Research Paper

Foxes, voles and waders: drivers of predator activity in wet grassland landscapes

Version: 3 Submitted: 2019-07-03

ABSTRACT

Impacts of generalist predators on declining prey populations are a major conservation issue, but management of this situation is constrained by limited knowledge of the factors influencing predator distribution and activity. In many declining populations of ground-nesting waders, high levels of nest and chick predation are preventing population recovery. Red foxes, Vulpes vulpes, are the main predator but their primary prey is small mammals. On wet grasslands managed for breeding waders, small mammals are concentrated in tall vegetation outside of fields, and nests closer to these patches are less likely to be predated. To assess whether these patterns result from fox attraction to small mammals, and thus the potential for management of tall vegetation to influence nest predation rates, we quantify seasonal and spatial variation in fox and small mammal activity in relation to tall vegetation patches. Across wet grassland sites, tall vegetation patches of any size (> 0.05 ha) supported small mammals and small mammal activity increased throughout the wader breeding season, while the use of fox track plots within fields declined seasonally. Although within field fox track plot use did not vary with distance to tall vegetation, over the 1064 nights of trail camera recording, foxes were seen in areas with tall vegetation on 13 nights compared with short vegetation on only two nights. These findings suggest that lower predation rates of lapwing nests close to tall vegetation could reflect fox attraction to areas with small mammal activity, but any such effects would primarily operate later in the breeding season, and may therefore primarily influence late nests and chicks.

Key words: Predation pressure; habitat management; landscape management; shorebirds; sward structure

INTRODUCTION

Predator-prey relationships are key ecological interactions that are increasingly the focus of conservation management (Smith et al. 2010, Woodroffe & Redpath 2015, Marshall et al. 2016). The increasing impacts of generalist mesopredators following extirpation of apex predators (Ritchie & Johnson 2009, Colman et al. 2014) has resulted in an urgent need to identify conservation management strategies that can reduce these impacts (Bolton et al. 2007, Bodey et al. 2010, Laidlaw et al. 2017). Interactions between predators and their prey can potentially be influenced by key aspects of landscape and habitat structure (Alterio et al. 1998, Carter & Bright 2002, Gorini et al. 2011), particularly if these influence the distribution of other prey types that are not the subject of conservation concern (Laidlaw et al. 2013).

The combination of increasing predator impacts alongside habitat loss can be severely detrimental for many wild bird popultations (Roos et al. 2018), with habitat degradation potentially facilitating increases in predation impacts (Thirgood et al. 2000, Evans 2004). For example, 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 et al. 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 et al. 2007, Smart et al. 2008, O'Brien & Wilson 2011). Efforts to improve wetland management within these areas, such as the maintenance of short swards and wet features, have been effective at attracting breeding waders (Smart et al. 2006, Eglington et al. 2008, 2010, Fisher et al. 2011). However, the impacts of predators of nests and chicks are severely constraining the recovery of these wader populations (Malpas et al. 2013, Roos et al. 2018), and most are continuing to decline (e.g. Hayhow et al. 2017).

A variety of management practices are already undertaken to reduce the impact of predators on breeding waders on grasslands, including lethal control (Bolton et al. 2007), exclusion fencing (Rickenbach et al. 2011, 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 or local-scale influence on predator activity (Smith et al. 2010). However, understanding how predators and prey are distributed across these landscapes could aid identification of land management options to reduce predation impact on breeding waders.

On wet grasslands in Western Europe, evidence from nest cameras shows the red fox (*Vulpes vulpes*, hereafter referred to as foxes) to be the main predator of wader nests, accounting for ~60% of recorded nest predation events across a range of studies (MacDonald & Bolton 2008). Foxes are a generalist predator whose varied diet predominantly comprises small mammals (Dell'Arte, Laaksonen, Norrdahl, & Korpimäki, 2007; Forman, 2005). Small mammal distribution could thus be an important driver of fox activity and distribution, and the associated nest predation risk experienced by ground-nesting birds. Breeding success of ground-nesting birds has also been linked to small mammal abundance (or a proxy of this measure) across a number of systems e.g. periodicity in high-arctic wader breeding success, as measured by proportion of juveniles in flocks, has been linked to lemming cycles (Summers and Underhill, 1987; Aharon-Rotman et al., 2015), reduced productivity of arctic-nesting geese has been recorded when voles are scarce (Nolet et al., 2013) and vole population irruptions have been associated with increased fecundity of North American dabbling ducks (Ackerman, 2002; Specht and Arnold, 2018).

Within wet grassland landscapes, small mammals are largely restricted to patches of taller, denser vegetation swards which typically occur only in verges outside of grazed fields (Laidlaw et al. 2013), and lapwing *Vanellus vanellus* nests that are closer to such verges are significantly less likely to be predated (Laidlaw et al. 2015), potentially as a result of foxes preferentially hunting small mammals (rather than wader nests) when verges are present. Modelling different scenarios of habitat management in these landscapes suggests that targeted expansion of the area of tall vegetation could potentially reduce nest predation rates by ~20% (Laidlaw et al. 2017), and manipulation of tall vegetation patches is a potentially practical and feasible tool, both in intensively managed reserves and across the wider countryside. However, the effectiveness of this management approach will depend on whether foxes do indeed concentrate their activity around patches of tall vegetation in these landscapes, which types of patches might be favoured and whether patch use varies seasonally.

While small mammals are known to be confined to tall vegetation patches in wet grasslands (Laidlaw et al. 2013), the extent to which their abundance varies with the size of these patches, and thus what size patches should be the target of management actions, is unknown. Similarly, understanding whether patterns of fox activity reflect seasonal variation in small mammal activity within these patches is important, as this could influence the location of managed patches in relation to the seasonal distribution of breeding birds. Consequently, here we quantify whether small mammal activity within tall vegetation patches varies with patch size and whether these patterns vary over the course of the breeding season. Then, to explore whether the resulting spatial and seasonal variation in small mammal activity is associated with fox distribution, we use fox track plots and trail cameras to quantify fox activity in relation to proximity to tall vegetation and how these patterns vary seasonally. We then use this information to consider the implications for adapting vegetation management in wet grassland landscapes to influence levels of wader nest predation.

