by predators, as they can be quickly traversed, which may lead to increased predation pressure within these edge habitats (Willson *et al.* 2001; Seymour, Harris, & White 2004). Therefore, the likelihood of nest predation in any location could be influenced by large-scale variation in accessibility caused by features such as deep ditches coupled with smaller-scale variation in accessibility caused by field wetness.

As well as barriers to movement, there are habitats within lowland wet grasslands that are likely to attract predators because of the conditions and resources they provide. The majority of land within lowland wet grasslands is managed to create short swards and wet features within fields to provide appropriate nesting and chick rearing habitat for wader species of conservation concern (Eglington *et al.* 2008; Rhymer *et al.* 2010). In these landscapes, areas of tall vegetation are generally only found as narrow verges outside fields, and previous studies have shown that these areas provide the only appropriate habitat for small mammals in these landscapes (Laidlaw *et al.* 2013). These verges may therefore attract foxes, both because of the small mammal prey that they support and the shelter they are likely to provide (Lucherini, Lovari, & Crema 1995). The distribution of habitat features that act as potential breeding sites for predators could also influence predation rates. For example, distance to fox earths, corvid nests or raptor nests can influence wader nest predation rates (Macdonald & Bolton 2008).

The anti-predator defence behaviour displayed by birds, including breeding waders, can be effective at dissuading predator presence close to nesting areas (Elliot 1985; Pettifor 1990). The benefit of multiple individuals engaging in anti-predator behaviour has been demonstrated by the ability of colony breeders of a single species to reduce predation rates, compared with solitary nesters (Andersson & Wiklund 1978; Götmark & Andersson 1984). Aggregations of lapwings *Vanellus vanellus* have been shown to experience lower levels of predation, possibly because their combined predator defence can act as a deterrent to predators (Seymour *et al.* 2003; Eglington *et al.* 2009).

Here we assess the influence of conservation management for breeding waders on the distribution and activity of red foxes within lowland wet grasslands. Firstly, we assess the extent to which foxes have been responsible for predation of nests of lapwing and redshank *Tringa totanus* on an area of managed lowland wet grassland in Eastern England. Between 2007 and 2011, the temporal and spatial distribution of foxes on this site has been monitored using baited track plots (e.g. Eglington *et al.* 2009). We collate these data to quantify the probability of fox use of track plots in relation to (i) field wetness as a potential barrier to fox movement, (ii) distance to tall vegetation that could provide shelter or small mammal prey and (ii) the number of nesting lapwing as a measure of their ability to deter foxes. Finally, to test whether fox activity was greater around patches of tall vegetation compared with field edges, we also deployed trail cameras along verges and within field edges.

Methods

Wader nest predation

This study took place at Berney Marshes RSPB reserve (52°35’N 01°35’E, National Grid reference TG4605). At this site the nesting success of breeding waders has been monitored intensively since 2003 (Redshank: 2003-2011; Lapwing: 2005-2011; Smart *et al.* 2006; Eglington *et al.* 2009; Bodey *et al.* 2010; Chapter 3). Annually, between 33 and 52 fields were monitored for breeding wader activity, with surveys being carried out every 4-5 days to locate as many nesting attempts as possible. Redshanks, which nest in tall vegetation, are not visible when incubating eggs and a late flushing response to disturbance in this species means that nests are located by systematic searching and incidental flushing of adults from concealed nests. In contrast, lapwing nest in open, short grassland, and nests can be located from a vehicle by observation of incubating adults. All nests since 2007 were spatially referenced with GPS and, for both lapwing (2007-2011) and redshank (2008-2011), nest temperature dataloggers have been deployed in a sample of nests (~50-150 lapwing and ~20-50 redshank nests *per annum*) to record the time of predation events. Nests were considered predated when their temperature profile deviated substantially and irreversibly from the normal incubation temperature (Bolton *et al.* 2007b). Predation events were categorised as being either diurnal or nocturnal (using the hours of Civil Twilight for Southern England). Between 2008 and 2010, nest cameras were also deployed on a smaller subsample of nests to record the identity of nest predators (9-38 lapwing and 4-17 redshank nests *per annum*), using technology and methodology developed by the RSPB (Bolton *et al.* 2007a).

Fox diet and distribution

The stomach contents of six foxes shot on the reserve during the wader breeding season (March to June) in 2011 (n=5) and 2012 (n=1) were analysed. All stomach contents were wet sieved over a 1 mm gauge sieve and identified, to species where possible, and the percentage of each prey type by volume was estimated by eye.

To determine the distribution of fox activity across the Berney reserve, baited track plots (Figure 1) were deployed during each wader breeding season between 2007 and 2011 (Eglington *et al.* 2009; Bodey *et al.* 2010; Cole 2010; Howell 2011). Plots were spread throughout the reserve in all years and located in key breeding wader fields, a variety of field edges, field centres and at different distances from wet features (Figure 2).

Figure 1 Fox track plot a) being constructed and b) having been visited by a fox; note the fox footprints and the removal of the buried bait in the centre of the plot.

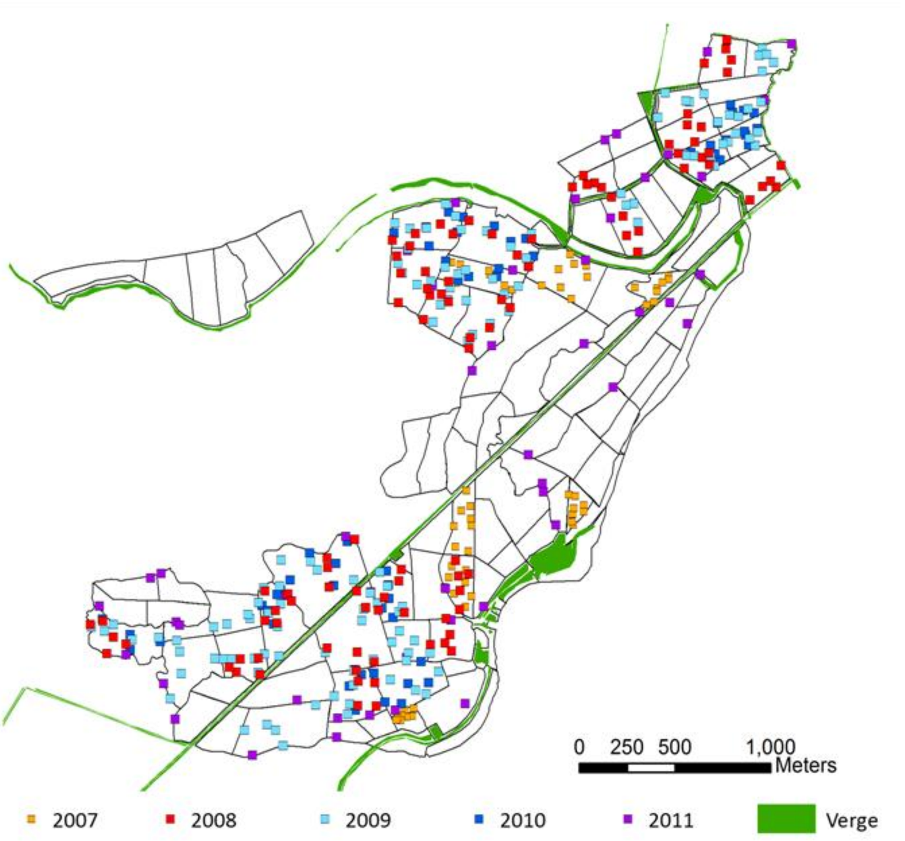

Figure 2 The distribution of fox track plots deployed on Berney Marshes RSPB each year between 2007 and 2011, and the distribution of all verges with tall vegetation.

Fox track plots consist of an area of ~1 m^2 from which turf is removed and replaced with a layer of ~30 - 50 mm of smoothed sand, covered with a fine layer of topsoil (following Eglington *et al.* 2009). Plots centres are baited with a buried small portion (~10 g) of a low-protein (5.5%), low-oil (2%) content dog food (brand name ‘Chappie’), which is a short-range bait that attracts foxes over a range of ~3 - 5 m (Eglington *et al.* 2009). The day the plots were set was considered the START DAY and each plot was checked every morning for nine consecutive nights, unless rainfall was sufficiently heavy to obscure prints, in which case the track period was extended until nine dry nights had been sampled. Plots were considered to have been used when fox footprints where detected, or when the bait had been dug up and consumed (Figure 1b). The day on which this occurred was recorded, and these plots were then removed from the study. Eglington *et al.* (2009) demonstrated the very high level of accuracy in identifying foxes from footprints on track plots with the use of nest cameras trained on a sub-sample of track plots.

To determine the daily use rate (DUR) of track plots, the Mayfield method was used (Mayfield 1961, 1975), in which the number of exposure days represents the time each track plot was monitored from deployment to being used by a fox:

$$DUR = \frac{\textit{Total number of monitored track plots}}{\textit{Total number of days track plots under observation}}$$

To assess whether fox activity was concentrated around verges, trail cameras (RECONYX™ PC800 HyperFire™) were deployed along 19 verges and along 19 edges of fields, for 28 consecutive nights each during April to June, to capture predator presence. Trail cameras were trained along the linear features of either verges with tall vegetation, or adjacent to ditches along field edges with short vegetation so that the coverage of predator routes between the two habitats was equivalent. Cameras were placed at chest height on either existing gate posts or posts added, with camera settings as default apart from ten pictures per trigger, with a ‘rapidfire’ delay between pictures and ‘max range’ during night mode.

Environmental conditions and breeding wader distribution

Within lowland wet grasslands, the extent of surface flooding is influenced by the management of water within the wider catchment area and local weather conditions. The amount of rainfall (monitored daily on site in a rain gauge) at Berney Marshes can vary greatly within and between years (Figure 3a). A carefully controlled management system of sluices and pumps within ditches (Armstrong 2000), and within-field management of wet features such as footdrains (shallow channels constructed to hold water, Eglington *et al.* 2008), is used to maintain a consistent pattern of slow drying of the site as temperature increases during the wader breeding season lead to higher evapotranspiration rates (Eglington *et al.* 2008). The extent of surface flooding is estimated in the last week of each month on the site by a single member of reserve staff, who estimates the proportionate cover of surface water on between 76 and 97 fields across the reserve each year (Figure 3b).

The area and distribution of all patches of tall (> 15 cm) vegetation within the reserve were mapped in ArcGIS v.9.3 (Figure 2) by digitising outlines from aerial photographs (Millennium Map 2000). The network of large, deep ditches that border fields and supply water across the lowland wet grassland landscape, was also digitised. As ditches are likely to act as barriers to the movement of ground-predators, and as predators are therefore most likely to access fields through gateways (the only dry access points between fields), the distance from the nearest gateway access point of each field to the nearest tall vegetation patch (the DRY DISTANCE,

Figure 4a) was measured in ArcGIS v.10. This distance was calculated using a cost-distance analysis, in which routes that crossed ditches were excluded by assigning them prohibitively high values of resistance to movement, while all other land-types were assigned no resistance to movement. All fox track plot locations were spatially referenced using GPS (Figure 2), allowing the direct DISTANCE TO EDGE of field from each track plot (i.e. the minimum distance from the field edge) to be measured in ArcGIS v.10 (Figure 4a). FIELD SIZE was also measured in ArcGIS v.10 for each focal field.

Around each track plot, a 100 m radius buffer was drawn in ArcGIS v.10, and all active (i.e. in the incubation stage at any point during the nine-day track plot monitoring period) lapwing NESTS WITHIN 100 M were counted (only for years since 2007, when spatial referencing of nests began). An additional measure of DISTANCE TO NEAREST NEST was used to represent the isolation of track plots from the closest active lapwing nest. These measures of lapwing density and isolation were included in the analyses to determine whether the local activity of breeding waders, and in particular defensive behaviour of nesting lapwing, was acting as a deterrent to fox movement. As not all fields were surveyed for nesting waders in all years, only track plots that were run in fields that were monitored for breeding waders (n = 385 plots) were included in the analysis.

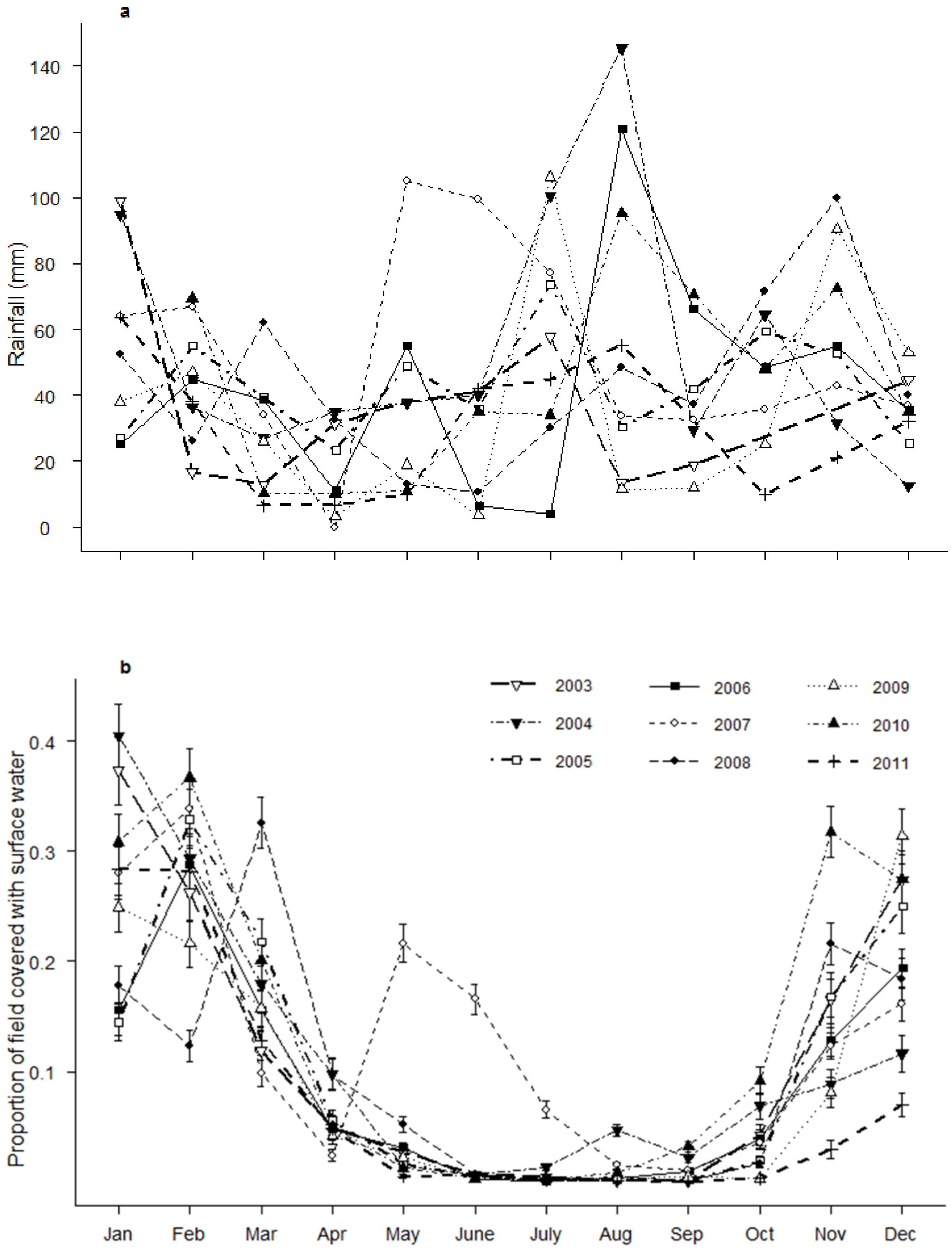

Figure 3 Monthly variation in (a) rainfall recorded at Berney Marshes and (b) the extent of surface flooding of fields (mean ± SE) recorded in the last week of each month, between 2003 and 2011.

Table 1 Description of the structure of models of fox track plot use rate and all response and explanatory variables. The maximal model is shown and was carried out in R (v 2.13.1).

Type	Variable	Distribution (link/offset)	Figure	Definition
Response	Fox track plot use rate	Binomial (logit)		Track plot (used / not used) accounting for days track plot was active; (cbind(track plot outcome, number days active)
Explanatory	Year			2007-2011
	Start day			Day after March 1st when track plot was started
	Distance to edge	m	4a	Distance from track plot to the field edge
	Dry distance	m	4a	Distance of route from track plot field gate to verge avoiding ditches between fields
	Nests within 100 m		4a	Number of active lapwing nests which occurred within 100 m of the track plot
	Distance to nearest nest	m	4a	Distance to nearest active nest which occurred when the track plot was run
	Field area	m^2		Area of field in which focal track plot located
	Surface water		4b, 5	Proportion of focal field covered by surface water during use of track plot

Response	Model structure
Fox track plot use rate	Year+ Start day+ Distance to edge+ Dry distance+ Nests within 100 m+ Distance to nearest nest + Field area+ Surface water+ Distance to edge*Surface water

Annual and seasonal variation in extent of surface water

Predator movement may also be influenced by the extent of SURFACE WATER present in fields, and this can vary within and between years (Figure 2). The positions of all footdrains (shallow channels of varying width that have been constructed to hold water within the fields) across the reserve have been spatially referenced with GPS and mapped. High water levels, resulting in water overtopping the footdrains and the formation of isolated pools, are maintained on the reserve over the winter months, and the maximum extent of surface water in fields was mapped in March of two years (2009 and 2011). From this map, a five category surface flooding score that reflected the range of surface flooding that occurs on the reserve was developed (mapped maximum extent, ~75%, ~50%, ~25% extent and water in footdrains only) and mapped in ArcGIS v.10 (Figure 4b).

