ORIGINAL ARTICLE

Predation of Lapwing *Vanellus vanellus* nests on lowland wet grassland in England and Wales: effects of nest density, habitat and predator abundance

Michael A. MacDonald · Mark Bolton

Abstract There is concern that predation of Lapwing *Vanellus vanellus* nests may create additional pressure on declining populations of this species in Europe. At seven sites in England and Wales, daily nest predation rates on 1,390 nests were related to variables using Generalised Linear Mixed Models. The strongest predictor was Lapwing nest density (number of nests within 100 m): predation rates declined as nest density increased. Since nocturnal species, probably mammals, have been identified as the major predators of Lapwing nests at these sites, these results suggest that Lapwings are able to deter mammalian predators or may settle to nest at high densities in areas with low predation pressure. At the site level, there was no relationship between Lapwing nesting density and fox density, and a positive relationship with Carrion Crow *Corvus corone* nesting density. There was a weaker effect of distance to field boundary: nests closer to boundaries were more likely to be predated. Weak interactive effects between crow density and both nest visibility and distance to vantage point were identified in models using a reduced subset of nests. These were counter-intuitive, did not persist in the larger data set, and do not have obvious explanations. If Lapwings nesting at high density *are* able to deter predators, there are implications for land management. Smaller areas could be managed within potential breeding habitat to encourage Lapwings to nest in dense colonies. Selection of larger fields for such management, where nests could be located far from the field boundary should improve the value of such measures.

Introduction

The population declines of waders breeding on lowland wet grassland habitat in UK are associated with habitat loss and degradation due to agricultural changes such as drainage and intensification of grassland management (Shrubb 1990; Wilson et al. 2004). However, while it is undeniable that appropriate habitat management is necessary to maintain or increase populations of waders, it has been suggested that increased nest predation is a possible additional cause of the declines of wader populations (Bellebaum 2002; Chamberlain and Crick 2003; Milsom 2005). Agricultural intensification may be linked to increased rates of predation on wader nests, as taller swards may compromise anti-predator vigilance, and homogeneous swards may reduce nest crypsis (Whittingham and Evans 2004). In addition, smaller population sizes might result in smaller breeding groups, which may be less able to defend nests against predators.

The decline of Lapwings *Vanellus vanellus* in the UK appears to be driven by reduced productivity, as ringing recoveries indicate that first-year and adult survival have increased in recent decades (Peach et al. 1994). Predation was the major cause of Lapwing nest failure in the 1990s, and constituted over 50% of nest failures in semi-natural habitats (which included wet grassland and other habitats aside from arable and pasture), up from around 30% in the 1960s (Chamberlain and Crick 2003). Other causes of nest

Communicated by F. Bairlein.

M. A. MacDonald (✉) · M. Bolton
Conservation Science, RSPB UK Headquarters, The Lodge,
Sandy SG19 2DL, UK
e-mail: michael.macdonald@rspb.org.uk

losses were destruction by agricultural activities (including trampling by stock), loss caused by weather, and desertion; destruction decreased as a proportion of nest failures in the 1990s.

Nest predator–prey relationships are ecologically interesting because, while nest predation is frequently the most common source of nest failure, eggs are generally relatively unimportant in the predators' diet, and thus nest predation may be incidental during other foraging behaviour (Vickery et al. 1992). Since the density of predators is not regulated by the abundance of nests, predators may apply continuous predation pressure even as prey nesting populations decline. High nest predation rates have been recorded for several wader species on wet grassland or similar habitats at a range of European sites (Green 1988; Grant et al. 1999; Hart et al. 2002; Ottvall 2005; Thyen and Exo 2005). Evidence suggests that wader nests are rarely targeted by their major predators, although they may switch to actively searching for them if alternative prey is scarce (Stillman et al. 2006).

The aim of the current study was to examine potential relationships between Lapwing nest predation rates, nesting densities, habitat features and the densities of two key species that have been implicated as important predators of Lapwing nests: foxes *Vulpes vulpes* and Carrion Crows *Corvus corone* (O'Brien 2001; Stillman et al. 2006). A clearer understanding of the factors influencing nest predation rates is necessary to inform potential habitat manipulations intended to reduce the impact of predators on breeding waders.