METHODS

Study sites

Variation in small mammal activity among patches of tall vegetation (areas larger than 400 m^2) was assessed on six wet grassland SITES (capital letter indicate model variables, Table 1) in east and south-east England (Strumpshaw Fen (52°61'N 01°46'E), Buckenham Marshes (52°60'N 01°47'E), Cantley Marshes (52°58'N 01°51'E), Ouse Washes (52°45'N 00°16'E), Nene Washes (52°57'N -00°06'E), Elmley Marshes (51°40'N 00°77'E)) and, in more detail, on a seventh site (Berney Marshes (52°35'N 01°35'E) (Figure A1). At the time of sampling, all of these sites were managed as nature reserves by the Royal Society for the Protection of Birds (RSPB), and management on these reserves is predominantly aimed at providing suitable habitat conditions for breeding waders, through maintenance of short swards (primarily delivered with livestock grazing) and surface wet features that contain water throughout the wader breeding season (Eglington et al. 2008, Fisher et al. 2011). Consequently, there are three distinct vegetation structures typically found within these wet grassland landscapes: short (i.e. <10 cm height) vegetation within the highly managed and often wet field centres, slightly taller (>10 cm) vegetation in the drier edges of fields (within 50 m of edge of field), and tall vegetation (>20 cm) outside fields, in verges that often follow paved roads, gravel tracks, railways and rivers (Laidlaw et al., 2013).

Small mammal distribution and activity

Small mammal activity 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 were 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 recording the number of squares that contained at least one whole or partial small mammal print; a maximum score of 48 was therefore possible from the two papers in each tunnel, and this metric of small mammal activity is used as a proxy for the amount of small mammal movement within the local area.

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 (>10 cm) vegetation 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. Within each reserve, sampled patches were spread across the site, with a mean distance between patches of 47.4 m ± 89.6 SD. Each of the 29 patches of tall vegetation on these reserves 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.

The area of each of the 29 tall vegetation patches was measured from aerial photographs in ArcGIS (ArcMap Version 9.3). Patch sward structure was measured during June and July 2011 and 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 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 et al. 2001).

On Berney Marshes, seasonal variability in small mammal activity in patches of tall vegetation was quantified in 25 patches spread throughout the reserve, along field verges (n = 14) and in field edges (n = 11). Patch size and sward structure was measured as described above. 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 late June 2011.

Fox distribution and activity

Tracking plots

To quantify the distribution of fox activity across Berney Marshes, baited track plots were deployed during each wader breeding season between 2008 and 2010 (Bodey et al. 2010, Cole 2010). Track plots were spread throughout the reserve in all years and located both at field edges and in the centre of fields (Figure A2).

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 on which each plot was 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 were detected and/or when the bait had been dug up and consumed. 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.

Trail cameras

To assess whether fox activity (i.e. the locations visited by foxes within this landscape) is concentrated around verges, trail cameras (RECONYX™ PC800 HyperFire™) were deployed at Berney Marshes to capture predator presence along 19 verges (with tall vegetation, >20 cm) and 19 field edges (with short vegetation, >10 cm), for 28 consecutive nights each during April to June 2011. Cameras were placed at height of around 1 m on either existing gate posts or new posts, with cameras set to record ten pictures per trigger, with a 'rapidfire' delay between pictures and 'max range' during night mode.

Environmental conditions and breeding wader distribution

The area and distribution of all patches of tall (> 10 cm) vegetation within the Berney Marshes reserve were mapped in ArcGIS v.9.3 (Figure A2) by digitising outlines from aerial photographs (Millennium Map 2000). The network of large, deep ditches that border fields and supplies water across the lowland wet grassland landscape, were also digitised. The DISTANCE TO VERGE for each spatially referenced track plot (Figure A2) was calculated in ArcGIS v.10 as the sum of the minimum distance from the plot to the field edge and the distance from the nearest gateway access point of that field to the nearest tall vegetation. To calculate this distance, a cost-distance analysis was used (following Laidlaw et al. 2017) 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. Ditches that surround these fields are likely to act as barriers to the movement of ground-predators, and predators are therefore most likely to access fields through the dry access provided by gateways. 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. This measure of lapwing density was included in the analyses to determine whether the local activity of breeding waders and, in particular, defensive behaviour of nesting lapwing, may be influencing fox movement. In all years 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 A2).

Annual and seasonal variation in extent of surface water

Using GPS locations of all footdrains (shallow channels of varying width designed to hold water within fields), the extent of SURFACE WATER within each field was estimated. High water levels, which result in pools forming around overtopped footdrains, are maintained on the reserve over winter, and the maximum extent of surface water in fields was mapped in March of two years (2009 and 2011). From these maps, a five-category surface flooding score that reflected the range of surface flooding across the reserve was developed (maximum extent, ~75%, ~50%, ~25% extent and water in footdrains only) and mapped in ArcGIS v.10. Surface flooding categories were assigned to each focal field over the season to capture seasonal reductions in surface flooding following Laidlaw et al. (2017).

Statistical analyses

General linear mixed models were used to determine the influence on small mammal activity (proportion of tracking paper with prints in each tunnel) of (a) patch size and sward density across six reserves (Table 1: Model 1), (b) patch location at Berney Marshes (Table 1: Model 2), and (c) patch size, interaction of patch size and time and sward density at Berney Marshes (Table 1: Model 3). 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. To account for non-independence of the four tunnels deployed in each sampling location, Models 1-3 (Table 1) include a random factor of tunnel identity nested within sampled habitat patch.

The daily use rate (DUR) of the track plots (over the nine night observation period) was modelled 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 1999). Details of the track plots model variables and interactions are in Table 1 (Model 4). 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 (used in Figure 4).

Non-significant ($p > 0.05$) interactions were removed by backwards deletion from full models. We used GLMM with function glmer in R 3.4.2 (R Core Team 2017).

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 R (v 3.4.2). The small sample size of cameras recording fox activity (4/38) prohibited a meaningful analysis of the frequency of verge and field use by foxes.

RESULTS

Variation in small mammal activity on wet grasslands

Across six wet grassland reserves in eastern England, small mammal activity increased significantly over the course of the season, with activity levels being more than three times higher in June than in April in all sites (Table 2 Model 1, Figure 2a). However, despite patch sizes in the six sites ranging from ~0.0004 to 0.05 km^2, small mammal activity did not vary significantly with patch area or sward density (Figures 2b and c).

Small mammal activity also 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 field edges, where vegetation was typically less dense (Table 2 Model 2, Figure 2d). Small mammal activity also did not vary with patch size at this site and this was also not influenced by the time in the season (Table 2 Model 3, Figure 2e). 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 swards, which were all in field edges (< 10% cover; Table 2 Model 3, Figure 2f). Small mammal activity in wet grasslands is therefore concentrated in field verges with dense vegetation, particularly later in the season when activity levels are greatest.