Surface flooding categories were assigned to each field containing a track plot as described in Table 2. For track plots run during March, the surface flooding on the reserve was classified as high, medium or low depending on the cumulative total rainfall from January to March (Table 2). For plots run during subsequent months (April to July), surface flooding was classified according to the rainfall during that month and the increasing effects of evapotranspiration as the season progresses (Table 2). The surface flooding category for each month in each year was then applied to each field in which track plots were run (Figure 5).

Table 2 Surface flooding scores assigned to months with high, medium or low rainfall (rainfall recorded daily in a rain gauge on Berney Marshes reserve) in periods before (Jan-Mar) and during the wader breeding season (FD = water in footdrains only).

Rainfall	Rainfall category range (mm)	Jan - Mar	April	May	June	July
High	Jan to March cumulative 12,501 - 16,500 (n=2) April, May, June or July 4501 - 10,500 (n=5)	100%	100%	75%	50%	25%
Medium	Jan to March cumulative 10,001 - 12,500 (n=4) April, May, June or July 2001 - 4500 (n=18)	75%	75%	50%	25%	FD
Low	Jan to March cumulative 0 - 10,000 (n=3) April, May, June or July 0 - 2000 (n=13)	50%	50%	25%	FD	FD

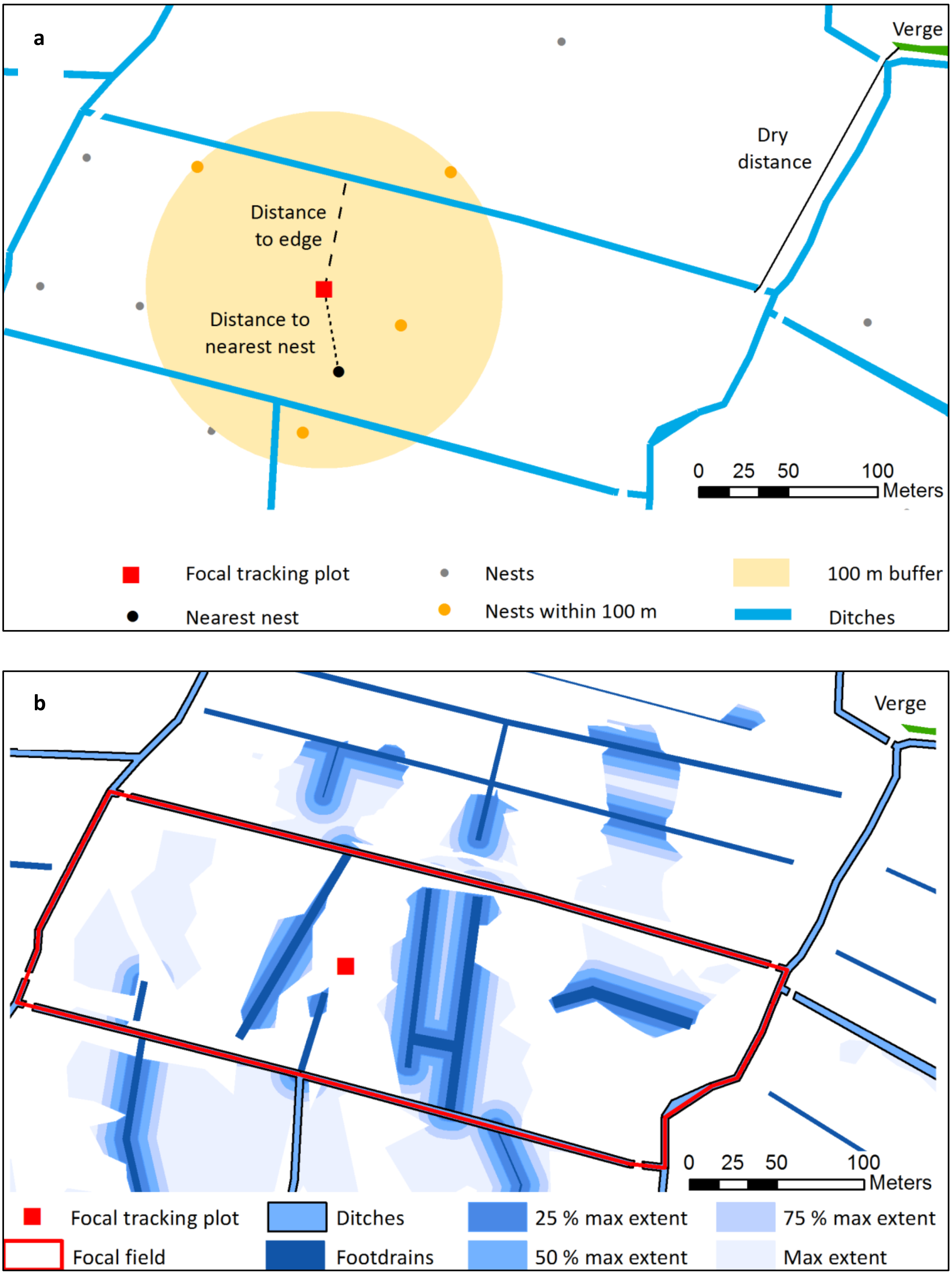

Figure 4 Illustration of the a) distance-related and b) surface flooding-related explanatory variables used in models of track plot use (see Table 1).

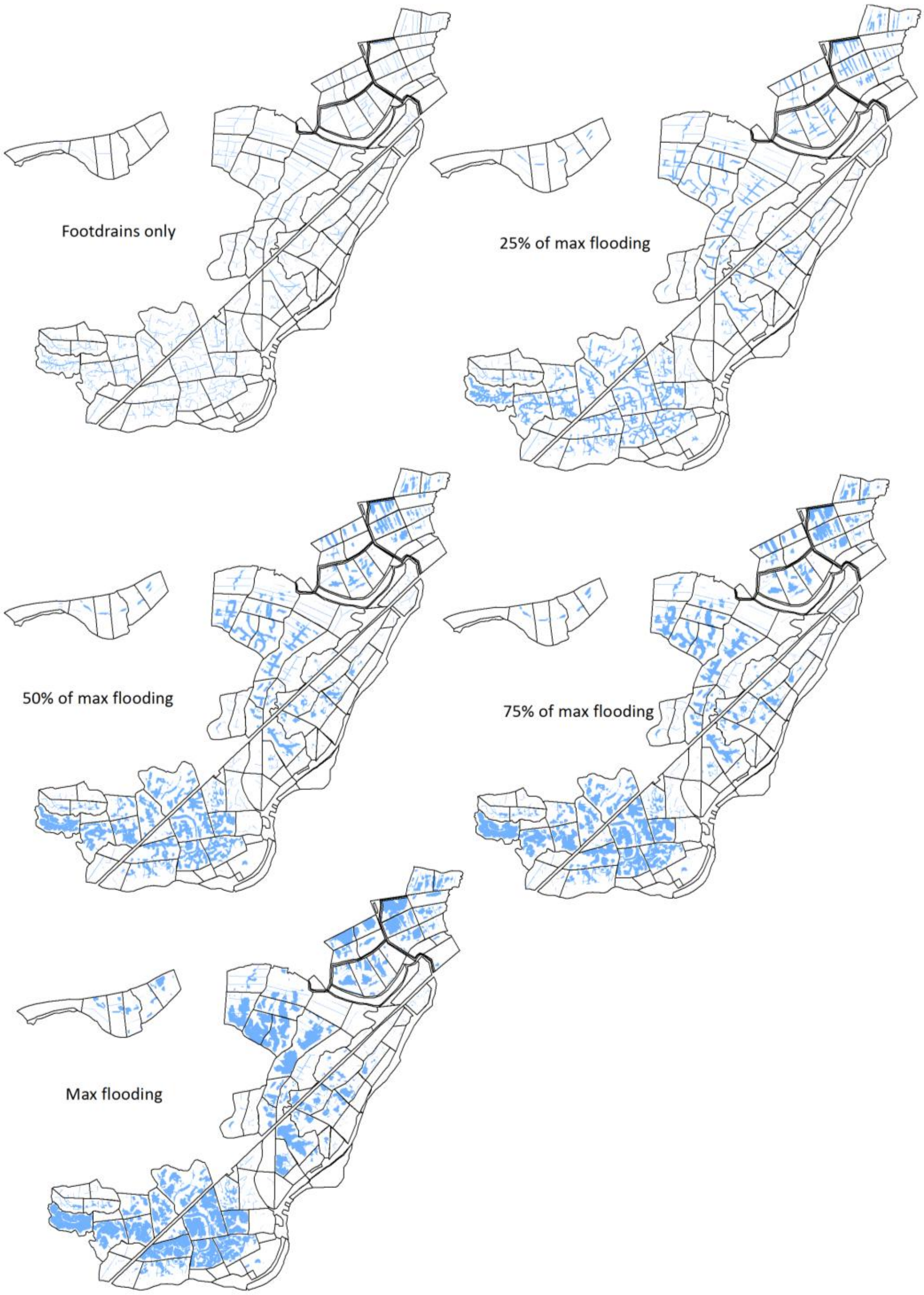

Figure 5 Representation of the extent of surface flooding across Berney Marshes in each of the five surface flooding categories, from footdrain-only to the maximum extent of flooding that was mapped using GPS in March 2009 and 2011.

Statistical analysis

The daily use rate (DUR) of the track plots (over the nine night observation period) was modelled with a GLM in R (v 2.13.1), using a formulation of Mayfield's (1961, 1975) method as a logistic model with a binomial error term, in which success (not used by fox) or failure (used by fox) was modelled with the number of exposure days as the binomial denominator (Aebischer 2009).

The DUR model (Table 1) incorporated annual and seasonal variation in use of plots by foxes by including YEAR and START DATE. In addition, the effects of track plot location relative to structures in the landscape were explored by including DRY DISTANCE, FIELD AREA, DISTANCE TO EDGE, SURFACE WATER, and the two-way interaction of DISTANCE TO EDGE*SURFACE WATER. The influence of nesting lapwing density on track plot use was explored by including the NESTS WITHIN 100 M and DISTANCE TO NEAREST NEST. Collinearity of predictor variables was checked. Daily use rates predicted from these models were then transformed to probabilities of not being used by a fox (S) by raising the daily non-use rate (1-DUR) to the power of the number of nights the track plots were run (nine). The probability of track plot use over the track period was then calculated as 1-S.

In fields containing both a fox track plot and an active wader nest during the same month (n = 31) the wader hatching success (redshank nests= 44; lapwing nests= 62) was compared between fields that contained track plots that were and were not used by foxes. See Chapter 3 for details on calculating hatching success.

The number of nights on which foxes were recorded on trail cameras in verges was compared to those recorded within fields using a Fisher’s exact test (SPSS v.18). The small sample size of cameras with fox activity (4/38) prohibited a meaningful analysis of the frequency of verge and field use by foxes.

Results

Evidence for the identity of wader nest predators

Of the 364 predated nests in which dataloggers were deployed, 310 (85%) were predated during the hours of darkness, indicating predation by mammals. Foxes were the only species identified on nest cameras (Table 3). Fox stomach content analyses showed that, of the five foxes controlled during the wader breeding season (May and June), two dogs contained easily identifiable remains of wader nests (Table 4). Of these, a dog controlled in June had egg shell fragments and three partially developed chicks within its stomach (Table 4). Taken together, this evidence strongly suggests that foxes are the main predator of wader nests at this site.

Table 3 Numbers of lapwing and redshank nests that were predated either diurnally or nocturnally, recorded from nest temperature dataloggers, and the identity of predators recorded by miniature nest cameras. Nest cameras only used from 2008-2010.

		Temperature dataloggers		Cameras
Species	Year	Diurnal	Nocturnal	Foxes
Lapwing	2007	10	34	-
	2008	2	23	5
	2009	3	40	3
	2010	9	110	5
	2011	9	42	-
	Total	33	249	13
Redshank	2008	9	15	0
	2009	3	7	2
	2010	6	32	9
	2011	3	7	-
	Total	21	61	11
Total		54	310	24

Table 4 Stomach contents (estimated % volume) of foxes controlled by shooting at Berney Marshes in 2011 and 2012

		% Stomach contents by volume								
Date shot	Sex	Lago-morph	Small mammal	Wader egg	Non-wader egg	Non-wader adult	Frog	Insect	Grass	Soil
01/03/2011	♂	80	0	0	0	20	0	0	0	0
09/05/2011	♂	0	0	60	0	0	0	10	30	0
16/05/2012	♀	0	5	0	8	85	0	2	0	0
17/05/2011	♂	100	0	0	0	0	0	0	0	0
08/06/2011	♀	0	0	0	0	0	0	15	15	70
09/06/2011	♂	0	0	20	0	0	5	1	25	49

Factors affecting the use of fox track plots

During the years in which track plots were deployed to monitor the temporal and spatial distribution of foxes, the distribution of plots was designed to explore different hypotheses, including fox use of linear features (Eglington *et al.* 2009), of field edges and centres (Bodey *et al.* 2010; Cole 2010) and of their distribution throughout the whole reserve (Howell 2011). However, track plots were widely distributed throughout the reserve in all years (Figure 2).

Between 32 and 48% of track plots were visited by foxes in each year of the study, with the exception of 2010, when nearly 95% of the track plots were visited (Figure 6a and 7). The likelihood of track plots being visited by foxes varied annually, with plots in 2010 more likely to be used than all other years (Table 5, Figure 6a). In all years except 2011 (when track plots were run throughout the wader breeding season), plots were run in the early season (mostly in April, to correspond with the first wader nesting attempts), and again in the late season (between mid-May and late June, to correspond with later nests and chick rearing; Figure 7). A lower proportion of track plots was visited during the late season (Figure 6b), particularly in 2008 and 2009 (Figure 7). There was a significant seasonal decline in the likelihood of track plots being used by foxes (Table 5, Figure 8a). Of the 385 track plots included in the analysis, 215 had no active lapwing nests recorded within 100 m (Figure 6e), and plots were significantly more likely to be used by foxes when there were fewer active lapwing nests within 100 m (Table 5, Figure 8b). Track plots with many (~7) surrounding lapwing nests were ~20% less likely to be used than plots with no nearby active nests (Figure 8b). Track plots were deployed in fields with a wide range of surface flooding (Figure 6h) but there was no significant relationship between the extent of surface water and the likelihood of fox use of track plots within those fields (Table 5).

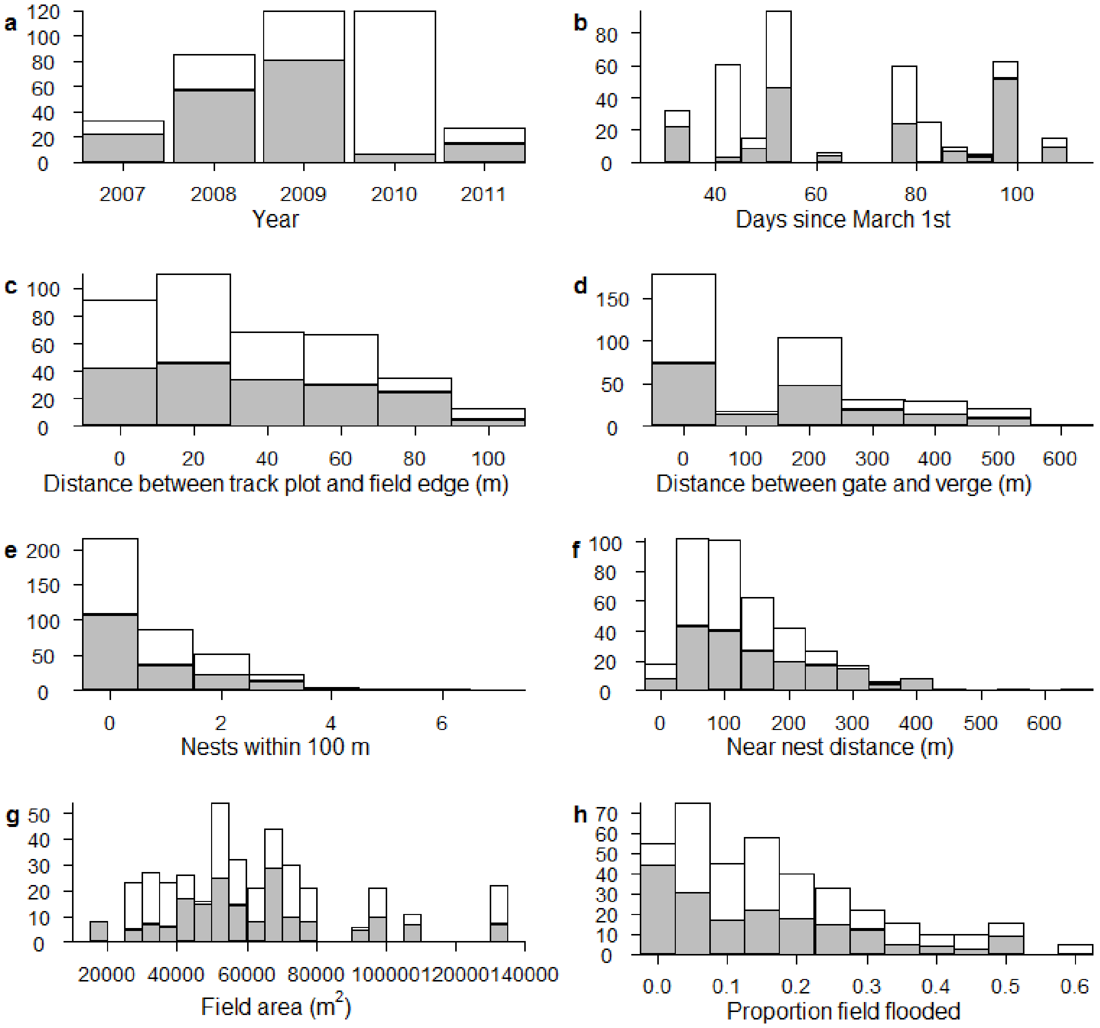

Figure 6 Numbers of track plots that were (open bars) or were not (grey bars) visited by foxes in relation to a) year, b) days since the 1st March, c) distance to edge of field, d) distance from field to verge, e) number of active lapwing nests within 100 m, f) distance to nearest active lapwing nest, g) field area, and h) proportion of field flooded.