Methods

Study sites

Lapwing nests were monitored over the period 1996–2003 at seven sites within two extensive blocks of wet grassland habitat: Aberleri (ABL), Ynys-hir (YNH), Penllyn (PNL), Penmaen Isa (PMI) and Lodge Park Farm (LPK) on the Dyfi estuary, Wales; and two sections of the Ouse Washes (OWA and OWB), England, that were separated by a 2-km section (Fig. 1). During this time, these sites formed part of a predator control experiment, in which foxes and crows were controlled at some sites in some years (Bolton et al. 2007). Where undertaken, fox control (by shooting) occurred from January to June, and crow control (largely through the use of Larsen traps) occurred from March to June. Crow control resulted in a reduction in territorial crows, but not of total crow numbers, while the effects of fox control varied between sites, since some sites had very low fox density even in the absence of lethal control measures (Bolton et al. 2007). There was also evidence that fox numbers declined more over consecutive years of control. Three of these sites are RSPB reserves, and were

Fig. 1 Location of study sites

Table 1 Predictor variables, means, minimums, maximums and quartile values for Lapwing *Vanellus vanellus* nest predation rates

Variable	Name	Count	Mean	SD	Min	25%	75%	Max
Distance (m)								
Vantage	VANT	1,163	77.6	66.9	2	30	100	500
Cover	COVER	1,113	75.3	66.5	0	28	100	400
Bound	BOUND	1,390	52.2	34.2	0	26.7	70.3	212.9
Mean visibility (m)	VIS	820	6.6	2.6	0	5	7.3	24
Field area (ha)	AREA	1,373	11.8	8.8	0.9	5.7	14.0	40.5
Nests within 100 m	M100	1,390	1.72	2.09	0	0	2	15
Fox density (mean no. seen per survey hour)	FOXDENSITY	1,373	0.541	0.668	0	0	0.87	2.6
Crow density (mean no. seen per survey hour)	CROWDENSITY	1,252	1.650	1.917	0	0.29	2.82	6.18

					0–300 m	300–1,000 m	>1,000 m
Distance to nearest crow nest	CROWNEST	1,086			161	309	616

					0–500 m	500–1,000 m	>1,000 m
Distance to nearest fox earth	FOXEARTH	1,390			194	596	600

thus managed in accordance with plans that characterise the operation of lowland wet grassland bird reserves, for which the provision of breeding habitat for waders is a high priority.

Lapwing nest predation

Lapwing nests were located by initially observing Lapwing behaviour from a suitable distance, usually from a vehicle, using binoculars and/or telescope. When behavioural observations indicated the presence of a nest, the area was searched on foot, and the nest marked with a cane placed at least 20 m away to avoid attracting predators (Galbraith 1987). The number of eggs was noted, and nest locations were mapped and grid references recorded. The fate of each clutch was determined by monitoring nests every 3–4 days, recording the number of eggs present each visit, and the number that hatched. Nests were considered to be predated if they were empty before the hatch date (predicted from egg density; Green 1984) and there was no evidence of hatched chicks (tiny eggshell fragments in the nest lining; adults alarm-calling) or of failure due to agricultural activities. For the purposes of the present analysis, nests were considered successful if they were not predated. Nest predation was recorded as a binary outcome (predated, not predated) and the exposure days (number of trials) for each nest was calculated following Mayfield (1961, 1975). In dealing with nests of uncertain outcome, we followed Manolis et al. (2000) calculating nest exposure days as the interval from the location of the nest to the last visit when the eggs were present.

Predictor variables

Variables that were considered potential predictors of nest predation rates were either collected during fieldwork, or were obtained from nest locations and digitised maps created in MapInfo Professional Version 7.8 (Table 1).