Variation in fox activity on wet grasslands

Between 32 and 48% of track plots were visited by foxes in each year of the study, except for 2010, when nearly 95% of the track plots were visited (Figure 3a). Between 40 and 60% of the track plots were visited by foxes regardless of distance to verge (Figure 3c). Relatively few track plots were situated in areas of high lapwing density, as these are now rare in this landscape (Figure 3d). There was a seasonal decline in the likelihood of track plots being used by foxes (Table 3, Figure 4a), from ~60% (April) to 30% (June). Use of track plots did not vary with distance to verge, nor was there any seasonal effect of distance to verge on track plot use (i.e. no significant interaction between season and distance to verge, Table 3). Similarly, track plot use did not vary with the extent of surface water in the surrounding field (Table 3). However, of the 325 track plots included in the analysis, 169 had no active lapwing nests recorded within 100 m (Figure 3d), and plots were significantly more likely to be used by foxes when there were fewer active lapwing nests within 100 m (Table 3, Figure 4b). Track plots with many (~7) surrounding lapwing nests were ~20%

less likely to be used than plots with no nearby active nests (Figure 4b).

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 (although number of individual foxes was not known), with foxes being recorded on 13 separate nights (of the 1064 camera-nights), while both within-field cameras only captured foxes on a single night each (Fisher's exact test, p=0.038). Thus, fox activity was more commonly recorded next to tall vegetation than in areas of short vegetation but very few foxes were recorded overall, and so these findings should be treated with caution.

DISCUSSION

Across wet grassland reserves that are managed primarily for breeding waders, small mammal activity increased significantly through the breeding season, but did not vary with patch size (> 0.05 ha, the minimum recorded in the study), but activity levels were greater in patches with dense ground-level sward structure. The activity measure 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. The consistently high late-season small mammal activity (tracking papers with ~80% print coverage), across all seven sites suggests, however, that similar seasonal changes in small mammal activity and patch structure are likely to operate across wet grasslands. Seasonal increases in small mammal activity are likely to reflect juvenile dispersal, which may increase use of lower quality habitats (e.g. Collins & Barrett 1997). The seasonal increase in small mammal activity in tall vegetation patches was mirrored by a decrease in fox use of track plots within fields. This suggests that fox distribution and activity in these wet grassland landscapes could be influenced by the distribution of small mammals and the vegetation patches in which they occur.

Previous work in this landscape has shown that predation of lapwing nests is lower near the tall vegetation of verges, with nests adjacent to verges having a ~60% predation probability compared to a ~90% predation probability for nests ~1 km from verges (Laidlaw et al. 2015, 2017). Verge vegetation structure is typically taller and denser than within-field vegetation because of a lack of grazing and water management. The presence of small mammals in verges, combined with the cover provided by this tall vegetation in an otherwise open landscape, could lead to fox activity being concentrated around these areas. Trail cameras placed next to tall vegetation recorded significantly more fox activity than cameras in areas with short vegetation, but foxes were recorded on only four cameras overall, and thus more evidence is needed to confirm this concentration of fox activity around tall vegetation.

While trail cameras suggested a possible concentration of fox activity close to tall vegetation, fox use of track plots did not vary with proximity to tall vegetation. This latter finding is consistent with previous studies which found no evidence of fox use of track plots being concentrated around field edges or close to linear features (Eglington et al. 2009). The contrast between track plots and cameras suggests that foxes do not avoid areas that are distant from tall vegetation (i.e. they occur throughout the landscape, in areas with and without tall vegetation). However, the concentration of trail camera records of foxes next to tall vegetation, and the lower predation rate of lapwing nests close to these areas (Laidlaw et al. 2015, 2017) suggests that foxes may stay close to tall vegetation when it is present. The seasonal decline in track plot use mirrors the seasonal increase in small mammal activity in field verges, and could thus reflect foxes increasingly concentrating their activity around field verges as the season progresses. As the density of the ground-level sward is particularly important for small mammals (Tattersall *et al.* 2000), the denser swards outside fields may provide the best substrate for small mammal runs to be constructed in vegetation with sufficient cover from predators. Over the course of the season, the vegetation within these habitats is also continually growing (Laidlaw et al. 2013) which, in combination with increasing small mammal abundance, could be making these habitats increasingly attractive to foxes as the season progresses. Wader nest and chick availability increases through April and May before declining rapidly in June (Eglington et al. 2008). Foxes may therefore be concentrating activity within fields when wader nests are abundant and small mammals are scarce, but switching to field verges when small mammal abundance increases and the number of wader nests declines. This would suggest that the presence of verges might be more likely to influence fox predation of late nests and chicks than of early nests. Verges may also provide perches and small mammal prey for avian predators, which can also be important predators of wader chicks (Mason et al. 2018).

Fox use of track plots was significantly less likely in areas with higher densities of nesting lapwing, which is consistent with previous studies showing that nest predation rates decline with increasing lapwing nesting densities (Eglington et al. 2009, Laidlaw et al. 2017). Lapwings have been shown to direct their mobbing defence behaviour at foxes during nocturnal observations (Seymour et al. 2003), and predator mobbing can be an effective form of nest defence (Elliot 1985). Foxes encountering lapwing mobbing, particularly by multiple individuals, may change their direction or speed of movement so that they are less likely to encounter a fox tracking plot. 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.

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. Our findings suggest that structure (especially ground-level sward density) of tall habitat patches is more important than patch size in determining small mammal distribution within these environments. Verges support the great majority of the main small mammal prey of mammalian and avian predators in wet grasslands. The management of verge structure and location is therefore key to encouraging small mammal populations in wet grasslands. As predation of wader nests is reduced in areas close to patches supporting small mammals (Laidlaw et al. 2015), encouraging small mammals through appropriate habitat creation may serve to both boost small mammal populations and reduce the unsustainably high levels of wader nest predation that occur across Europe at present (MacDonald & Bolton 2008).

Establishing and encouraging dense verge vegetation in wet grassland landscapes could therefore potentially increase the prey available for generalist predators. Verge creation could be a flexible management tool as relatively small areas of verge can provide suitable conditions for small mammals. The tall vegetation patches in this study were selected as being representative of those currently available in the landscape, and were predominantly narrow verges that bordered tracks, paths or rail and river embankments. There is, however, scope for altering verge configuration, for example through the addition or maintenance of tall grasses and reeds along ditches. Tall vegetation could also be developed within fields that are either not appropriate for breeding waders (e.g. very dry fields, Eglington et al. 2008), or likely to be poorer quality (e.g. fields that lack foraging areas for chicks, (Eglington et al. 2010), by reducing levels of grazing and cutting.

The findings of this study also suggest that there may be potential 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. Future work that aimed to track foxes using GPS collar technology could be used to determine fine-scale predator use of wet grassland landscapes, and therefore usefully inform future habitat manipulations aimed at altering their behaviour, ultimately to reduce predation on breeding waders.

Experimental manipulations of habitat management to create tall vegetation patches at differing distances from breeding wader fields would allow the interaction between small mammal distribution, predator activity and wader nest predation to be assessed. The design and creation of tall habitat patches for small mammals within lowland wet grassland landscapes could then potentially become an important management tool to reduce levels of predation of breeding waders and to encourage greater species and habitat diversity within grassland landscapes.