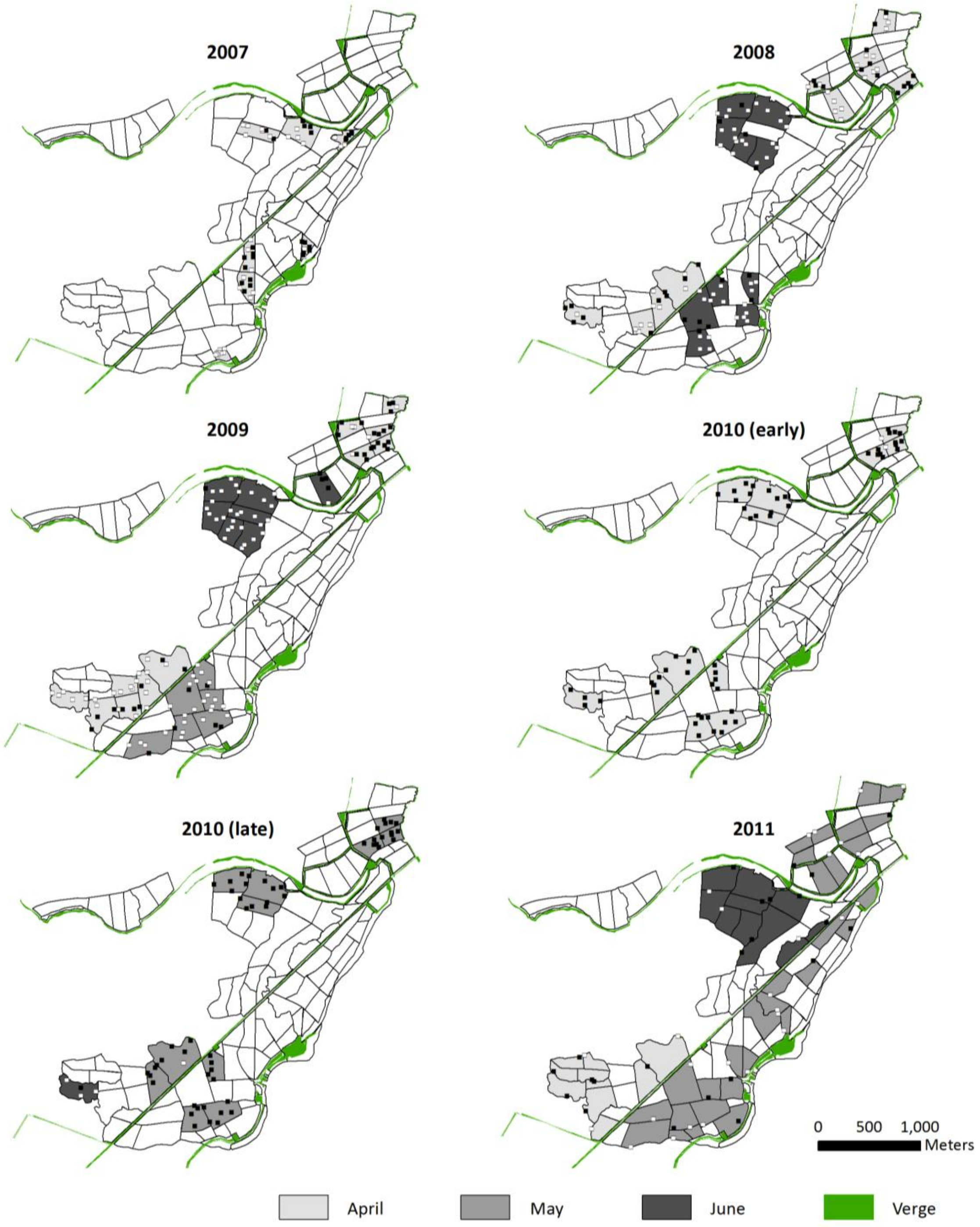

Figure 7 The distribution of track plots that were (■) and were not (□) visited by foxes in relation to the month of deployment between 2007 and 2011 at Berney Marshes. Fields in 2010 were sampled twice, all other fields sampled in only one month.

Table 5 Results of a GLM (with binomial errors) of track plot use over a nine-night period. Minimum models are shown above the dashed line, and non-significant variables (with estimates from the full model) are shown below the dashed line. Estimates and SE are logits, with 2007 acting as a reference year.

Variable	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.615	0.340	-7.687	<0.001
Year (2008)	0.805	0.389	2.071	0.038
Year (2009)	0.649	0.380	1.707	0.088
Year (2010)	2.444	0.349	7.005	<0.001
Year (2011)	1.147	0.458	2.506	0.012
Start day	-0.014	0.004	-3.499	<0.001
Nests within 100 m	-0.218	0.068	-3.193	0.001
Distance to edge	0.005	0.005	1.025	0.305
Dry distance	-0.001	0.001	-1.253	0.210
Distance to nearest nest	-0.001	0.001	-0.920	0.357
Field area	$-0.2\text{x}10^{-5}$	0.000	-0.622	0.534
Surface water	1.476	0.976	1.512	0.131
Dist to edge*Surface water	-0.028	0.023	-1.224	0.221

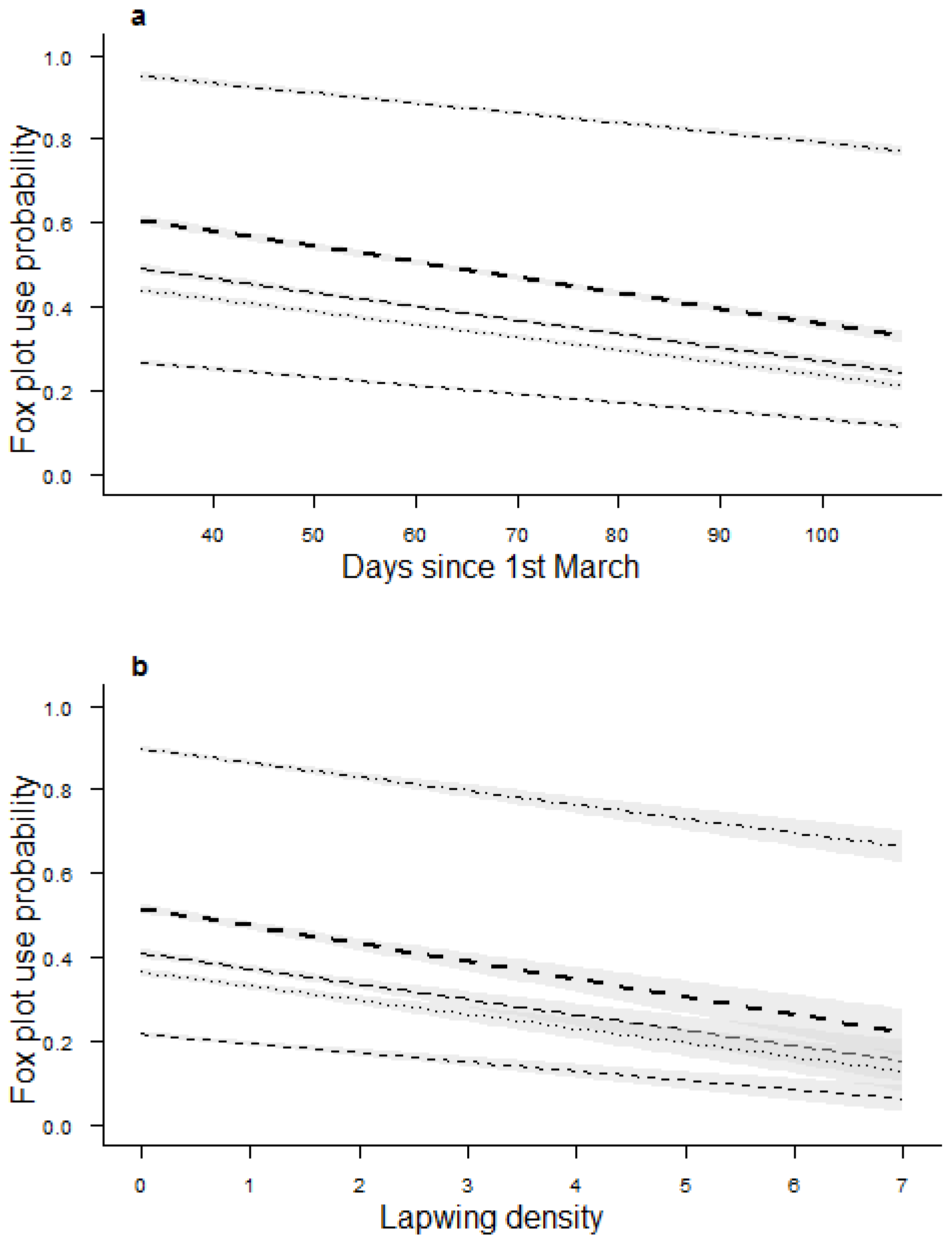

Figure 8 Changes in the predicted probability of fox use of track plots over 9-night study periods with increasing a) time since the 1st of March and b) number of active lapwing nests within 100 m. Symbols represent years (2007: dashed line; 2008: long-dashed line; 2009: dotted line; 2010: dot-dashed line; 2011: thick dashed line). Predictions (with shaded se) used are from models in Table 5.

Across the wader breeding season we found no difference in the likelihood of hatching between lapwing nests in fields that had or hadn't recently had fox activity recorded. However there was an indication that redshank nests in fields where foxes had recently been identified were less likely to successfully hatch, although this was not a significant difference.

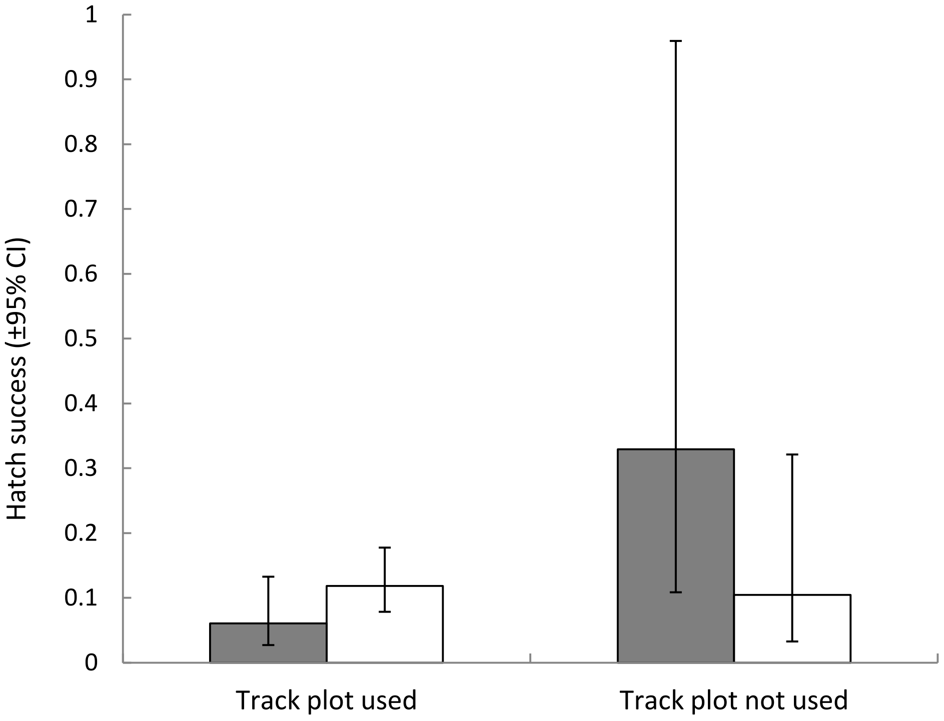

Figure 9 Hatching success of redshank (closed bars) and lapwing (open bars) nests in fields that had fox track plots that were or were not used by foxes in the month in which the nest was found. Overlapping 95% confidence intervals indicate no significant differences in hatching success across all groups.

Of the 19 trail cameras located along verges with tall vegetation and 19 along field edges with short vegetation, foxes images were captured at two verge and two field edge locations. However, the trail cameras that were located along verges recorded significantly more fox activity, with foxes being recorded on 13 separate nights, while both within-field cameras only captured foxes on a single night each (Fisher's exact test, one tailed, $p<0.001$; Figure 10).

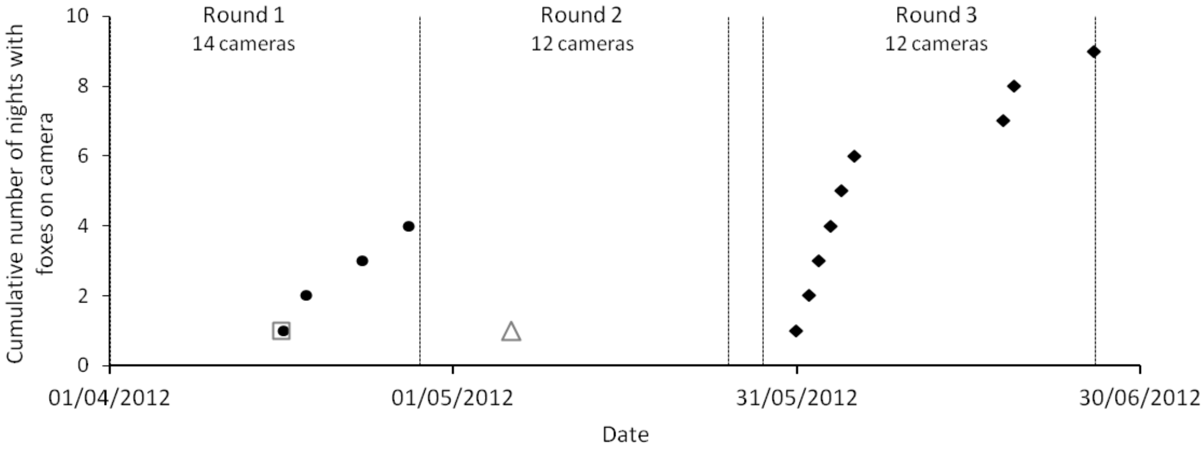

Figure 10 Dates on which fox images were captured on trail cameras located on two verges (filled symbols) and two within-field locations (open symbols) at Berney Marshes reserve. A total of 38 trail cameras were run across three time periods. Double vertical line between round 2 and 3 indicates the small time gap between these monitoring periods.

Discussion

Predation is a key driving force in the population dynamics of ground-nesting birds (Tapper, Potts, & Brockless 1996), and the effects of predation can interact with habitat change to alter the predation risk faced by local populations (Evans 2004). Predation is an important limiting factor for wader breeding success, with examples ranging from lapwing within German polders (Bellebaum & Bock 2009), black-tailed godwit *Limosa limosa limosa* in Dutch wet grassland (Schekkerman, Teunissen, & Oosterveld 2009) and grassland monocultures (Kentie *et al.* 2013), and nesting golden plovers *Pluvialis apricaria* in the uplands of England (Whittingham, Percival, & Brown 2002). As there is evidence that high levels of nest predation are limiting nesting densities and preventing the recovery of wader populations (Stillman *et al.* 2006), action to manage predation is likely to be needed to maintain species of conservation concern. To ensure that management of predators is targeted and effective, their identities need to be determined and the factors that influence their distribution and movements need to be elucidated.

In this study, red foxes were confirmed as the main predator of nesting waders at a major lowland wet grassland site in Eastern England, using diet composition and evidence from nest cameras and temperature loggers. This evidence concurs with previous findings in other European studies of breeding wader predation. For example, Macdonald & Bolton (2008) found that foxes were responsible for 132 of 216 nest predation events caught on camera across several European studies. Overall, the hatching success of wader nests was similar in fields where fox presence had been confirmed using fox track plots and fields without noted fox activity. The influence of landscape features (e.g. surface water and cover vegetation) and prey defence behaviours (e.g. group mobbing of predators) on the activity and distribution of this predator were explored using five years of data on fox activity patterns. Trail cameras trained on field verges captured significantly more fox images than those trained along field edges, suggesting that fox movement through the reserve is influenced by the distribution of verges, which provide the only tall vegetation in this landscape (Laidlaw *et al*. 2013). However, within-fields, fox use of track plots was unrelated to distance to the field edge, distance to the nearest verge or by the extent of surface flooding. Track plot use was, however, significantly less likely in areas with higher densities of nesting lapwing, and also varied significantly between years and declined over the course of the wader breeding season. Thus, while fox movement through the landscape may be influenced by the location of patches of tall vegetation, the primary factor influencing within-field fox distribution and movement appears to be density of nesting lapwings. Local nesting densities may therefore be a major driver of the likelihood of nests being predated.

Fox use of track plots was significantly less likely in areas with higher densities of nesting lapwing. Lapwings have been shown to direct their mobbing defence behaviour at foxes during nocturnal observations (Seymour *et al.* 2003), which has been shown to be an effective nest defence (Elliot 1985). Mobbing behaviours are able to provide information on the direction of a predation threat (Frankenberg 1981), which can facilitate group mobbing in sites with high densities of nesting lapwing. Foxes encountering lapwing mobbing, particularly by multiple individuals, may change their behaviours so that they were less likely to encounter a fox tracking plot, by dissuading them from staying in the vicinity and/or increasing their speed of movement through the landscape. Focussing habitat management in areas that can support high densities of nesting lapwing may therefore be among the most effective of measures to reduce predator impacts. However, low levels of fox track plot use at high lapwing densities could also result from reduced attraction to bait in the presence of abundant wader nests on which to forage. To distinguish between these two different hypotheses, the influence of lapwing density on nest predation rates must also be assessed directly.