An index of nest concealment (VIS) was measured when each nest was first located. The maximum distance from which the nest was visible was recorded in three directions separated by arcs of 120°. The mean of the three values was used as the predictor variable. The area of the field (AREA) in which each nest was located was calculated from MapInfo. During fieldwork, the distances to cover (COVER), typically tall vegetation, such as irises or reeds, and to vantage points (VANT), such as posts, trees or bushes, were recorded.

Following mapping of nest locations and digitising maps of the study sites, we calculated the distance to the field boundary (BOUND), which could be a ditch, riverbank, fence, hedge, or a combination of these. During fieldwork monitoring Lapwing nests, and with the assistance of land managers, fox earths and crow nests were located and mapped: the distances from these to Lapwing nests were calculated using MapInfo following map digitisation (FOXEARTH and CROWNEST, respectively). We placed these into three categories: near (0–300 m for crow nests, 0–500 m for fox earths); moderate (300–1,000 m for crow nest, 500–1,000 m for fox earths); and distant (>1,000 m for both). We used these categories to ensure sufficient cases in each distance class and for biological reasons (foxes are more likely to forage further from dens than crows from nests). Although nests and earths were mapped on each

study site, no data were available on the location of crow nests and fox earths on land adjacent to study sites. On study sites where no fox earths or crow nests were recorded, nests were categorised as distant from earths/nests. It is unlikely that this will have resulted in significant mis-classification of categories, since study sites were located in regions of relatively low fox densities (Webbon et al. 2004), and our surveys recorded low numbers of foxes at these sites.

While the sites in this study were under predator control for some or all of the study period, we were not interested in predator control per se, but the resulting density of predators, regardless of the management regime. Fortnightly surveys of crows and foxes, the suspected major predators of Lapwing nests, were made (Bolton et al. 2007). We used a single figure representing crow and fox density at each site for each year: the number of territorial crows per hour of survey, averaged across all surveys (CROWDENSITY); and the number of adult foxes per hour of survey, averaged across all surveys (FOXDENSITY).

Using the mapped locations of Lapwing nests and data on their period of activity, the number of nests within 100 m of the active nest was calculated in MapInfo as a measure of nest density (M100). This was calculated on a weekly basis, so includes all nests that were concurrent within 1 week

Data analysis

We modelled the daily predation rate of each nest as a binomial trial (predation outcome/exposure days), following the principles outlined by Aebischer (1999) for nest survival analysis. To investigate the contribution of the predictor variables to variation in daily nest predation rate a generalised linear mixed model (GLMM) was fitted to the data, using a binomial error distribution, logit link function, and exposure days as the binomial denominator. Models were implemented using PROC GLIMMIX of the SAS® (v. 9.1) statistical package (Littell et al. 1996), specifying site and site × year as random terms. The potential non-independence of data from sites within each of the two extensive grassland blocks (Dyfi estuary and Ouse Washes) was addressed by the incorporation of a blocking factor into all models.

We anticipated that the habitat features (such as nest crypsis) affecting nest predation rates were more likely to be important in situations where the predator species dependent on such features (in this case, visual predators such as crows) occurred at high density. We therefore included the interactions between predictor variables and both crow density and fox density in the models, in addition to the main effects. We did not fit other interaction effects since they did not represent biologically meaningful hypotheses.

Complete data were available for around one-third of nests, so we examined the fit of two models. The first included nests for which all environmental variables were measured ($n = 505$), for which the maximal model was:

$$\text{Daily predation risk} = \text{BLOCK} + \text{SITE} + \text{YEAR} + \text{VIS}$$
$$+ \text{VANT} + \text{AREA} + \text{M100} + \text{FOXEARTH}$$
$$+ \text{CROWNEST} + \text{COVER} + \text{FOXDENSITY}$$
$$+ \text{CROWDENSITY} + \text{FOXDENSITY} \times (\text{VIS} + \text{VANT}$$
$$+ \text{AREA} + \text{M100} + \text{FOXEARTH} + \text{COVER})$$
$$+ \text{CROWDENSITY} \times (\text{VIS} + \text{VANT} + \text{AREA} + \text{M100}$$
$$+ \text{CROWNEST} + \text{COVER}) + \text{FOXDENSITY}$$
$$\times \text{CROWDENSITY}$$