LITERATURE CITED

Aebischer, N. J. 1999. Multi-way comparisonsand generalized linear models of nest success: extensions of the Mayfield method. *Bird Study* 46:22-31.

Alterio, N., H. Moller, & H. Ratz. 1998. Movements and habitat use of feral house cats Felis catus, stoats Mustela erminea and ferrets Mustela furo, in grassland surrounding Yellow-eyed penguin Megadyptes antipodes breeding areas in spring. *Biol. Conserv.* 83:187-194.

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

Bodey, T. W., J. Smart, M. A. Smart, & R. D. Gregory. 2010. Reducing the impacts of predation on ground-nesting waders: a new landscape-scale solution?. *Asp. Appl. Biol.* 100:167-174.

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

Bowers, M. A., & S. F. Matter. 1997. Landscape ecology of mammals: relationships between density and patch size. *J. Mammal.* 78:999-1013.

Carter, S ., & P. Bright. 2002. Habitat refuges as alternatives to predator control for the conservation of endangered Mauritian birds. Pages 71-78*in* C. . Veitch and M. . Clout, editors.*Turning the tide: the eradication of invasive species. Proceedings of the International* Conference on Eradication of Island Invasives.

Cole, T. 2010. Reducing the impacts of predation on ground-nesting waders : a new landscape-scale solution? *MSc Thesis, Wildlife Management Conservation, University of Reading.*

Collins, R. J., & G. W. Barrett. 1997. Effects of habitat fragmentation on meadow vole (*Microtus* pennsylvanicus) population dynamics in experiment landscape patches. *Landsc. Ecol.* 12:63-76.

Colman, N. J., C. E. Gordon, M. S. Crowther, & M. Letnic. 2014. Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. *Proc. R. Soc. B Biol. Sci.* 281:20133094-20133094.

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

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

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

Elliot, R. D. 1985. The exclusion of avian predators from aggregations of nesting lapwings (Vanellus vanellus). *Anim. Behav.* 33:308-314.

Evans, K. L. 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. *Ibis (Lond. 1859).* 146:1-13.

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

Gibbons, D. W., A. Amar, G. Q. A. Anderson, M. Bolton, R. B. Bradbury, M. A. Eaton, A. D. Evans, M. C. Grant, R. D. Gregory, G. M. Hilton, G. J. M. Hirons, J. Hughes, I. Johnstone, P. Newbery, W. J. Peach, N. Ratcliffe, K. W. Smith, R. W. Summers, P. Walton, & J. D. Wilson. 2007. The predation of wild birds in the UK: a review of its conservation impact and management. *RSPB Res. Rep. no 23,* RSPB, Sandy, UK.

Gorini, L., J. D. C. Linnell, R. May, M. Panzacchi, L. Boitani, M. Odden, & E. B. Nilsen. 2011. Habitat heterogeneity and mammalian predator-prey interactions. *Mamm. Rev.* 42:55-77.

Hayhow, D. B., M. A. Ausden, R. B. Bradbury, D. Burnell, A. I. Copeland, H. Q. P. Crick, M. A. Eaton, T. Frost, P. V. Grice, C. Hall, & S. J. Harris. 2017. The state of the UK's birds 2017.

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

Laidlaw, R. A., J. Smart, M. A. Smart, & J. A. Gill. 2015. Influence of landscape features on nest predation rates of grassland-breeding waders. *Ibis (Lond. 1859).* 157:700-712.

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

MacDonald, M. A., & M. Bolton. 2008. Predation on wader nests in Europe. *Ibis (Lond. 1859).* 150:54-73.

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

Marshall, K. N., A. C. Stier, J. F. Samhouri, R. P. Kelly, & E. J. Ward. 2016. Conservation Challenges of Predator Recovery. *Conserv. Lett.* 9:70-78.

Mason, L. R., J. Smart, & A. L. Drewitt. 2018. Tracking day and night provides insights into the relative importance of different wader chick predators. *Ibis (Lond. 1859).* 160:71-88.

Mayfield, H. F. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73:255-261.

Mayfield, H. F. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87:456-466.

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

Rickenbach, O., M. U. Grüebler, M. Schaub, A. Koller, B. Naef-Daenzer, & L. Schifferli. 2011. Exclusion of ground predators improves Northern Lapwing *Vanellus vanellus* chick survival. *Ibis* (Lond. 1859). 153:531-542.

Ritchie, E. G., & C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecol. Lett.* 12:982-998.

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

Seymour, A. S., S. Harris, C. Ralston, & P. C. L. White. 2003. Factors influencing the nesting success of Lapwings Vanellus vanellus and behaviour of Red Fox Vulpes vulpes in Lapwing nesting sites. *Bird Study* 50:39-46.

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

Smart, J., J. A. Gill, W. J. Sutherland, & A. R. Watkinson. 2006. Grassland-breeding waders: identifying key habitat requirements for management. *J. Appl. Ecol.* 43:454-463.

Smith, R. K., A. S. Pullin, G. B. Stewart, & W. J. Sutherland. 2010. Effectiveness of predator removal for enhancing bird populations.. *Conserv. Biol.* 24:820-829.

Stewart, K. E. J., N. A. D. Bourn, & J. A. Thomas. 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. *J. Appl. Ecol.* 38:1148-1154.

Team, R. C. 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Thirgood, S. J., S. M. Redpath, D. T. Haydon, P. Rothery, I. Newton, & P. J. Hudson. 2000. Habitat loss and raptor predation: disentangling long- and short-term causes of red grouse declines. *Proc. R. Soc. B Biol. Sci.* 267:651-656.

Wilson, A. M., M. Ausden, & T. P. Milsom. 2004. Changes in breeding wader populations on lowland wet grasslands in England and Wales: causes and potential solutions. *Ibis (Lond. 1859)*. 146:32-40.

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

Woodroffe, R., & S. M. Redpath. 2015. When the hunter becomes the hunted. *Science 348*:1312-1314.

Table 1. Description of the structure of models of small mammal (SM) and fox track plot use rate and all response and explanatory variables. The maximal model is shown and was carried out in R (v 3.4.2).