The annual variation in fox distribution reflected in the use of track plots could have been influenced by differences in the layout of track plots in each year of the five-year study. Track plots were deployed to explore fox use of linear wet features (Eglington *et al.* 2009), field edges and centres (Bodey *et al.* 2010; Cole 2010) and to compare the effectiveness of different tracking methods (Howell 2011), and thus the location of track plots varied between years. However, plots were widely distributed within and between fields in all years, and the lack of any effect of distance to edge or field wetness suggests the study design was not likely to result in the observed substantial annual variation. Annual variation could reflect changes in management on the reserve during the period of study, particularly the ongoing control of foxes that could influence fox abundance (Fletcher *et al.* 2010). However, the numbers of foxes killed on the reserve were similar throughout the study, with between 2 and 9 individuals controlled in each year. In particular, there was no large reduction in fox control in 2010 that could account for the high rates of track plot use during that year. Even without lethal control the number of foxes within the site could vary annually due to natural death or recruitment into the population, which could be influenced by the amount of their main prey that is available. The behaviour of individual foxes may also have influenced the use of track plots, for example, individual foxes may vary in their hunting ability, techniques or levels of neophobia, or they may learn over time to exploit seasonally available resources.

The decline in track plot use over the season may have been influenced by seasonal variation in prey abundance. For example, small mammal prey activity increases through spring and summer (Laidlaw *et al.* 2013), and wader nest and chick availability increases through April and May before declining rapidly in June (Eglington *et al.* 2008). Foxes may be more likely to take the bait provided within the track plots when natural prey is scarce early in the season, and their foraging effort within fields may decline when the abundance of wader nests and chicks declines at the end of the wader breeding season, resulting in a decreased likelihood of encountering track plots.

Track plots can be effective techniques for quantifying fox distribution, and running them for consecutive nights allows the number of nights elapsed until fox use to be used as a measure of fox activity. However, track plots cannot be used to assess spatial variation in fox activity, as repeat baiting of plots in the same location could mean that repeat visits by foxes are incentive-driven rather than reflecting their natural behaviour and distribution. Thus, while track plots are well-suited to addressing questions on the influence of landscape structure on fox movement and distribution, alternative methods of tracking individual foxes are likely to be necessary to identify spatial variation in fox activity.

During this study, trail cameras were trained along 19 different verges and 19 field edges throughout the reserve, and were operational for 28 days each. Despite this level of coverage, fox images were captured on only two verge and two within-field locations. However, the two verge locations were repeatedly used by foxes over several nights, while the within-field locations were used only once. Trail cameras can thus give more information on spatial variation in fox activity than track plots, and this evidence suggests that foxes may repeatedly use verges as cover or as routes through the reserve. Foxes prefer cover-rich habitats both for resting and to move through during daylight hours (Lucherini, Lovari, & Crema 1995). Areas of tall vegetation can therefore potentially provide both shelter and access to small mammal prey, which also favour these habitats (Laidlaw *et al.* 2013).

Implications for wet grassland management

The information on fox distribution and activity on wet grassland provided by this study can potentially be used to inform future management of wet grassland landscapes. In particular, the findings suggest that there may be potential for the removal and relocation of verges to reduce levels of fox activity close to nesting lapwing, and to concentrate management to attract waders into areas that can support nesting densities that are high enough to provide protective benefits of anti-predator mobbing. The removal of safe diurnal resting sites for foxes, to try and reduce their density within the local landscape has previously been posed as a possible management option (Stillman *et al.* 2006). Firstly, however, there needs to be an assessment of the potential for such manipulations to have substantial impacts on predation rates of nesting waders. Currently our predictions of how changes in management would influence predator species are held back by our limited understanding of predator response to changes in landscape structure. Future work that aimed to track foxes using GPS collar technology could be used to determine predator use of wet grassland landscapes, and therefore usefully inform future habitat manipulations aimed at altering their behaviour, ultimately to reduce their predation on breeding waders.

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Chapter 5

Using drivers of wader nest predation rates to inform future habitat management

Summary

1. Conservation management that focuses on the provision of species' key habitat and dietary requirements can also benefit from considering the impact of those actions on other species that interact with the target species of conservation concern. Understanding the consequences of habitat management for the distribution of species of conservation concern, and for the activities and impacts of their predators, can potentially improve management recommendations.
2. In Western Europe, many lowland wet grasslands are managed to encourage breeding wader populations, most of which have declined rapidly in recent decades. These species typically require short vegetation, high water levels and surface wet features but, even with provision of such habitat structure, many populations are limited by high levels of predation on eggs and chicks.
3. We investigated the effect of landscape structures designed to attract breeding waders, and environmental conditions within nesting fields, on nest predation rates of lapwing, *Vanellus vanellus*, and redshank, *Tringa totanus*. To assess the potential for future manipulation of these conditions to substantially influence nest predation rates, we develop a series of realistic management scenarios and quantify predicted levels of nest predation in each scenario.
4. Lapwing nests in fields far from patches of tall verge vegetation are significantly more likely to be predated and, in dry fields (< 30% surface water) nests in field centres have a ~15% higher predicted probability of being predated than those near the edge. Conversely, in wet fields (> 30 % surface water), nests near the edge are ~10% more likely to be predated than those in the centres. For both lapwing and redshank, nest predation rates were also lower in areas with high lapwing nest densities.
5. Modelled scenarios of future changes in surface water and the distribution of verges indicated that a 25% reduction in surface flooding could increase levels of lapwing nest predation by up to ~3%. The current drought management plan for the site, which focuses water resources in particular areas, is predicted to result in predation rates that are only slightly higher (~1%) than current levels. Scenarios in which reduced surface flooding are combined with removal of verge habitat resulted in significant increases of ~10% in lapwing nest predation rates.
6. Combining the identification of environmental factors associated with nest predation with modelled scenarios of realistic habitat modifications can be a useful tool for assessing the potential magnitude of demographic consequences of management actions.

Introduction

There is growing recognition of the need for conservation practices to be developed from a strong evidence-base of the consequences of management interventions (Sutherland *et al.* 2004; Pullin *et al.* 2013). Traditionally, conservation actions have been experience-based, with limited evaluation of their effectiveness (Pullin *et al.* 2004). Information derived from monitoring and research is often inaccessible to conservation practitioners, who frequently have to rely on ecological intuition in the development of land management strategies (Pullin & Knight 2005). However, predictions from habitat association models can be used to consider the potential magnitude of impact of specific future management scenarios that are appropriate to a given context or location. Developments in the use of GIS-based visualisations of predictions from habitat association models can also help in assessing the implications of future habitat management planning (Swetnam *et al.* 2005).

A particularly complex issue in conservation management is the influence of predation on species of conservation concern. Reducing impacts of predation is rarely straightforward (Bolton *et al.* 2007; Bodey *et al.* 2010; Malpas *et al.* 2013), and several studies have shown that control of one predator species can result in increased impacts of other predators, through processes such as mesopredator release (Conner, Rutledge, & Smith 2010; Ellis-Felege *et al.* 2012; Brook, Johnson, & Ritchie 2012). Understanding the influence of habitat management on both target species of conservation concern and other constituents of the wider foodweb, particularly species that may interact with target species through competitive interactions or predation, may help to address this issue.

Conservation management tends to focus on creating habitat conditions that can provide resources for species of concern (e.g. food or nesting sites). The development of appropriate habitat management strategies when predation is an important driver of the demography of target species can be helped by understanding the factors influencing levels of predation. The structural complexity of habitats can influence predation rates, for example nest predation rates of greater snow geese *Anser caerulescens atlanticus* L. are lower in wetlands with a more complex structure than in mesic tundra (Lecomte *et al.* 2008). The configuration of different habitats in the landscape can also influence predation risk, with lower predation rates of ground-nesting bird species often being reported in areas containing mosaics of different habitat types, such as patchworks of grass and heather (Whittingham, Percival, & Brown 2001), or grasslands cut at different times (Schekkerman, Teunissen, & Oosterveld 2008).

Commercially managed wet grasslands typically have high levels of drainage and grazing and support very low levels of biodiversity. However, conservation management within this habitat to reinstate and maintain high water levels and short vegetation (Eglington *et al.* 2008; Fisher *et al.* 2011) has been successful at attracting breeding waders, particularly to nature reserves (Ausden & Hirons 2002; Smart *et al.* 2008; O'Brien & Wilson 2011). Populations of breeding waders across Western Europe have been declining in recent decades, and predation impacts on the reproductive stage (Chapter 3) have been identified as a factor that may be limiting population recovery (Macdonald & Bolton 2008; Schekkerman, Teunissen, & Oosterveld 2009; Kentie *et al.* 2013; Malpas *et al.* 2013). Management of landscapes for breeding waders can have direct impacts on the predation pressure experienced by nesting birds, for example, high densities of waders surrounded by habitats such as agricultural land with very low prey densities may attract high numbers of predators. Management intended to benefit breeding waders can also potentially have indirect impacts upon wader nest predation by altering habitat conditions for other species present in the lowland wet grassland food web. On wet grasslands in Western Europe, camera evidence has shown foxes to be the main predator of wader nests (Macdonald & Bolton 2008). The diet of this generalist predator in the UK is dominated by small mammal species, such as field voles, (Forman 2005), which are largely restricted within this landscape to tall areas of vegetation in field verges (Laidlaw *et al.* 2013). Verge distribution may impact the influence of predators in wet grasslands, as there is evidence that proximity to tall vegetation can influence wader nest predation rates (Chapter 3), and that foxes may use verges disproportionately as they move through these grasslands (Chapter 4). Verge vegetation is generally not subject to any specific management actions in these landscapes, however, manipulations of their distribution and/or structure could be relatively easy to implement, through cutting, grazing and planting regimes.

Habitat management carried out on reserves to benefit breeding waders is largely concentrated within fields, through manipulations of vegetation and surface water conditions. Shallow channels known as footdrains can be used to move water from the ditches at the edge of fields to the centre of fields. Fields with greater densities of footdrains that have water overtopping into floods have been found to have a significantly greater probability of supporting nesting lapwing (Eglington *et al.* 2008), and these wet features also provide much of the invertebrate food supply for wader chicks (Eglington *et al.* 2010). Surface water and footdrains within fields could potentially hinder movement of mammalian predators, which could reduce wader nest predation rates in wet fields or areas and concentrate them in drier, more accessible locations. On RSPB reserves managed for breeding waders, the planned response to the increased risk of years with low rainfall are reserve-specific drought plans that prioritise resources to specific fields, ensuring the maintenance of water in footdrains and associated surface floods remain for as long as possible during the wader breeding season. As nesting adult lapwing can show strong predator defence behaviour, including group-mobbing of predators (Elliot 1985a), the implications of management actions to alter habitat structure may also vary in relation to nesting densities (Stillman *et al.* 2006).

Here we assess the potential implications of different conservation actions targeted at breeding waders for nest predation rates of lapwing *Vanellus vanellus* and redshank *Tringa totanus*. We use a nine year study of wader breeding demography in east England to quantify the probability of nest predation for lapwing and redshank in relation to environmental conditions in the surrounding area and local wader nesting densities. We then use the predictions from these models to explore the potential impact on nest predation rates of a range of future scenarios of habitat and landscape structure that could be achieved through management.

Methods

Study site

The study took place at Berney Marshes RSPB reserve (52°35’N 01°35’E, National Grid reference TG4605). Habitat management on this reserve is predominantly aimed at providing suitable nesting conditions for breeding waders within fields, through maintaining short swards and surface wet features (pools and footdrains) that are capable of containing water throughout the wader breeding season (Eglington *et al.* 2008)). The vast majority of the landscape comprises short swards; however, patches of taller vegetation also occur as verges bordering roads, tracks, railway embankments and riverbanks and comprise about 5% of the landscape (Chapter 2).

Wader nest monitoring and survival

The nesting success of breeding waders has been monitored intensively at Berney Marshes since 2003 (Smart *et al.* 2006; Eglington *et al.* 2009; Bodey *et al.* 2010, Chapter 3). Between 33 and 52 fields were studied each year, with surveys being carried out every 4-5 days to locate as many nesting attempts as possible (Chapter 3, Figure 1). Redshanks, which nest in taller vegetation, are not visible when incubating eggs and a late-flushing response to disturbance means that nests are located by systematic searching and incidental flushing of adults from concealed nests. In contrast, lapwings nest in open grassland, and these more visible nests are thus located through observation of incubating adults from a vehicle. All nest locations have been spatially referenced since 2005 for redshank, and 2007 for lapwing (Table 1 and Chapter 3: Figure 1).

The date on which each nest was first located (FIND DAY) provides an indication of when nests were active (with the majority of nests being found within 10 days of laying). To determine the period of activity of any nest, the estimated lay date of nests was calculated from measurements of egg length and breadth at the widest point (0.1 mm, egg volume = egg length * egg breadth^2) and egg mass (0.1 g) inserted into a regression equation derived from successful nests (Smart 2005):

$$\textit{Lay date} = \textit{FIND DATE} - ((\textit{Laying period} + \textit{Incubation period}) - \textit{Number of days to hatching}))$$

$$\textit{Number of days to hatching} = (271919 * (\textit{egg mass} / \textit{egg volume}) - 113.88)$$

Where L = laying period (5 days for both species) and I = incubation period (26 and 24 days for lapwing and redshank, respectively). Lay dates are calculated for each egg within a nest, and then averaged per nest.

All nests were marked and visited a minimum of every five days, and more regularly near their estimated hatch date, to determine their fate. Nests were considered successful if one or more eggs hatched, and predated nests were defined as those that were empty without any eggshell fragments in the nest to indicate hatching (Green, Hawell, & Johnson 1987).

Table 1 Descriptions of wader nest predation rate and predicted lapwing predation rate response variables, and all explanatory variables used in modelling their probabilities. Maximal models for each analysis of lapwing (L) and redshank (R) predation rate are shown and were carried out in R (v 2.13.1).

Type	Variable	Distribution (link/offset)	Explanation
Response	Wader predation rate	Binomial (logit)	For lapwing and redshank separately, nest outcome (predated (P) / hatched (H)) accounting for the no. of days the nest was active; (cbind(predated outcome, number days active)
	Predicted Lapwing predation rate	Binomial (logit)	Proportion of nests predicted to be predated in different management scenarios (see Table 2)
Explanatory	Year		Lapwing: 2005-2011; Redshank 2007-2011
	Find day		Days after March 1st when nest was first located
	Distance to edge	m	Distance from nest to the field edge
	Dry distance	m	Total distance of route from field entrance (gateway) to nearest verge without crossing ditches between fields
	Nests within 100 m		Number of active lapwing nests within 100 m of the nest
	Near nest distance	m	Distance to nearest lapwing nest active at the same time as the focal nest
	Field area	m^2	Area of field in which focal nest was located
	Surface water		Estimated proportion of field covered by surface water (measured monthly)
	Scenario type		See Table 2 for scenarios

Response	Model structure
Wader predation rate	
	Year+ Find day+ Distance to edge+ Dry distance+ Nests within 100 m+ Near nest distance+ Field area+ Surface water+ Distance to edge*Surface water
Predicted Lapwing predation rate	
	Year + Scenario type + Year*Scenario type

To determine the time and date of nest failures, Ibutton dataloggers (Maxim Integrated Products Ltd, CA, USA) have been placed in a random selection of nests (between 40 – 85% of all nests monitored) since 2007. These loggers record a temperature trace at specified intervals, usually every seven minutes in this study, and allow the date and time of predation to be identified from the sharp decline in nest temperature. For nests where the exact date of predation was not known, the failure day was taken as the midpoint between visits. Nests that were deserted (33), flooded (11) or trampled (54) without any evidence of prior predation were excluded from the analyses of hatched (594) and predated (760) nests.

To determine the daily nest predation rate (DPR), the Mayfield method was used (Mayfield 1961, 1975), which takes account of the number of 'exposure days' (the number of days between nest location and predation/hatching) and thus controls for the increased likelihood of locating nests that survived for longer periods:

$$DPR = \frac{\textit{Total number of monitored nests predated}}{\textit{Total number of days nests were under observation}}$$

Environmental conditions and breeding wader distribution

Patches of tall vegetation, which are generally field verges, provide the only appropriate habitat for small mammals in this landscape (Laidlaw *et al.* 2013), and may thus be an important source of prey for mammalian predators. In addition, these patches may offer direct shelter for predators. At Berney Marshes, foxes have been shown to be the main predator of breeding wader nests (Chapter 4), and evidence from trail cameras suggests that fox activity may be concentrated along verges (Chapter 4). Consequently, nest predation rates may vary in relation to distance from these patches. The distribution of all patches of all tall (> 15 cm) vegetation within the reserve were mapped in ArcGIS v.9.3 by digitising outlines from aerial photographs (Millennium Map 2000).

The GPS locations of all lapwing and redshank nests were recorded, allowing the DISTANCE TO EDGE of nearest field from each nest (i.e. the minimum distance from the field edge) to be measured (Figure 1a). DRY DISTANCE from the nearest gateway access point of each focal field containing a nest to the nearest tall vegetation patch was also calculated (Figure 1a). This distance was calculated using a cost-distance analysis, in which routes that crossed ditches were excluded by assigning them prohibitively high values of resistance to movement, while all other land-types were assigned no resistance to movement. FIELD AREA was also measured for each focal field (Figure 1a). All areas and distance measurements were calculated in ArcGIS v.10.

For all lapwing and redshank nests, the distance to the nearest other active lapwing nest was calculated (NEAR NEST DISTANCE), to explore the effect of nest isolation on predation rates. In addition, the number of active lapwing nests within a 100 m buffer area around each focal nest was also calculated (NESTS WITHIN 100 M) to explore the effect of local nesting densities on predation rates. Only proximity to nests of lapwing were considered as this species exhibits the strongest mobbing behaviour of predators, the likely mechanism by which higher nesting densities reduces predation (Macdonald & Bolton 2008), and the concealed nature of redshank nests means that they unlikely to respond to predator presence before lapwing. Active lapwing nests were defined as those being incubated for at least one day during the incubation period of the focal nest. The active period of nests was calculated using the predicted lay date and the predation or hatch date recorded on temperature loggers or estimated as date between last two visits when no temperature logger present.