The second included only those variables that were measured for all (or almost all) nests ($n = 1{,}373$), for which the maximal model was:

$$\text{Daily predation risk} = \text{BLOCK} + \text{SITE} + \text{YEAR} + \text{M100}$$
$$+ \text{AREA} + \text{BOUND} + \text{FOXEARTH} + \text{FOXDENSITY}$$
$$+ \text{FOXDENSITY} \times (\text{M100} + \text{AREA} + \text{BOUND}$$
$$+ \text{FOXEARTH}).$$

BLOCK, SITE and YEAR were forced into the model at all times, except as explained as follows. The minimal adequate model was obtained using a backwards deletion procedure that involved fitting the maximal model, then sequentially removing non-significant interaction effects and non-significant main effects that did not appear in significant interactions, and then refitting the model until no non-significant variables or interactions remained.

Results

Nest predation rate

A total of 1,390 nests were monitored on the seven sites over 20,719 nest exposure days; 451 nests were predated. Mayfield estimates of the proportion of nests surviving to hatching for each site-year indicated a wide variation among site-years, although there was no main effect of site or year in the selected models. Across all sites and years, the daily predation rate was 0.02177 ± 0.001 SE. Assuming 31 exposure days from laying to hatching (Galbraith 1988), the calculated predation rate was 49.5% of nests (95% confidence limits: 46.2–52.5% of nests predated).

Relationships between predictor variables and nest predation

Nest density was the strongest predictor of daily nest predation rate, in both the model using all cases, and the

reduced subset of cases for which all data were available (Tables 2, 3; Fig. 2). The non-significant BLOCK term could not be retained in the final model of the reduced subset of nests, due to limitations imposed by reduced degrees of freedom, and site was specified as a fixed effect due to difficulties with model convergence. Nest predation was less likely for nests that had more Lapwing nests within 100 m ($P < 0.001$). YEAR and BLOCK did not prove to be significant predictors, but were retained in the final models.

In the model using all cases, distance to field boundary was also a significant predictor ($P < 0.05$), with nests further from field boundaries suffering lower rates of predation (Fig. 3). In the model using the reduced number of cases, there was a significant main effect of distance to vantage point, as well as significant interactions between crow density and nest visibility, and crow density and distance to vantage point (all $P < 0.05$). The main effect of distance from vantage point on nest predation rates was negative, but there was a positive interaction between this variable and crow density. Predation rates were lower for nests closer to vantage points when crow density was higher, and higher for nests closer to vantage points when crow density was lower. The main (but non-significant) relationship between nest visibility and predation rate was negative (i.e. more visible nests were more likely to be predated), but the significant interaction between nest visibility and crow density was negative. Predation rates were lower for more visible nests when crow density was higher, and higher for more visible nests when crow density was lower.

Table 2 Model term effects and standard errors, for model containing all cases

Term[a]	Level	Estimate	SE	P
Intercept		−4.3382	0.3978	<0.0001
BLOCK				0.2277
	DYF	0.4211	0.3079	0.2277
	OWW	0	–	–
YEAR				0.1427
	1996	1.0683	0.396	0.0105
	1997	1.1464	0.4012	0.0069
	1998	0.6086	0.4423	0.1749
	1999	0.6263	0.4223	0.1461
	2000	0.4657	0.4300	0.2841
	2001	0.8623	0.4808	0.0800
	2002	0.9221	0.4213	0.0349
	2003	0	–	–
M100		−0.2288	0.03408	<0.0001
BOUND		−0.0033	0.0015	0.0257

[a] See Table 1 for explanation of abbreviations

DYF Dyfi estuary, *OWW* Ouse Washes

Table 3 Model term effects and standard errors, for model containing reduced cases