Type	Variable	Distribution (link/offset)	Definition
Response	SM activity	Normal (identity)	Prop. Of the 48 grid squares with SM prints
	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)
Explanat-ory	Site	6 sites	Six lowland wet grassland reserves in the East of England
	Time period	Early:middle: late	Early (late March to early April); middle (May); or late (June) for 9 nights each
	Time	10 periods	Consecutive time periods of 9 nights each, from April - July
	Location	Field:verge	Patch location, either within fields or verges outwith fields
	Patch area	Continuous	Area (log 10 transformed) of tall vegetation patches
	Lower sward density	Continuous	Sward density in late season
	Year	3 years	2008-2010
	Start day in season	Continuous	Day after March 1^{st} when track plot was started
	Distance to verge	Continuous	Distance to field edge plus route from focal field gateway to nearest verge avoiding ditches (m)
	Nests within 100 m	Continuous	Number of active lapwing nests which occurred within 100 m of the track plot
	Field area	Continuous	Area of field in which focal track plot located (km^2)
	Surface water	Proportion	Proportion of focal field covered by surface water during use of track plot
Model	Response	Model structure	
1 (Six sites)	SM activity	Site + Time period + Patch area + Lower sward density + (1|Patch/Tunnel)	
2 (Berney)	SM activity	Time + Location +Time*Location + (1|Patch/Tunnel)	
3 (Berney)	SM activity	Time + Patch area + Lower sward density + Time*Patch area (1|Patch/Tunnel)	

(con'd)

4 (Berney)	Fox track plot use rate	Start day + Distance to verge + Nests within 100 m + Field area + Surface water + Start day* Distance to verge + (1|Year)

Table 2. Results of generalised linear mixed models exploring the influence on small mammal activity of Model 1: patch area and sward density at all reserves (controlling for site and seasonal (time period) variation), Model 2: patch location at Berney Marshes (controlling for seasonal variation); and Model 3: patch area and sward density at Berney Marshes (controlling for seasonal variation). Both maximum models and minimal models with R2 are shown.

Model	Fixed effects	X^2	*df*	*p*
1	Site	33.610	5	**<0.001**
	Time period	398.065	2	**<0.001**
	Patch area	0.274	1	0.600
	Lower sward density	0.722	1	0.395
Minimal model				
R^2=60.8%	Site	34.998	5	**<0.001**
	Time period	398.065	2	**<0.001**
2	Time	389.521	9	**<0.001**
R^2=51.4%	Location	43.377	1	**<0.001**
	Time*Location	259.509	9	**<0.001**
3	Time	305.7525	9	**<0.001**
	Patch area	0.0319	1	0.858338
	Lower sward density	11.8139	1	**<0.001**
	Time*Patch area	14.0206	9	0.121594
Minimal model				
R^2=37.8%	Time	304.039	9	**<0.001**
	Lower sward density	15.127	1	**<0.001**

Table 3. Results of generalised linear mixed model (with binomial errors) of Model 4: track plot survival over a nine-night period. Both the maximum model and the minimal model ($R2=19\%$) are shown. Estimates and SE are logits.

Variable	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.511	0.489	-5.131	**<0.001**
Start day	-0.274	0.104	-2.626	**0.009**
Distance to verge	-0.160	0.101	-1.584	0.113
Nests within 100 m	-0.254	0.087	-2.923	**0.003**
Field area	-0.086	0.084	-1.020	0.308
Surface water	0.081	0.101	0.803	0.422
Start day * Distance to verge	-0.108	0.091	-1.191	0.234
Minimal model				
(Intercept)	-2.493	0.475	-5.249	**<0.001**
Start day	-0.328	0.091	-3.608	**<0.001**
Nests within 100 m	-0.258	0.082	-3.130	**0.002**

Fig. 1. The distribution of tall vegetation patches outside fields (black), and within fields (light grey) in which small mammal activity was recorded. The locations of non-surveyed verge vegetation (dark grey) across Berney Marshes and surrounding farmed grassland are also indicated. Fields where fox plots were run for at least one year between 2008 and 2010 indicated by hashed lines, see Figure A1 for details.