Annual and seasonal variation in extent of surface water

Annual and seasonal variation in the extent of surface water in each month and year was estimated using the procedures described in Chapter 4 (pages 108-111), but with distances measured from focal nests (Figure 1) rather than focal fox track plots.

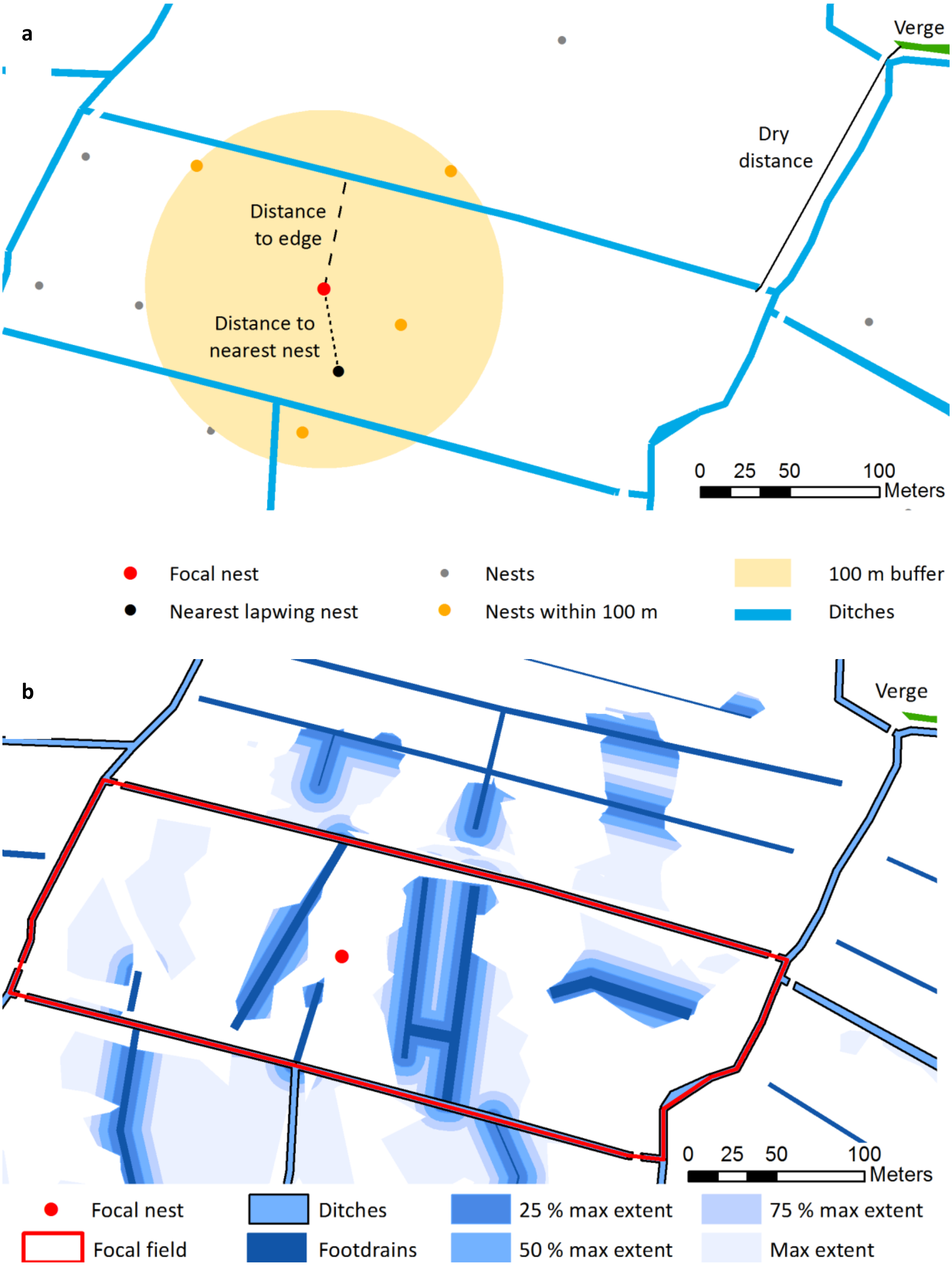

Figure 1 Illustration of the environmental metrics (see Table 1) of a) distance of focal nest to field edge, nearest active nest (including active nests within 100 m buffer) and dry distance to tall vegetation of verge and b) range of extents of surface wetness of focal fields, from water in footdrains only up to the maximum extent recorded in focal fields.

Scenario testing methods

A range of feasible management scenarios in which water levels or verge configuration could be manipulated were identified from discussions with the site manager (Table 2). Three scenarios manipulating the extent and distribution of water within the landscape were explored (Table 2). Firstly, the estimated extent of surface flooding in each field for each month and year (Chapter 4: Table 2 and Figure 5) was subject to a 25% increase (WETTER scenario) or decrease (DRIER scenario) in surface flooding (Table 2). The third scenario reflected the current drought management plan on the reserve. An increase in the frequency of drought conditions has resulted in the development of a plan in which existing sluices, pumps and deep ditches would be used to retain high water levels on 15 fields grouped into six blocks across the reserve (Figure 2a), while water levels on the remaining fields would be unmanaged and would be likely to dry at faster rates than non-drought years (Table 2).

Three scenarios manipulating the verge configuration within the reserve were also devised with the reserve site manager, for all verges under the ownership or control of the RSPB (Table 3, Figure 2b-d). These scenarios represented realistic options for verge removal, addition, and restructuring to create continuous ‘corridors’ of verge habitat along which predators may move. The verge scenarios were modelled initially using existing extent of surface water, and were then modelled in combination with the three water manipulations, resulting in nine combinations of scenarios (Table 3).

To explore the potential change in lapwing nest predation rates for these management scenarios, DRY DISTANCE and SURFACE WATER (Table 1) were recalculated for each scenario, and applied to the recorded distribution of nests in each year from 2005 to 2011. These new values were then incorporated within the model describing the predation rate of lapwing nests, and used to predict the expected predation rate in the conditions associated with each scenario.

Figure 2 The location of a) fields on which high water levels would be maintained in the drought plan scenario and of verge distribution in the scenarios of verge b) removal, c) creation of corridors and d) addition of verge (note this map also shows the current verge distribution). For levels of site wetness see Chapter 4; Figure 5.

Table 2 Descriptions of the three scenarios in which water levels are manipulated, and the resulting extent of surface water (FD=footdrain only, 25%, 50%, 75% or 100% of maximum mapped surface flooding extent in each field) in months with high (H), medium (M) or low (L) rainfall (see Chapter 4: Table 2 for definitions).

				March			April			May			June			July		
	Scenario	Description		H	M	L	H	M	L	H	M	L	H	M	L	H	M	L
	Current situation	Data used in minimum model		100	75	50	100	75	50	75	50	25	50	25	FD	25	FD	FD
Water manipulation	Wetter	Increase surface flooding by 25%		100	100	75	100	100	75	100	75	50	75	50	25	50	25	25
	Drier	Decrease surface flooding by 25%		75	50	25	75	50	25	50	25	FD	25	FD	FD	FD	FD	FD
	Drought plan	Implementation of the planned management in the event of a drought in which water is maintained on 15 selected fields (through pumping). Water levels on all other fields decreases by 25% each month, until water is only present in footdrains).	Dry fields	100	75	50	50	50	25	25	25	FD	FD	FD	FD	FD	FD	FD
			Wet fields	100	75	50	75	75	50	50	50	25	25	25	25	25	FD	FD

Table 3 Descriptions of the three verge manipulation scenarios, and the nine combinations of verge and water manipulation that were modelled (see Table 2 for descriptions of water manipulations)

Manipulation	Description	Combination of scenarios
Verge remove	Removal of all verges over which reserve staff have control to leave the minimum amount of tall vegetation on site (only remaining on the railway verges and in three copses).	Verge removal + Wetter Verge removal + Drier Verge removal + Drought plan
Verge corridor	Verge removal and creation to result in only two continuous "corridors" of tall vegetation through the reserve, one following the railway and one the river bank.	Verge corridor + Wetter Verge corridor + Drier Verge corridor + Drought plan
Verge addition	Potential verge creation at all suitable locations identified by Site Manager.	Verge addition + Wetter Verge addition + Drier Verge addition + Drought plan

Statistical analysis

Variation in daily nest predation rates for lapwing and redshank were explored separately in general linear models in R (v 2.13.1), using a formulation of Mayfield's (1961, 1975) method as a logistic model with a binomial error term, in which success (hatched) or failure (predated) was modelled with the number of exposure days as the binomial denominator (Aebischer 2009).

These daily nest predation rate models for lapwing and redshank incorporated annual and seasonal variation in predation risk by including YEAR and FIND DATE and, to explore the effects of nest location relative to habitat structures, by including DRY DISTANCE, as well as FIELD SIZE, DISTANCE TO EDGE, SURFACE WATER, and the two-way interaction of DISTANCE TO EDGE*SURFACE WATER to account for the potentially different levels of accessibility of nests within fields created by surface water. The capacity for lapwing group-mobbing of predators to protect nearby nests was explored by including NEAR NEST DISTANCE and the NESTS WITHIN 100 M.

DPRs predicted from these models were then transformed to predation probabilities by estimating nest survival rates over the incubation period (S), by raising the daily survival rate (1-DPR) to the power of the species incubation periods (from first egg laid: redshank = 30 days; lapwings = 32 days; Crick, Baillie, & Leech 2003; Kragten & De Snoo 2007). Nest predation probability over the incubation period was then calculated as 1-S.

The full general linear model comparing the predicted proportion of lapwing nests predated under different management scenarios included YEAR, SCENARIO TYPE and their interaction, and used a binomial error structure. The interaction term was non-significant, indicating that the shapes of these relationships were consistent between years, so the interaction was removed, but both main effects were retained in the model regardless of whether they remained significant. Model estimates and the 95% confidence intervals are presented for each scenario in each year.

Results

The number of nests monitored each year ranged from ~50 – 200 for lapwing and ~25 – 70 for redshank, with most nests monitored in 2010 (Figures 3a and 4a). The high predation rate in 2010, with around two-thirds of monitored nests being predated, resulted in a high re-nesting rate, accounting for the increased sample size in that year. Between 38 and 68% of lapwing and 22 and 87% of redshank nests were predated in each year (Figures 3a and 4a), with nest predation occurring throughout the season in both species (Figures 3b and 4b). Predation of both lapwing and redshank nests occurred throughout the range of environmental variables (field area, field flooding, distance to tall vegetation, distance to field edge) and measures of nesting activity (near nest distance and number of nests in the surrounding 100 m) (Figures 3c-h and 4c-h).

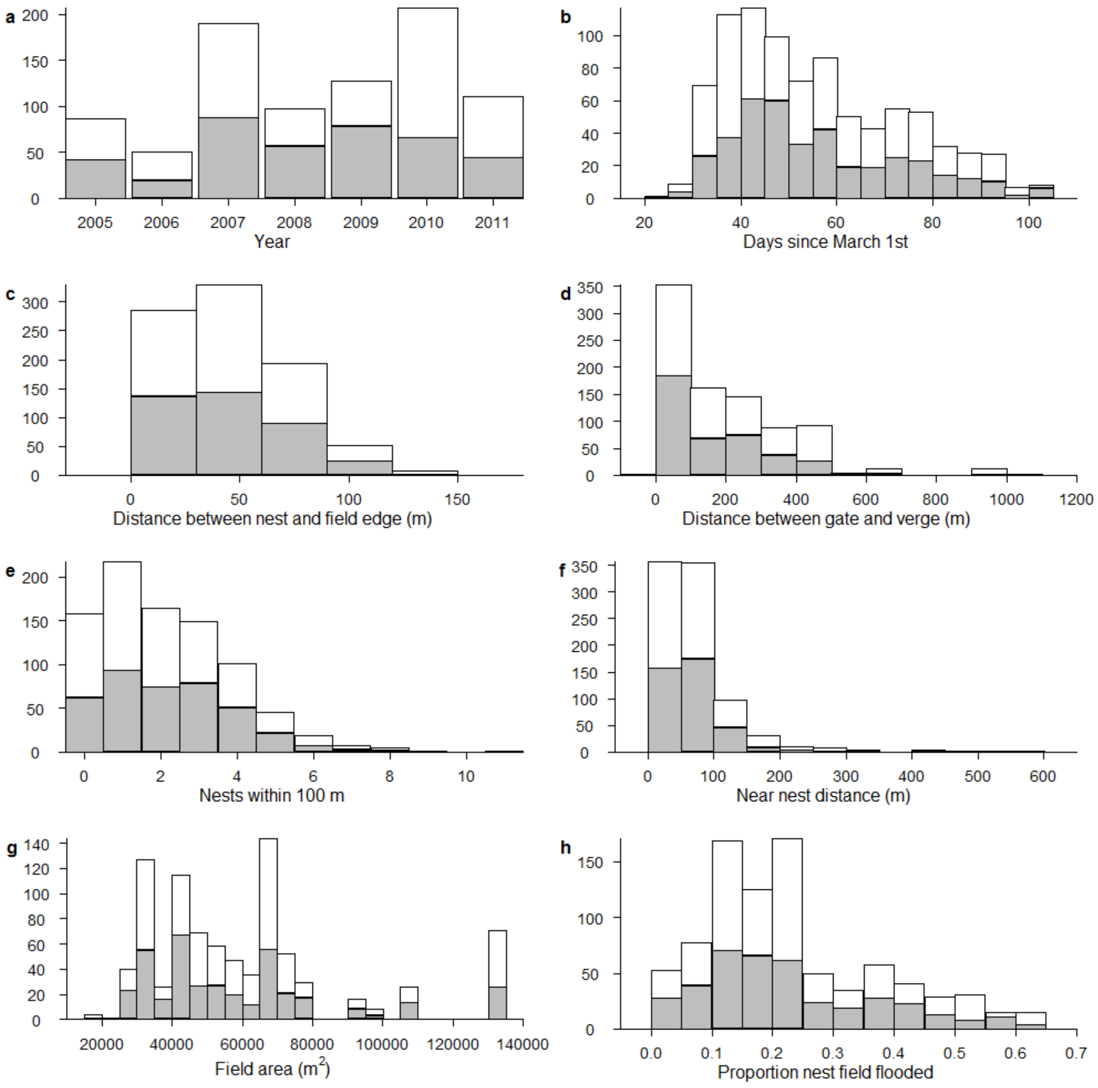

Figure 3 Number of lapwing nests that were predated (white) and hatched (grey) for different a) years, b) days since the 1st March, c) distances to field edge, d) distance between gate of field to verge, e) number of active lapwing nests within 100 m, f) distance to nearest active lapwing nest, g) field areas, and h) proportion of field flooded.

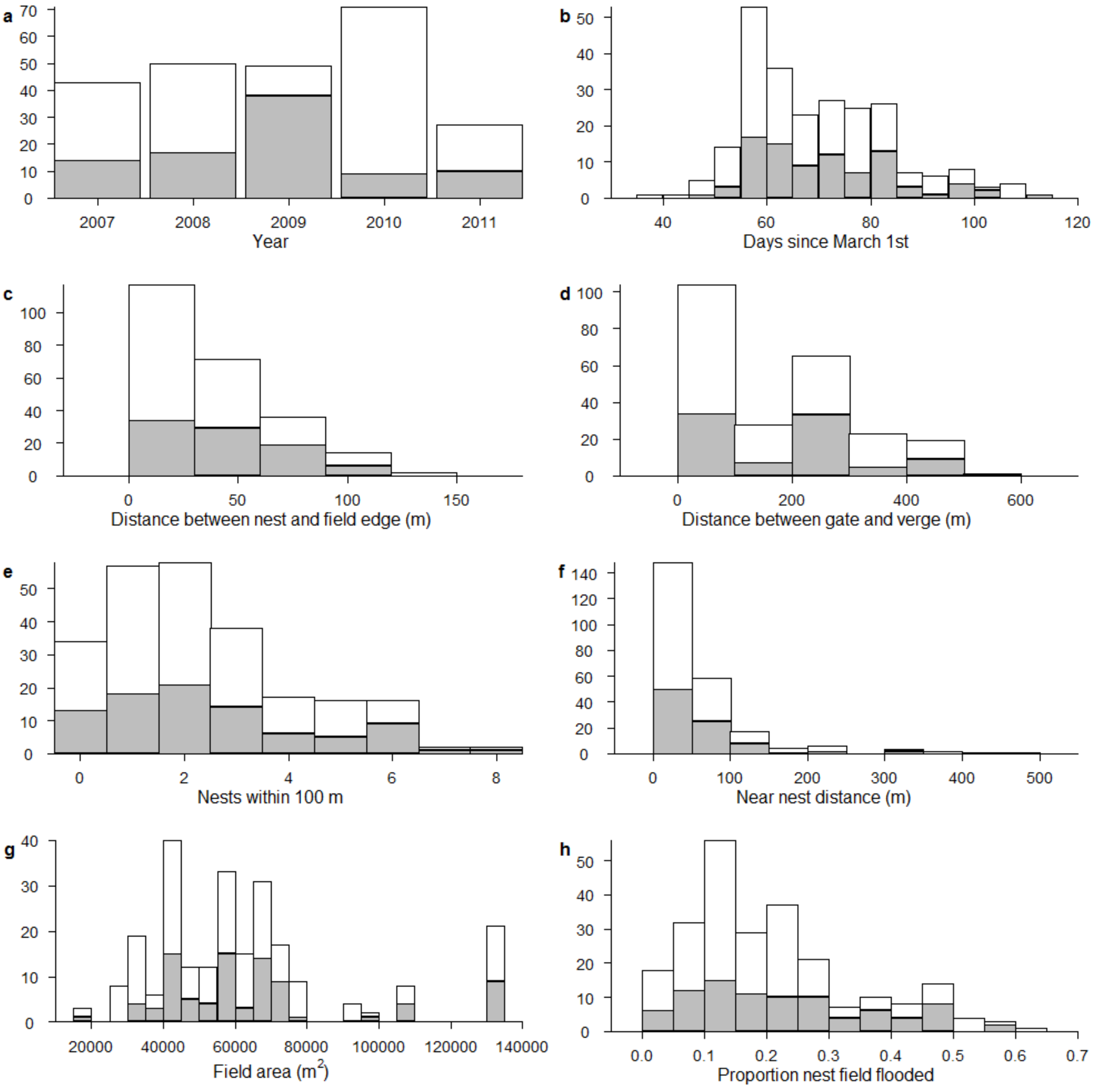

Figure 4 Number of redshank nests that were predated (white) and hatched (grey) for different a) years, b) days since the 1st March, c) distances to field edge, d) distance between gate of field to verge, e) number of active lapwing nests within 100 m, f) distance to nearest active lapwing nest, g) field areas, and h) proportion of field flooded.

Lapwing nest predation increased significantly with distance to tall vegetation, with the likelihood of predation increasing by ~60 to 90% as the distance to verge increased up to 1 km (Figure 5a, Table 3a). Isolated lapwing nests were significantly more likely to be predated (Figure 5e, Table 3a) and predation probability also increased very slightly with field area (Figure 5b, Table 3a). Although there was no significant main effect of surface water on predation probability, a significant interaction term showed that lapwings nesting within dry fields (< 30% surface water) had a higher predicted probability of being predated if they are further from the field edge (Figure 5c, Table 3a). Conversely, in wet fields (> 30% surface water) nests near the edge were more likely to be predated (Figure 5d, Table 3a). Redshank nest predation probability decreased significantly with increasing lapwing density (no. nests within 100m) but was unrelated to any other environmental variables (Figure 5f, Table 3b).

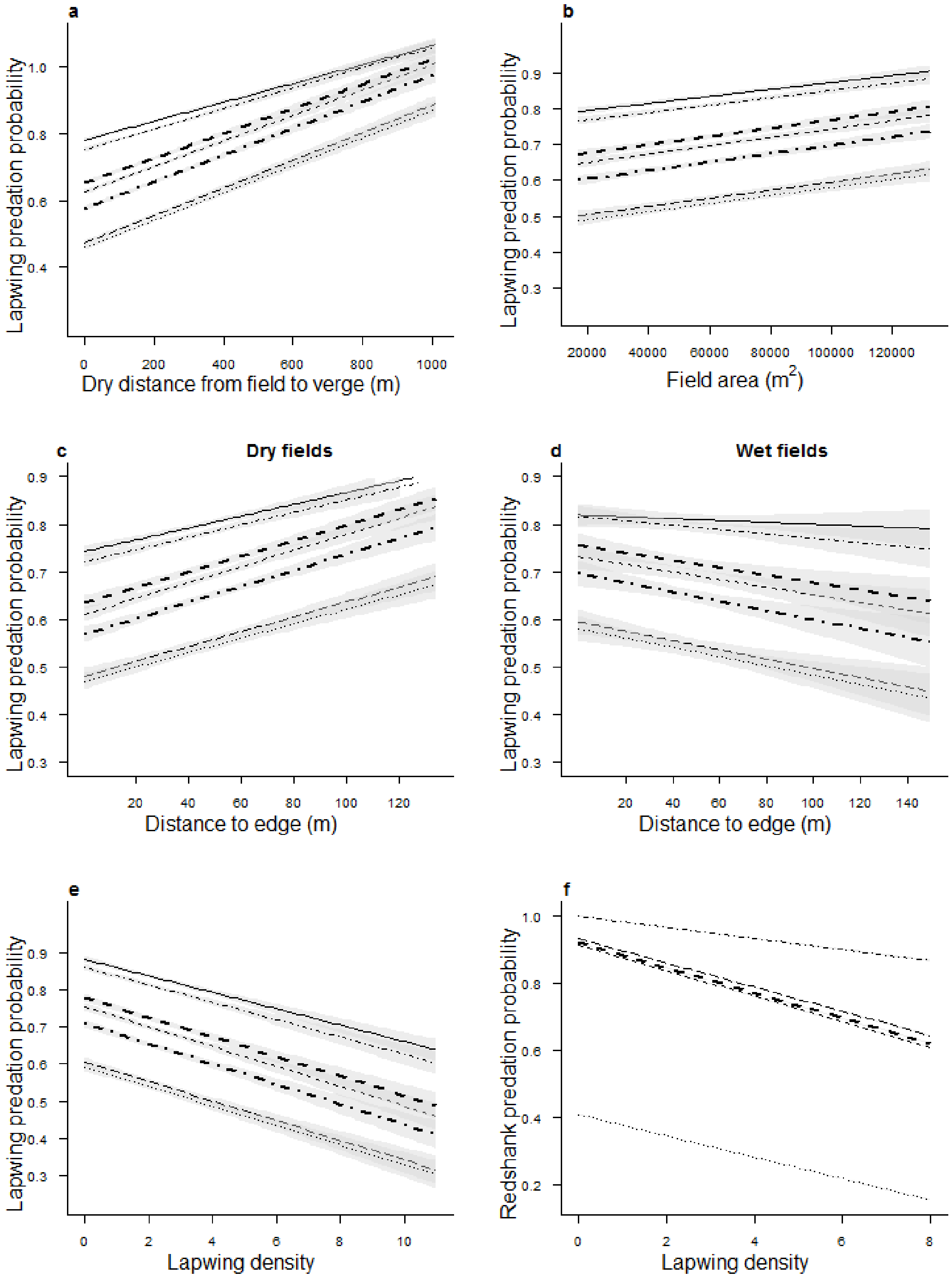

Figure 5 Predicted nest predation probability over the incubation period for lapwing with a) increasing distance verge, b) increasing field area, c) an increasing distance to edge in dry fields and d) wet fields, e) increasing number of active lapwing nests within 100 m, and f) for redshank with increasing number of active lapwing nests within 100 m. Lines represent years (2005: thick dot-dash line; 2006: solid line; 2007: dashed line; 2008: long-dashed line; 2009: dotted line; 2010: dot-dashed line; 2011: thick dashed line). Predictions and 95% confidence intervals (shown by shading around lines) are from models in Table 3.

Table 3 Results of a GLM (with binomial errors) of nest predation probability for a) lapwing and b) redshank. Minimum models are shown above the dashed lines, and non-significant variables excluded from the minimum model (with estimates from the full model; see Table 1) are shown below the dashed lines. Estimates and SE are in logits.

a

Variable	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-4.303	0.243	-17.693	<0.001
Year (2006)	0.461	0.247	1.867	0.062
Year (2007)	0.177	0.184	0.958	0.338
Year (2008)	-0.258	0.226	-1.141	0.254
Year (2009)	-0.267	0.217	-1.233	0.218
Year (2010)	0.555	0.181	3.065	0.002
Year (2011)	0.329	0.203	1.623	0.105
Distance to edge	0.011	0.004	3.121	0.002
Dry distance gate to verge	0.001	0.000	5.845	<0.001
Nests within 100m	-0.095	0.029	-3.304	0.001
Field area	0.000004	0.000002	2.114	0.035
Surface water	1.043	0.688	1.516	0.129
Dist to edge*Surface water	-0.030	0.013	-2.230	0.026
Find day	-0.001	0.003	-0.247	0.805
Near nest distance	0.001	0.001	1.769	0.077

b

Variable	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.504	0.213	-11.776	<0.001
Year (2008)	0.086	0.263	0.328	0.743
Year (2009)	-1.506	0.359	-4.193	<0.001
Year (2010)	0.688	0.237	2.909	0.004
Year (2011)	0.030	0.316	0.094	0.925
Nests within 100m	-0.125	0.047	-2.669	0.008
Find day	-0.003	0.008	-0.371	0.711
Dry distance to gate	0.002	0.006	0.289	0.773
Dry distance gate to verge	0.0002	0.001	0.283	0.777
Near nest distance	-0.003	0.001	-1.849	0.065
Surface water	-1.012	1.085	-0.933	0.351
Dry distance*Surface water	-0.015	0.024	-0.609	0.543
Field area	-0.000001	0.000	-0.241	0.809

The scenarios that represented a reduction in surface water resulted in an increase in the predicted predation of lapwing nests from the current situation (mean across all years: 69.8% ± 0.4 SE; drier scenario: 72.9% ± 0.4; Figure 6a) but this difference was not significant (Table 4). Under the proposed reserve drought plan, which maintains high water levels in a few selected areas of the reserve, predicted predation rates (71.0% ± 0.4) were lower than for the drier scenario (Figure 6a), and did not differ significantly from the current situation (Table 4). Increasing the amount of surface water resulted in a slight but non-significant decrease in predicted predation rates of lapwing nests reduced (66.8% ± 0.4).

The scenarios of verge removal and verge restructuring to create corridors both resulted in significant increases in predicted predation probability for lapwing nests (removal: 78.5% ± 0.5; corridors: 78.2% ± 0.5; Figure 6b; Table 4). Adding more verge habitat had very little effect on the likelihood of lapwing nests being predated (69.8% ± 0.4), but on this site there is only scope to create new verges on one area of the reserve (Figure 2d). When the wet and verge scenarios were combined, verge addition scenarios again had no significant change in predicted predation probabilities, and all scenarios with verge removal and corridor creation had significantly higher predicted predation probabilities than the current situation (Figure 6c, Table 4), with the verge removal and drier fields combination resulting in the highest average predation probability (81.0% ± 0.5; Figure 6c; Table 4).

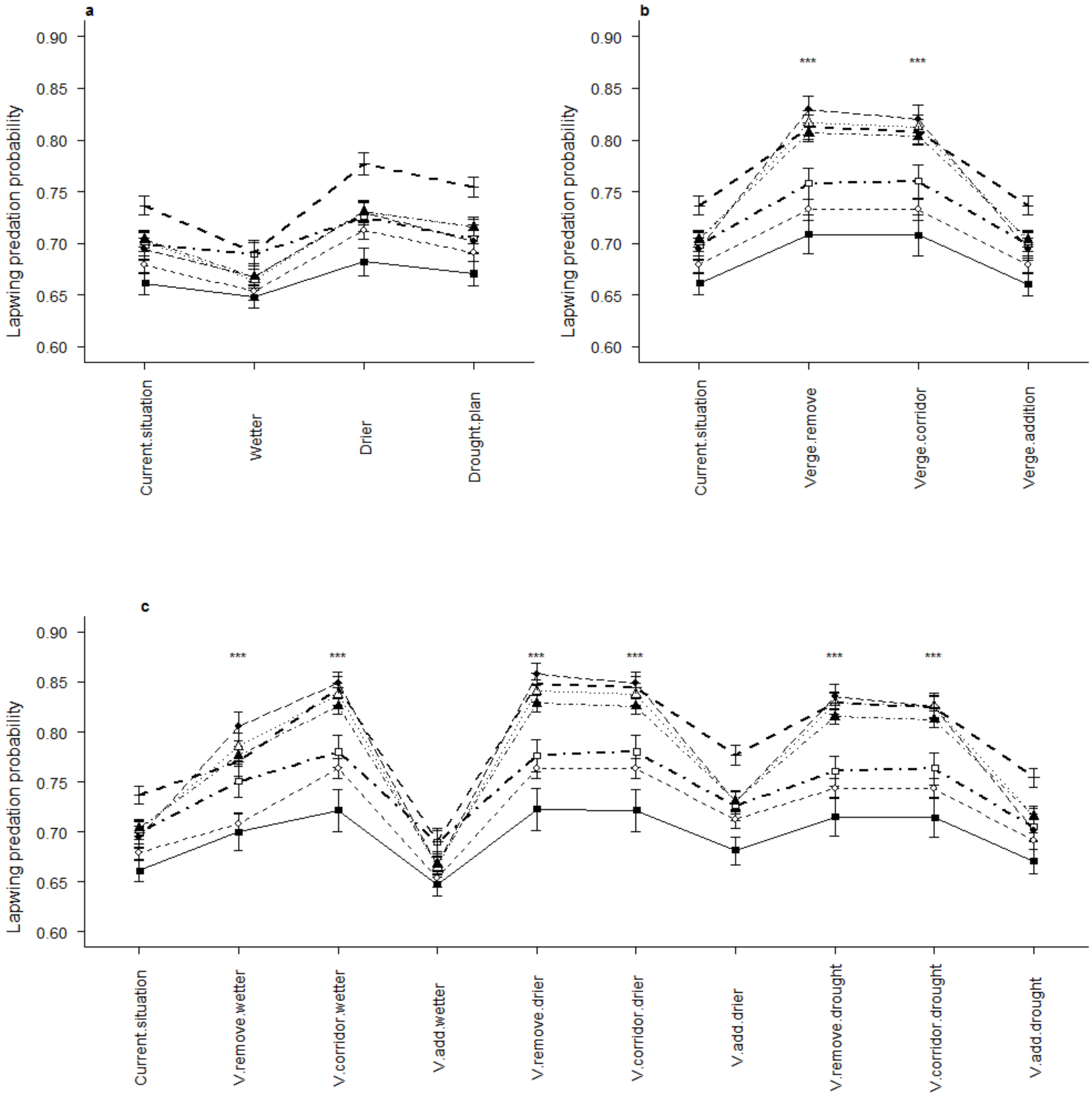

Figure 6 Predicted nest predation probability over the incubation period for lapwing under different scenarios of a) surface wetness, b) verge vegetation configuration and c) combinations of scenarios (see Table 2 for descriptions). Lines represent different years (2005: open square, thick dot-dash line; 2006: closed square, solid line; 2007: open circle, dashed line; 2008: closed circle, long-dashed line; 2009: open triangle, dotted line; 2010: closed triangle, dot-dashed line; 2011: cross, thick dashed line). Scenarios that differed significantly from the current situation model are denoted by ***.

Table 4 Results of a GLM (with binomial errors) of predicted probabilities of lapwing nest predation. Estimates and SE are in logits, with 2005 acting as a reference year.

Variable	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.778	0.094	8.269	<0.001
Year (2006)	-0.227	0.098	-2.310	0.021
Year (2007)	-0.108	0.073	-1.471	0.141
Year (2008)	0.167	0.086	1.945	0.052
Year (2009)	0.150	0.081	1.860	0.063
Year (2010)	0.123	0.074	1.673	0.094
Year (2011)	0.253	0.084	3.009	0.003
Wetter	-0.140	0.103	-1.357	0.175
Drier	0.152	0.106	1.428	0.153
Drought plan	0.056	0.105	0.534	0.593
Verge removal	0.455	0.111	4.098	<0.001
Verge corridor	0.440	0.111	3.970	<0.001
Verge addition	-0.0001	0.105	-0.001	0.999
Verge removal + Wetter	0.305	0.109	2.809	0.005
Verge removal + Drier	0.615	0.114	5.395	<0.001
Verge removal + Drought plan	0.513	0.112	4.583	<0.001
Verge corridor + Wetter	0.602	0.114	5.290	<0.001
Verge corridor + Drier	0.602	0.114	5.290	<0.001
Verge corridor + Drought plan	0.499	0.112	4.462	<0.001
Verge addition + Wetter	-0.140	0.103	-1.358	0.174
Verge addition + Drier	0.152	0.106	1.427	0.154
Verge addition + Drought plan	0.056	0.105	0.533	0.594

Discussion

Targeted conservation actions that focus on the specific requirements of single species can also inadvertently influence other constituents of the foodweb, including species that may interact directly with the target species. For example, management of habitat conditions and landscape structure may also influence predators of target species, and thus indirectly influence the effectiveness of conservation management. An increased understanding of predator activity can potentially help to avoid negatively affecting species of conservation concern, but opportunities to explore predator activity in relation to conservation management are rare (Amar & Redpath 2005). In this study, the collation of seven years of intensive monitoring data on the breeding success of two species of wader has allowed the identification of environmental conditions associated with differing levels of nest predation. Lapwing nests were significantly more likely to be predated if they were far from tall vegetation, far from field edges in dry fields, close to field edges in wet fields, and when there were fewer other lapwing nesting in the surrounding area. Redshank nests were also significantly more likely to be predated when there were fewer lapwing nesting nearby, suggesting that the protective effect of lapwing mobbing predators can extend to other species. Habitat management within wetland environments needs to be able to adapt efficiently to potential future extreme climatic events (e.g. droughts or very high rainfall) that could influence environmental conditions. Modelling of the potential impact of future environmental changes resulting from realistic management scenarios of changes in surface wetness and verge distribution indicated that substantial and biologically relevant changes in predation rates (up to ~10%) could occur in response to particular management scenarios, assuming that both nest distribution and predator activity would operate in the same way as at present.

The tall vegetation that is found only in field verges in this landscape is a habitat that has been found to be associated with higher levels of fox activity (Chapter 4). Lapwing nests in close proximity to areas of tall verge vegetation have a reduced likelihood of being predated, perhaps as a result of predators concentrating their foraging activities on alternative prey, such as small mammals within the verges (Laidlaw *et al.* 2013). The increase in lapwing nest predation as distance from tall verge vegetation increases may also suggest that, in these more open areas, far from verges, predators may concentrate more on wader nests as the only available prey, or they may opportunistically locate wader nests as they move through the landscape.

Within lowland wet grasslands the configuration of wet features can create complex within-field habitat structures which mammalian predators may find difficult to navigate. Wet features are generally more frequent in the centre of fields (Bodey *et al.* 2010) and, in wet fields, lapwing nests further from the edge had lower probabilities of predation. This suggests that high degree of surface flooding may create barriers to predator movement into the centre of fields; either by physically preventing movement, by dissuading predators from attempting to gain access, for example to avoid risk of injury (Berger-Tal *et al.* 2009), or through aversion to contact with wet surfaces (Harri, Mononen, & Sepponen 1999). In addition, in very wet fields, lapwing may nest closer to field edges to avoid flooding of nests, and predator hunting behaviour may be more efficient along narrow field edges, especially if nest densities are higher, as foxes have been shown to spend more time and effort in prey-rich patches (Mukherjee, Zelcer, & Kotler 2009). In fields with only small areas of surface wetness there may be little or no barrier to predator movement. Consequently, in dry fields, predators may be more likely to encounter nests in field centres, particularly if they no longer restricted to dry field edges to traverse fields.