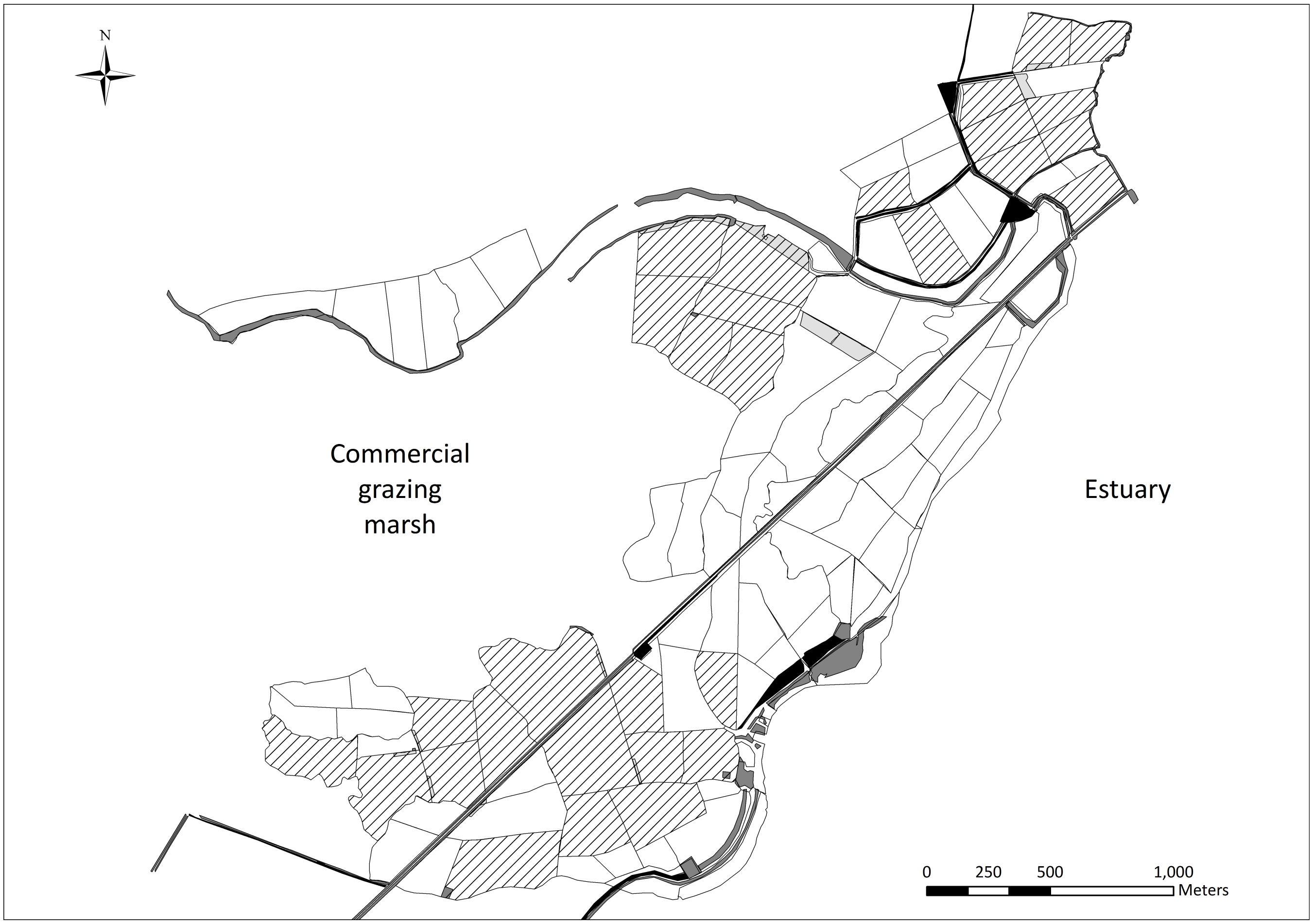


Fig. 2. Small mammal activity (percentage cover of tracking papers with small mammal prints) a) on six wet grassland nature reserves (mean ± SE) during early (open bars), mid (light grey bars) and late season (dark grey bars) and, on tall vegetation patches across these six reserves (Buckenham:!, Cantley:!, Strumpshaw:!, Ouse Washes:!, Nene Washes:!, and Elmley Marshes:!) that vary in b) area and c) ground-level sward density (Table 2 Model 1). d) Seasonal variation in small mammal activity in tall vegetation patches in verges (closed bars) and field edges (open bars) at Berney Marshes, between 27 March and 25 June 2011 (Table 2 Model 2), and small mammal activity across 25 tall vegetation patches varying in e) area, f) ground-level sward density, and located either in verges (closed) or within fields (open) at Berney Marshes (Table 2 Model 3).

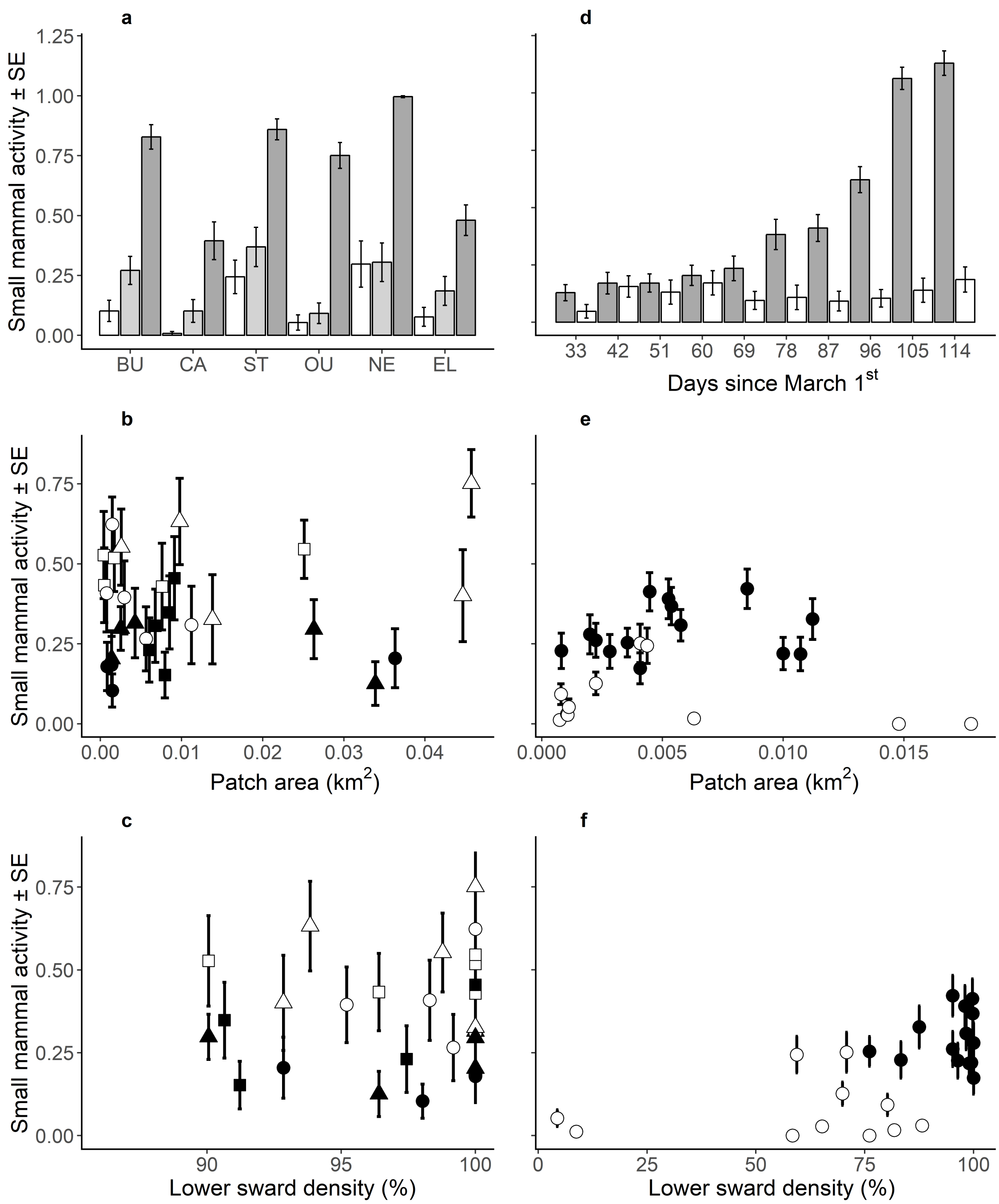


Fig. 3. Numbers of track plots that were (open bars) or were not (grey bars) visited by foxes in relation to a) year, b) days since the 1st March, c) distance to verge, d) number of active lapwing nests within 100 m, e) field area, and f) proportion of field flooded.

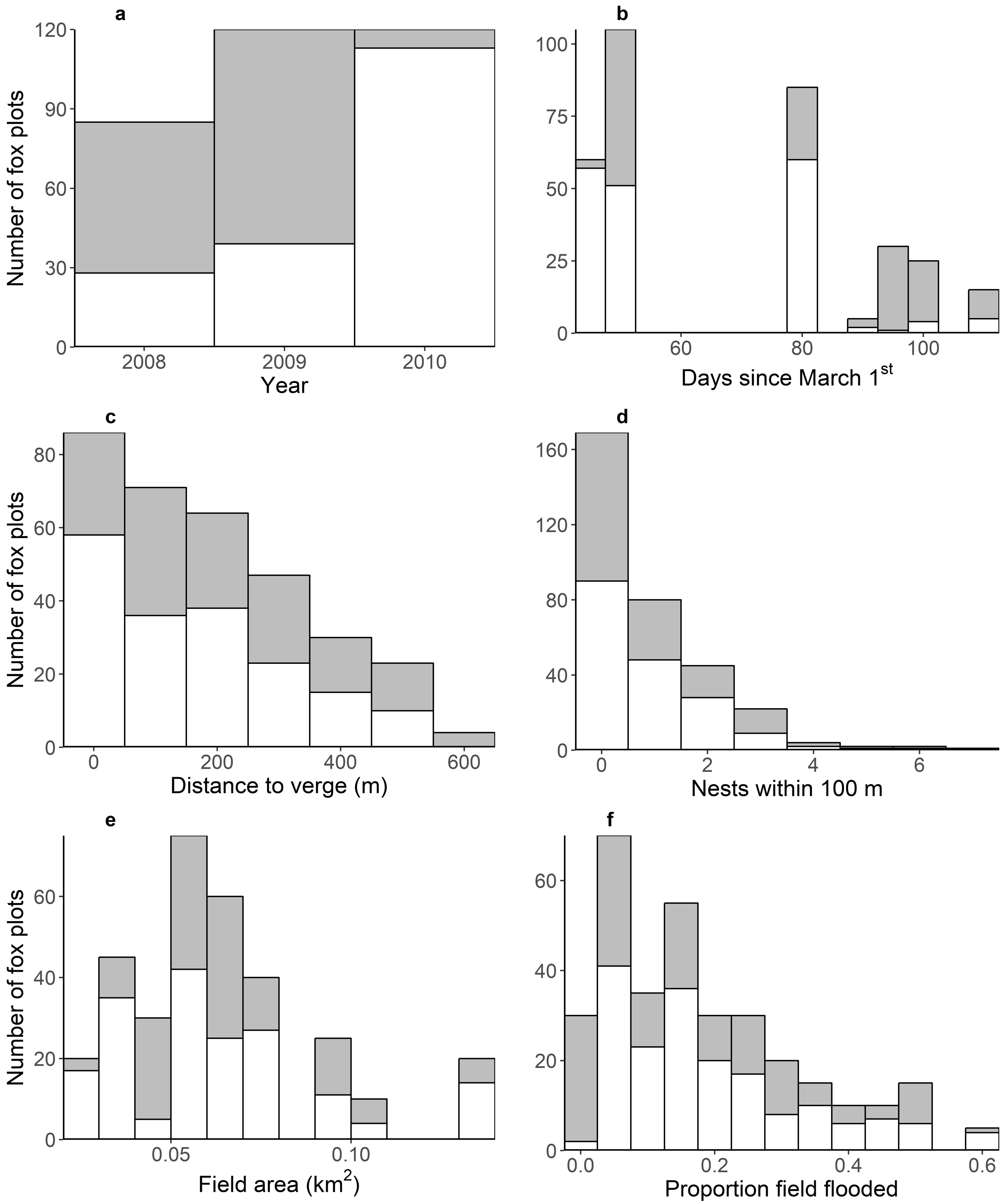
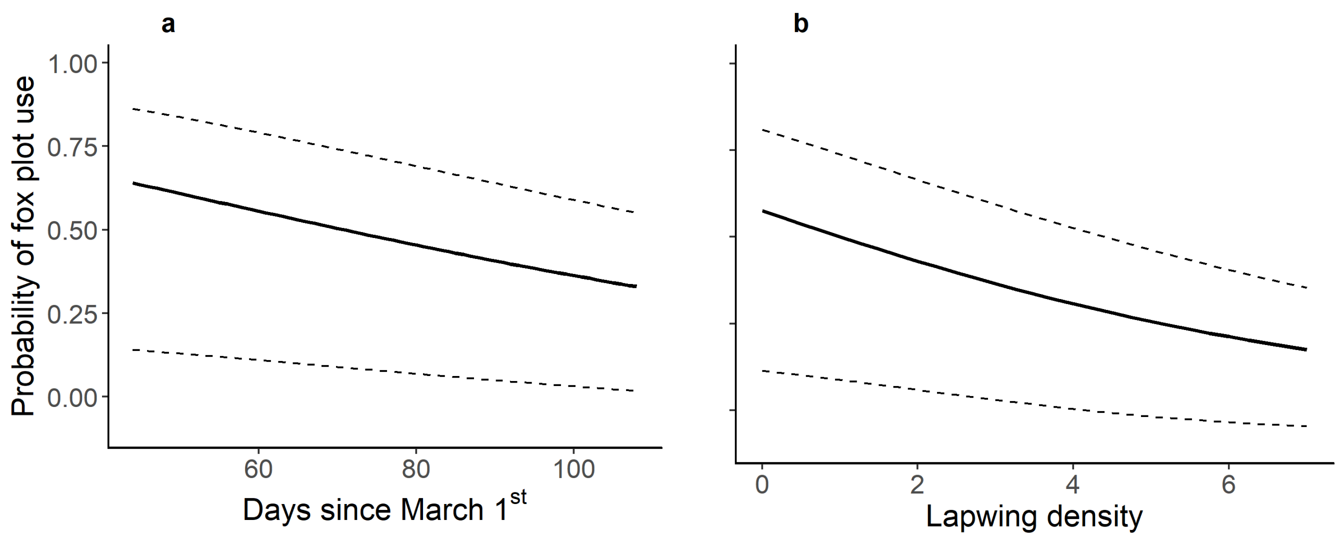


Fig. 4. Changes in the predicted probability of fox use of track plots (± 95% CI) over 9-night study periods with increasing a) time since the 1st of March and b) number of active lapwing nests within 100 m. Predictions used are from models in Table 3.