The well-documented predator mobbing behaviour of breeding lapwing (Elliot 1985b) is likely to contribute to the reduced level of nest predation in areas of high lapwing nesting density. Similar protective effects of high wader nesting densities have been demonstrated in studies with artificial nests (e.g. in grey plover *Pluvialis squatarola*, Larsen & Grundetjern 1997). Neighbouring species may also benefit from this defensive behaviour, as redshank nest predation probabilities were also lower in areas with high densities of nesting lapwing. This apparent nest protection gained from lapwing may result from the physical mobbing of predators by adult lapwing, the early warning of predator presence that might be provided by species such as lapwing that nest in the open, or through dilution of predation risks in areas of high prey density (Hamilton 1971), especially as concealed redshank nests are likely to be harder for predators to locate (Götmark *et al.* 1995). Evidence from Chapter 4 on the reduced use of fox track plots in areas with high densities of lapwing, together with the lower predation rates of both wader species at high nesting densities, may indicate that fox foraging activity in these areas is being reduced rather than deflected onto alternative targets.

Scenario-testing of the potential impact of future management

Intensification of farming and climate change have been highlighted as two of the major conservation issues facing breeding bird populations in Britain (Ausden & Fuller 2009). However, the way in which these processes will change habitats and influence species is not always clear. Current habitat management of lowland wet grassland to benefit breeding waders relies on manipulating both the water within the landscape and the vegetation structure of fields (Smart *et al.* 2006; Eglington *et al.* 2010). Scenario testing is one way in which the potential magnitude of responses to changing management actions can be explored, in order to help develop conservation policies that will continue to be effective in a changing world (Peterson, Cumming, & Carpenter 2003). Although the scenarios explored in this study all related to nature reserve management, they can potentially also inform land management decisions in the wider countryside, for example through the ongoing development of agri-environment scheme options.

The implementation of water storage and pumping regimes to increase surface flooding at Berney Marshes and other similar sites would be a costly and difficult task. Consequently, a reserve drought plan has been proposed, in which limited water resources would be concentrated in a small number of fields. These fields have been selected as they have the most suitable hydrology and topography, ensuring water retention is most feasible within these areas of the reserve. Encouragingly, overall levels of predation pressure faced by nesting lapwing under the drought plan were predicted to only increase by ~1%, indicating that this planned reallocation of resources may not substantially influence predator effects, probably because increases in predation rates of nests in the centres of the larger number of dry fields would be offset by reduced predation rates on nests in the centres of wet fields. Scenarios in which the whole reserve became wetter or drier also had no significant change in overall nest predation rates. However, the estimates of lapwing predation probability are derived using the geographical distribution of past nesting attempts. Eglington et al. (2008) showed that lapwing nest distribution is influenced by water in the landscape, with higher nesting densities occurring close (within 50 m) to areas with surface flooding. Consequently, changes to the extent of surface water may also result in changes to wader nesting distribution, which may then alter their predation probability. The scenarios presented here could be developed to incorporate predicted changes in nesting distribution in response to altered management regimes. For example, the drier scenario could result in fewer waders being attracted to nest at the site. In addition, downstream costs of a drier scenario could include those not considered within this analysis, such as reduced survival of chicks, due to reduced growth rates (Eglington *et al.* 2010) and increased risk of predation (Kentie *et al.* 2013).

The scenarios of verge removal and creation within the reserve were constrained because not all verges are under the ownership or management of the RSPB (e.g. the railway line bisecting the reserve), and there are relatively few roads and tracks suitable for verge creation (as most fields are separated by deep ditches). Despite these limitations, both removal of tall vegetation and creation of corridors of continuous verges were predicted to result in significant increases of ~8% in nest predation rates. While no combination of proposed management changes predicted significant declines in the predation rates, the combined influence of verge addition and increased wetness of fields suggested a potential decline in predation of ~3%. The scenarios represented here also assume that predator behaviour is constant during these changes in the landscape that they use. Given the ability of foxes to adapt to new situations, as exemplified by their impact as an invasive species (Harding, Doak, & Albertson 2001; Saunders, Gentle, & Dickman 2010), it is unlikely that this species would not respond to landscape alterations, particularly if food resources were scarce. In particular, the effectiveness of creating corridors of tall vegetation that would provide routes of movement for predators through the landscape may rely upon foxes strongly preferring to stay close to verges, which may be their preference within a reserve where they are controlled.

Implications for managing predator impacts on wet grasslands

At Berney Marshes, the impact of predator control has previously been found to decrease the probability of lapwing nest predation from ~90% to ~65% (Bolton *et al.* 2007). During our study, average lapwing predation probability was ~70%, and the scenario-testing suggested that predation rates of ~65-85% could result. By contrast, previous studies have shown that predator exclusion is capable of reducing nest predation levels from ~66% to only 16% after fence construction (Malpas *et al.* 2013). The estimated magnitude of reduction in predicted nest predation pressure of ~10% through modelling the manipulation of landscape conditions suggests that, in theory, it may be possible to alter predation rates through changing landscape structure. Given the important role of nest predation in limiting recovery of declining wader populations, and the prohibitive costs associated with exclusion of predators from large areas of breeding habitat, such relatively easy management approaches are attractive. However, field manipulations of environmental conditions are likely to be necessary to assess their impact on wader nesting densities, predator behaviour and, ultimately, the levels of predation experienced at both the nest and chick stage so that impacts on overall productivity can be estimated. If management of landscape and habitat structure on wet grasslands can substantially influence nest predation rates, these techniques may also be applicable in wider countryside management, for example through development of the management options and targeting of agri-environment schemes. However, this may first depend on establishing whether the relationships between environmental drivers and wader nest predation are similar on reserves and in the wider countryside.

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General Conclusions

In this thesis, I have assessed the effect of management for breeding waders on aspects of the wider foodweb within lowland wet grasslands, and used these findings to improve understanding of patterns of wader nest predation in this landscape. I found that, within wet grassland landscapes managed for breeding waders, small mammals are almost entirely restricted to patches of tall vegetation, which are rare and typically occur in verges that are outside fields and follow linear features in the landscape (e.g. tracks, railways and rivers). Lapwing nest predation rates are lower when nests are closer to these verges and when the area of verge in the landscape surrounding nests is higher. Lapwing nest predation is also influenced by an interaction between field wetness and the distance from the edge of fields, such that lower predation rates occur closer to field edges in drier fields, and further from field edges in wetter fields. Nest predation rates of lapwing and redshank, and fox visitation rates at fox tracking plots, are lower when densities of nesting lapwing are higher. I then used this information to consider the potential influence of future changes in reserve management on breeding waders. In this concluding section, I will consider wider implications of this work and potential directions for future research.

The lowland wet grassland foodweb

As the ranges of many breeding wader species in Western Europe are increasingly restricted to nature reserves and sites managed within agri-environment schemes (Ausden & Hirons 2002; Smart *et al.* 2008; O'Brien & Wilson 2011), the management implemented in these areas is of utmost importance. I explored how management to provide appropriate habitat conditions for breeding waders (Smart *et al*. 2006; Eglington *et al*. 2008) influences other species within the lowland wet grassland foodweb. A variety of techniques to measure small mammal distribution and activity (including live trapping, field sign surveys and ink tracking tunnels) were used throughout Berney Marshes RSPB reserve, and this work showed that small mammals are predominantly found in tall vegetation, and within lowland wet grassland, such tall vegetation is typically rare and restricted to verges outside fields (Chapter 1). Ink tracking tunnels were also used to measure small mammal activity in tall vegetation patches of differing size, sward structure and level of connectivity to other patches throughout Berney Marshes RSPB reserve, and on six other wet grassland RSPB reserves in the east of England, and this work showed that small mammal activity increases with sward density, but there is little effect of patch size (Chapter 2). Within verges, levels of small mammal activity are relatively consistent, irrespective of patch characteristics, and there was no evidence for increased levels of small mammal activity within fields adjacent to verges (Chapter 2).

The nesting distribution and hatching success of lapwing (913 nests monitored over seven years) and redshank (255 nests monitored over nine years) has been intensively monitored at Berney Marshes. These long-term data were extremely important in allowing exploration of nest predation patterns in a range of conditions. Collation and analysis of these data within a GIS framework allowed me to show that the probability of predation of lapwing nests increases with distance from the nearest verge, and decreases with increasing area of surrounding verge, while the probability of redshank nest predation was not significantly influenced by proximity to or area of nearby verge (Chapter 3). Reduced lapwing nest predation rates close to verges could potentially be influenced by the presence of small mammals, the main prey of many predators of wader nests, and/or the cover afforded by tall verge vegetation, attracting predators to those areas. The lack of influence of verges on redshank could be because their different nest site characteristics (nests concealed in tall clumps of grass) alter the manner in which nest predation operates, or because the smaller sample of redshank nests prevented identification of relationships with environmental factors.

The activity of foxes at Berney Marshes during the wader breeding season has been measured with fox track plots over the last five years. Collation and analysis of these data within a GIS framework allowed me to show that fox use of plots varies annually, declines seasonally and is lower in areas of the reserve with higher lapwing densities (Chapter 4). The decline in plot use with lapwing nesting density suggests that lapwing predator defence behaviour may influence fox distribution and behaviour. Alternatively, areas with high lapwing density may be found in areas where foxes are less likely to visit because of their habitat preferences (Stillman *et al.* 2006).

To consider the potential for management of field conditions and habitat structure in wet grasslands to influence wader nest predation rates, I then developed models of nest predation that included within-field surface water conditions and verge locations. These models showed that lapwing nest predation probability is greater (a) further from edges in drier fields, but nearer field edges in wetter fields, (b) further from verges (using routes that do not cross ditches) and (c) when nests are more isolated (Chapter 5). By contrast, redshank nest predation probability is only influenced by lapwing densities, with isolated nests having higher predation rates (Chapter 5). These analyses suggest that manipulation of field wetness, verge distribution and lapwing nesting densities could potentially influence levels of wader nest predation. The scenarios that were developed to explore realistic manipulations of these parameters at Berney Marshes suggested that reductions in nest predation of only up to ~3% may be possible, if wader distribution and predator behaviour are consistent under these new habitat conditions.

Over the course of the study, significant annual variation was found in nest predation of both lapwing and redshank, and fox use of track plots. This annual variation could have been driven by differences in fox use of the reserve, for example, through differences in numbers or behaviour of individual foxes. Annual records of fox control in the pre-wader breeding season at Berney indicate that numbers of shot individuals were relatively constant (mean ± SD: 6.9 ± 2.3, range = 2-9 individuals shot per year) between 2005 and 2011, but fox control ended by April in the majority of years, so numbers of foxes on the reserve during the breeding season are unknown and are difficult to quantify using existing methods. The behaviour of foxes within the reserve could also be influenced by fluctuations in the abundance of their main small mammal prey, in which case nest predation pressure may be linked to numbers of small mammals, as has been shown in the Netherlands (Beintema & Muskens 1987).

No long-term small mammal monitoring has been carried out at Berney, but annual variation in the breeding success of predators such as owls, for which small mammals are the main component of the diet, have previously been linked to variation in small mammal abundance (Petty & Fawkes 1992). In open grasslands, the main avian predator that primarily consumes small mammals is the barn owl, *Tyto alba*, and their diet largely comprise field voles, bank voles and *Apodemus spp.* (Love *et al.* 2000). To assess whether years with high barn owl breeding success (which could reflect high small mammal abundance) were also years with low wader nest predation (which could result from foxes concentrating on small mammals), we used data from the British Trust for Ornithology Nest Record Scheme (Crick, Baillie, & Leech 2003) to explore the association between annual levels of wader nest predation at Berney and barn owl brood size within Norfolk. In the Nest Record Scheme, volunteer observers locate nests and record their contents and success. As many barn owls now use nest-boxes, large sample sizes are available for this species. Brood size was used because it is likely to be an indicator of the prey available to feed young. Although the brood sizes of barn owls in Norfolk did vary substantially between 2003 and 2011 (Figure 1a), there was no correlation between average annual brood size of barn owls and the average level of nest predation for either lapwing or redshank (Figure 1b and c). However, variations in abundance of small mammals may occur at more local scales than the regional scale at which barn owl brood size can be measured, and thus direct measurements of small mammal abundance at the locations at which wader breeding success is measured may be needed to be able to fully explore the influence of small mammal abundance on fox activity and impact on waders. Monitoring of small mammal activity at Berney Marshes has continued since the completion of this thesis, and will hopefully continue into the future.

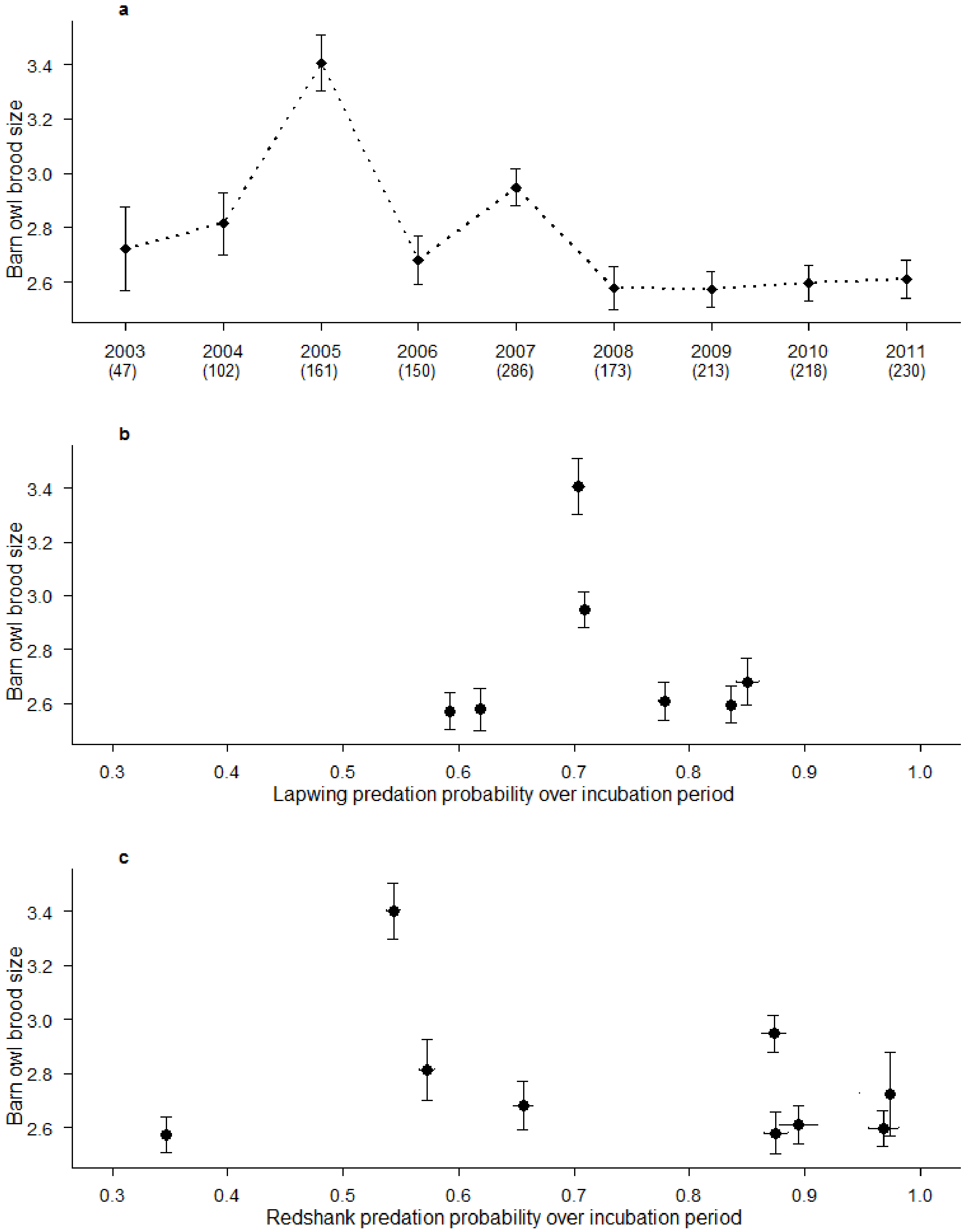

Figure 1 Annual variation in a) mean (± SE) barn owl brood size in Norfolk (data from British Trust for Ornithology Nest Record Scheme, sample size for each year in parentheses), and associations between mean barn owl brood size and mean ± SE nest predation rates at Berney Marshes for b) lapwing (r =-0.05, p =0.91) and c) redshank (r =-0.26, p =0.50).

Identity and impact of predators of breeding waders within lowland wet grassland

Since 2007, more than 350 dataloggers have been deployed in lapwing and redshank nests at Berney Marshes, and these loggers have shown that 85% of predated nests were taken at night, and the 24 nest cameras that have captured predation events since 2008 only ever recorded foxes, implicating foxes as the main predator at Berney Marshes. However, the eggs of ground-nesting birds can be predated by a wide range of predator species, including mammals and birds (Macdonald & Bolton 2008). In wet grassland landscapes, several corvid species are common, and are assumed to be a major wader nest predator. The evidence from dataloggers suggests that this is unlikely, as there are no nocturnally-active avian predators in the UK. An opportunity to explore the timing of nest predation by corvids arose during this study when an experiment using artificial nests of quail eggs monitored by nest cameras (Bolton *et al.* 2007a) was carried out to investigate the influence of nest location within fields on predation probability. In 22 fields across the reserve, one artificial nest was placed at the field edge and two nests were placed in field centres (>50 m from the edge). Unfortunately, given that this study aimed to explore vulnerability to fox predation, 53 of the 63 predated nests were subject to avian predation (22 crow *Corvus corone*, 13 jackdaw *Corvus monedula*, 8 magpie *Pica pica* and 10 rook *Corvus frugilegus*, 10 predator spp. unidentified). The average latency between nest construction and avian predation was very short (1.4 days ± 1.9 SD) suggesting that individual birds either witnessed nest construction, or could very quickly find these nests. However, the timing of predation by corvids was always during daylight (Figure 2), which is the inverse of the time of predation events of lapwing nests (Eglington *et al.* 2009b, Chapter 4). The use of artificial nests in this case was therefore unhelpful in identifying effects of nest location on predation by foxes, but it did provide strong supporting evidence that avian predators are not a major contributor to wader nest predation at this site. These artificial nests, although located in fields with varying levels of lapwing nesting density, did not have any adults specifically defending them from predators. The protection provided by aggressive adults protecting nests may therefore be one of the reasons for the low contribution of avian predators to the overall predation of wader nests.

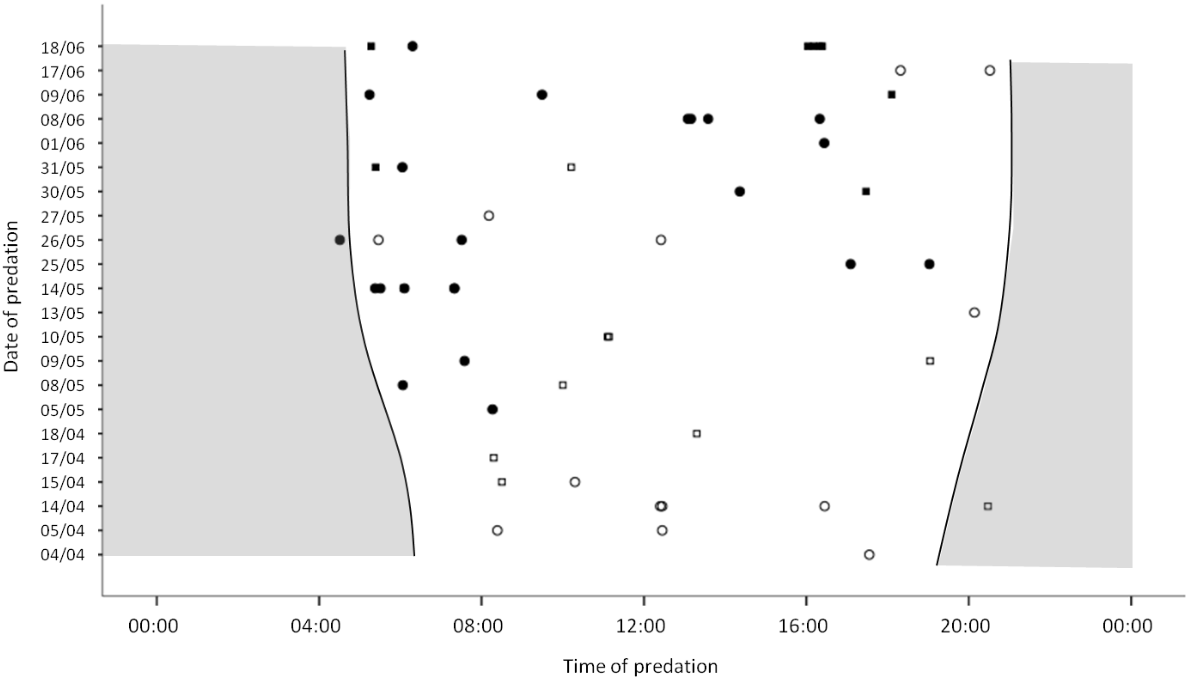

Figure 2 Date and time of predation events of artificial nests at Berney Marshes. Shaded areas represent the hours of darkness and the points are predation events by crow (●), jackdaw (○), magpie (▪) and rook (□).

This thesis has focussed on understanding the larger-scale and long-term processes that influence wader predation rates and, in particular, the interaction between wader nest predation, fox distribution and the distribution of their primary prey; small mammals. A primary aim of the research has been to identify ways in which management could potentially be used to reduce the influence of foxes. However, reduced levels of nest predation by foxes could potentially increase levels of predation by other species, such as stoats *Mustela ermine* and weasels *Mustela nivalis*.

An early aim of this study was to investigate the relative distributions and activity of foxes and mustelids within lowland wet grassland, after initial studies on Berney had suggested that mustelid activity may be higher in areas of low fox abundance (Robertson 2009). The ink tracking tunnels that were deployed to measure small mammal activity were specifically designed to also capture mustelid activity, and thus to allow the distribution and activity of mustelids within lowland wet grassland landscape to be explored. However, the use of tunnels by mustelids was very low, with prints being recorded on only 3% of tunnel checks in 2010 and 2011 (Figure 3). This is in comparison to the small mammal prints, which were used extensively in chapter 1 and 2 to explore the distribution and activity of prey in the landscape, where 24% of tunnels recorded prints. Water vole *Arvicola amphibius* prints were also recorded but only in 2% of tunnels. The very low use of tracking tunnels by mustelids, and the lack of any mustelid predation events being recorded by nest cameras at Berney Marshes, provides little evidence to suggest whether these species could pose an increased threat to wader nests in the future. In particular, mustelid use of tracking tunnels was too low to assess whether annual variation in mustelid activity was associated with differences in nest predation rates by foxes. However, monitoring of other predator species during any manipulation that is aimed at disrupting fox predation may help to explore these interactions in more detail.

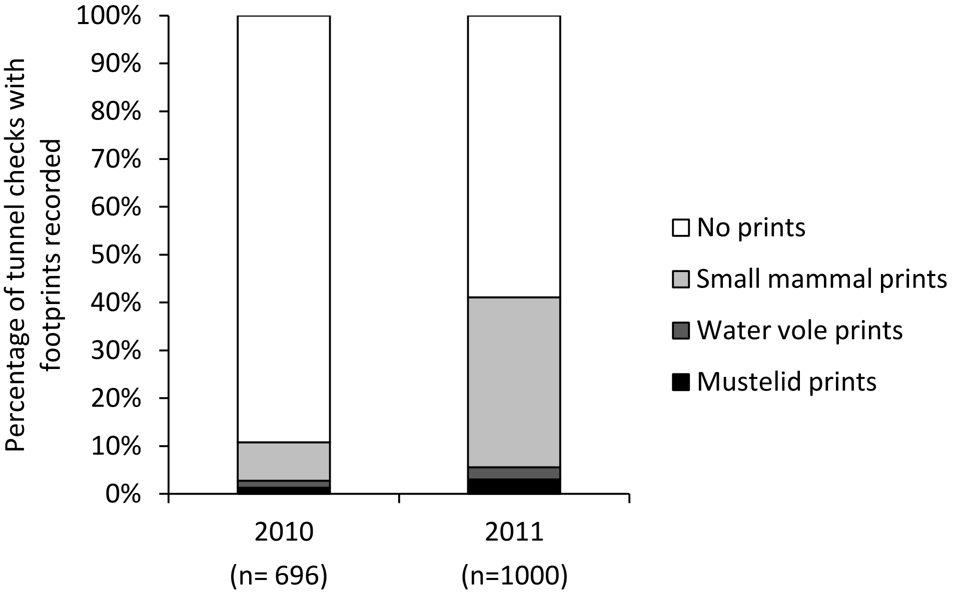

Figure 3 Percentage of tunnel checks on which prints from small mammals, watervoles or mustelids were recorded.

While this thesis has concentrated on the identification and impact of nest predators of waders in lowland wet grassland, predation at the chick stage is also contributing to population limitation in these species (Malpas *et al.* 2013) and avian predation may be more likely at this life stage (Schekkerman, Teunissen, & Oosterveld 2009). Many of the avian predators of wader chicks (e.g. kestrel *Falco tinnunculus*, marsh harrier *Circus aeruginosus* and buzzard *Buteo buteo*) also have small mammals within their diet (Underhill-Day 1985) and are potentially using tall vegetation habitats as foraging or nesting locations or as perches. Management aimed at improving conditions for small mammals could therefore also have implication for these raptors. Determining the impact of drivers identified as important for nest predation on the fate of chicks will be an important nest step in assessing the possible implications of future management actions.

Management of lowland wet grassland landscapes to reduce wader nest predation

i) Implications for reserve management

The data used to explore predation patterns here are from the only long-term monitoring of wader nest predation rates in the UK. Although these data are from a single site, the 500 ha nature reserve at Berney Marshes is typical of reserves managed intensively for breeding waders, and foxes are often the main predators of wader nests at these sites (Bolton *et al.* 2007b). Between 2005 and 2011, the breeding lapwing population at this site has been stable/increasing, even though productivity in most years has been lower than levels estimated to be necessary for population stability or growth (General Introduction, Figure 3b). In 2005, an area of arable land adjacent to the reserve was bought by the RSPB and reverted to wet grassland; this site was immediately colonised by breeding lapwing (Eglington *et al.* 2009a), suggesting that Berney may also be attracting lapwing from other sites.

The analyses reported in this thesis show that lapwing nest predation rates between 2007 and 2011 have been ~68-72%. The modelled scenarios of alternative landscape management reported in Chapter 5 suggest that nest predation rates of ~65-85% could result from some management scenarios, if wader distribution and fox behaviour remain consistent. This increase in predation rates is greater than the annual variation in predation rates, and would be very unlikely to be sustainable. None of the scenarios predicted significant decreases in overall nest predation rates, but the strong protective effect of high wader nesting densities on nest predation suggests that maintaining and protecting areas with high breeding densities is likely to be very important.

ii) Implications for wider countryside management

Following the Making Space for Nature report (Lawton *et al.* 2010), there is increasing recognition that conservation efforts to recover populations of previously widespread species should follow a landscape-scale approach in which more and bigger protected sites are better managed and, importantly, these sites become more joined up within the landscape. Within a lowland wet grassland context, agri-environment schemes such as Environmental Stewardship are the main government-funded mechanism for delivering improved habitat around and between protected sites to join up habitats in the landscape. The current government investment is considerable, at £15.1 million *per annum* to maintain over 50,000 ha (21.6% of UK total, Natural England 2012) of coastal and floodplain grassland using options designed to deliver habitat for breeding waders (HK9/11/13 and HK10/12/14).

This thesis has highlighted the need for wader breeding habitat that can attract and support high densities of breeding lapwing capable of providing effective anti-predator behaviour, that can lead to lower predation of both lapwing and redshank nests. These findings would therefore support the use of targeted Higher Level Stewardship (HLS) options in appropriate areas of the wider countryside. Encouraging breeding waders to nest at low densities in poorer quality habitats through Entry Level Stewardship (ELS) schemes may therefore risk resulting in high nest predation rates (Kentie *et al.* 2013). Habitat manipulations capable of reducing nest predation rates are particularly attractive, however, without a greater understanding of the behaviour of predator species we may just be changing the storyline without altering the ending of the tale. This may result in the conservation community being forced into using conspicuous interventions, such as the use of fencing to protect whole reserves from terrestrial predators.

iii) Rewilding of lowland wet grassland in the UK

In addition to bottom-up approaches of manipulating landscapes to reduce predation rates of nests, there is growing interest in conservation approaches that focus on the withdrawal of management. The concept of creating very large, naturally-functioning landscapes (RSPB 2011) could include top-down control of the predators of breeding waders within lowland wet grassland in the UK. Large carnivore top predators are the natural top-down mechanism of controlling medium-sized predators within ecosystems (Elmhagen & Rushton 2007). Mesopredators that have been released from the suppression of natural predators have been shown to increase predation on small prey (Ritchie & Johnson 2009), and red foxes are a prime example of a predatory species that has been released from the control imposed by its top predators. The reintroductions of top predators could potentially provide the top-down control on red foxes required to lessen their predatory impact upon breeding waders (Sæther 1999). For example, recolonisation by lynx *Lynx lynx* in Fennoscandia has been associated with a decrease in the suppression of prey and competitors by red foxes (Ritchie *et al.* 2012).

Within the UK, there is interest in reinstating the natural predators of red foxes, such as lynx and wolf *Canis lupus* (Wilson 2004). At present, the most suitable habitat for reintroductions is likely to be in areas of the Scottish Highlands that can provide the appropriate conditions for large home ranges of top predators and high densities of wild ungulate prey (Wilson 2004). A possible alternative in the east of England could be the translocation of top avian predators, with white-tailed eagle *Haliaeetus albicilla* reintroductions having been considered in Suffolk in recent years, and eagle owls *Bubo bubo* now breeding in some areas of England (Melling, Dudley, & Doherty 2008). In the intensively farmed landscape of lowland England, reintroduction of top predators is a controversial issue. A major stumbling block preventing the more widespread consideration of top carnivore reintroduction is that of perceived risks, both to humans and livestock, although it has been argued that this attitude is perhaps hypocritical when we take it for granted that Indian villagers should live with the risk of tigers for the benefit of global biodiversity (Taylor 2009). Future work on the impact of top predator reintroductions upon foxes and mustelids would be of interest, however, methods of management within the wider countryside that would be supported and implemented by landowners is the current priority.

Future directions

Improving understanding of predator movements within lowland wet grassland

The methods used in this thesis to explore fox distribution and activity provided only discrete snapshops of predator locations, e.g. fox track plot use and camera images. Fox scat transects are also carried out on the reserve and, in 2011 deployment of small, inert plastic beads (Polyethylene, Plastibution LTD, UK) in bait that were subsequently found in scats showed that individual foxes are traversing large areas of the reserve (Figure 4). A range of other tracking techniques were attempted during this study (e.g. ink fox track plots, fox bite tubes and cards), however, none were found to be both practical and used by foxes. Tracking foxes using GPS technology embedded in collars was attempted, but limitations in the available techniques that are acceptable to RSPB animal ethics meant that catching foxes during the wader breeding season was impossible. Future work using GPS technology to track the moments of foxes within lowland wet grassland habitats would be extremely useful in determining the mechanisms through which environmental drivers of nest predation were operating. Tracking individuals may allow detailed assessments of how foxes use specific habitats within these landscapes, and may give an indication of the level of individual specialisation on food sources such as wader nests.

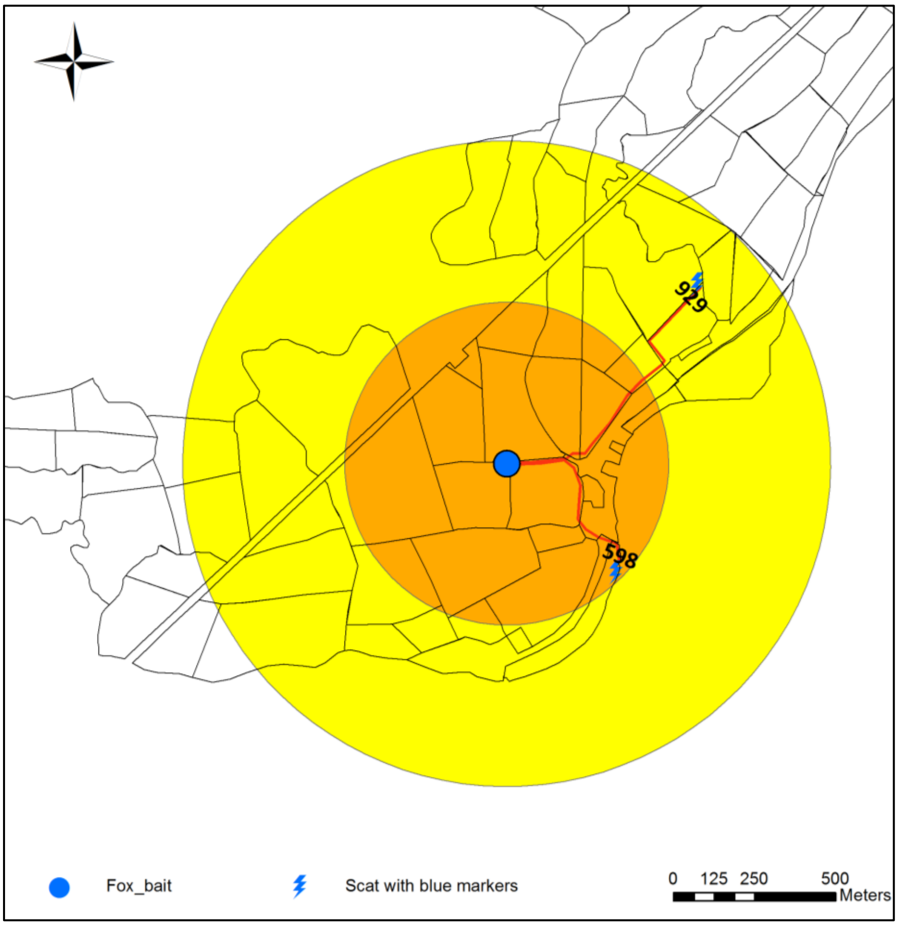

Figure 4 Location of fox bait containing plastic markers at Berney Marshes deployed in March 2011, the location of two scats containing plastic markers subsequently located during scat transects and the shortest routes (show by red line) between bait and scat locations avoiding ditches (see Chapter 4 for details).

Exploring environmental drivers of nest predation in the wider countryside

The likely differences between reserves and the wider countryside in the predation processes experienced by lowland waders, coupled with the large investment in lowland wet grassland agri-environment options, means it is important to maximise the benefits of these options for target species. If the results presented in this thesis are to be used to influence future management of the countryside to reduce the impacts predators have on breeding waders, future work needs to test the predictions of models derived from Berney Marshes by monitoring wider countryside sites over a large spatial-scale. An understanding of these processes could lead to adaptation of current agri-environment options or development of new options as a non-lethal way of managing wader nest and chick predation in the landscape.

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