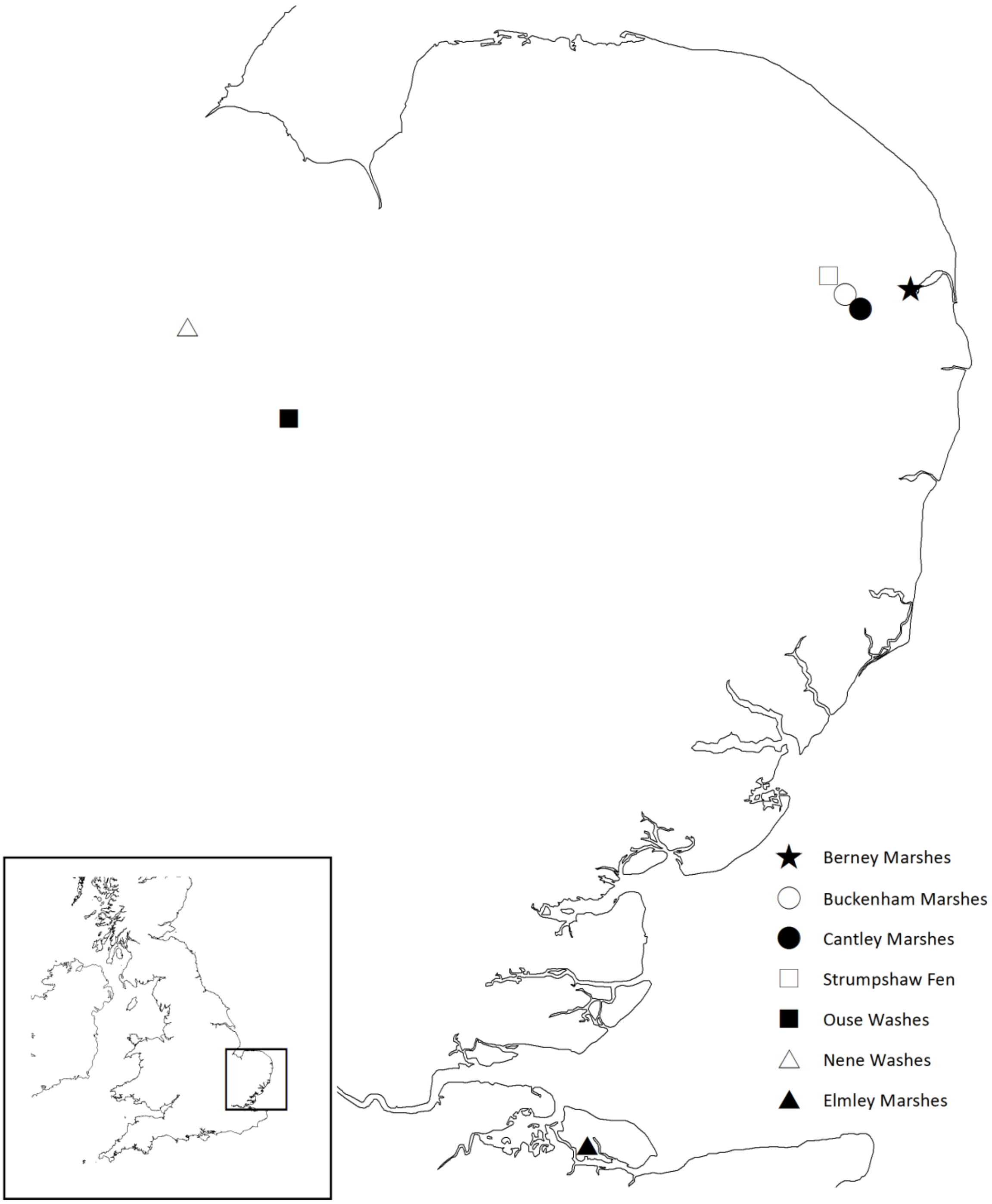


Figure A1 Locations of the seven RSPB-managed (at time of sampling) wet grassland nature reserves in the east of England (inset) used in the study, including the main study site at Berney Marshes.

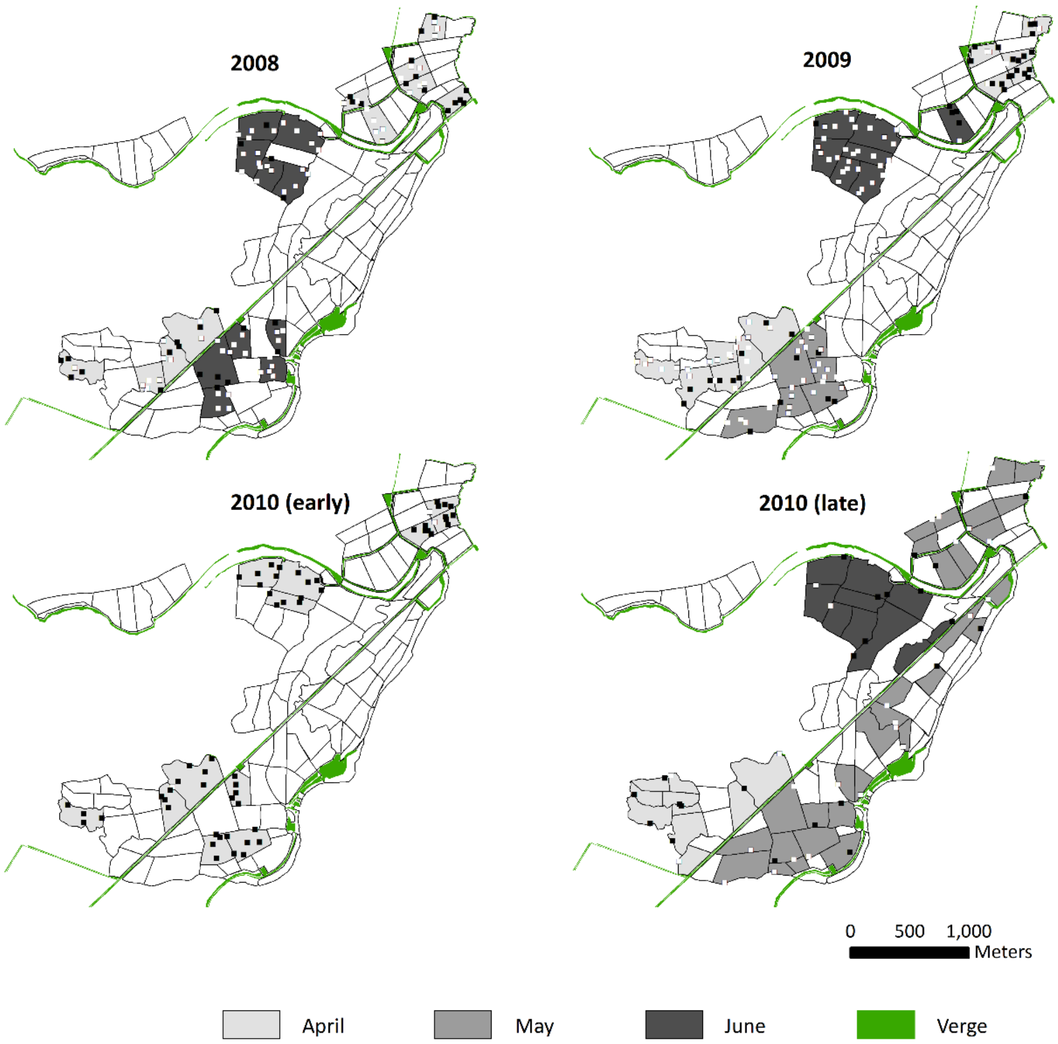


Figure A2 The distribution of track plots that were (▪) and were not (▫) visited by foxes in relation to the month of deployment between 2008 and 2010 at Berney Marshes. Fields in 2010 were sampled twice, all other fields sampled in only one month.