Term[a]	Level	Estimate	SE	P
Intercept		−4.0441	1.034	0.0003
SITE				0.6128
	ABL	−0.3318	0.8565	0.7017
	LPK	−0.107	0.8208	0.8974
	OWA	−0.6352	0.9162	0.4963
	OWB	0.2597	0.7921	0.7469
	PMI	−0.8086	0.7659	0.3006
	PNL	0.2625	0.8017	0.7463
	YHR	0	–	–
YEAR				0.5640
	1997	0.8673	0.6498	0.1955
	1998	0.2351	0.7221	0.7479
	2000	0.2391	0.6707	0.7245
	2001	0.3909	0.9488	0.684
	2002	0.9939	0.7069	0.1754
	2003	0	–	–
M100		−0.3298	0.06774	<0.0001
VIS		0.09822	0.0634	0.122
VANT		−0.0093	0.00369	0.0123
CROWDENSITY		0.3222	0.264	0.2275
VIS × CROWDENSITY		−0.055	0.02764	0.0474
VANT × CROWDENSITY		0.0042	0.00197	0.0334

[a] See Table 1 for explanation of abbreviations except as below

ABL Aber Leri, *LPK* Lodge Park Farm, *OWA* Ouse Washes A, *OWB* Ouse Washes B, *PMI* Penmaen Isa, *PNL* Penllyn, *YHR* Ynys Hir. See Fig. 1 for locations
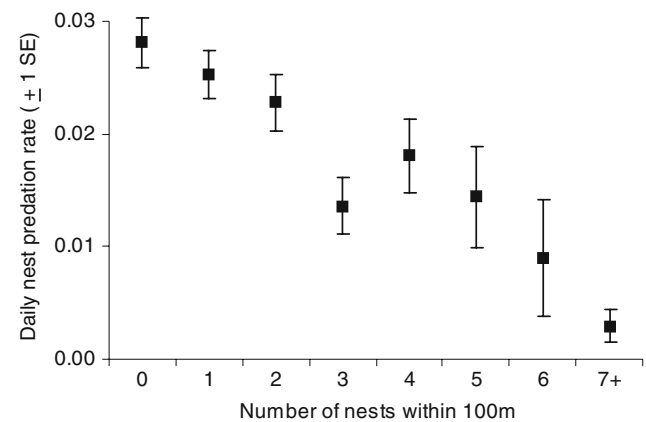

Fig. 2 Daily predation rate according to number of Lapwing *Vanellus vanellus* nests within 100 m

Discussion

Predation rates observed at the sites over the 8-year period indicated that around 50% of nests were lost to predation. This rate is moderate in relation to other studies: the
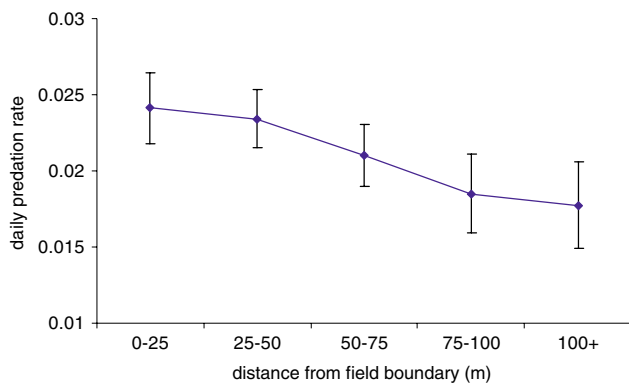
Fig. 3 Daily predation rate (±SE) according to distance from field boundary

median value from 219 other site-years or studies recently reviewed was 57.2% (MacDonald and Bolton, unpublished data). However, in combination with losses to other causes, which in the present study reduced total nest survival to just 37.2%, such levels of nest predation are likely to result in hatching rates that are insufficient to maintain stable populations. The effects of nest failure rates on Lapwing populations, even at the local scale, are difficult to determine, because re-nesting has not been taken into account, and because population trends are strongly influenced by chick survival, adult survival, immigration and emigration (Bellebaum 2001; Bolton et al. 2007). .

Nest density and predation rates

All models showed a strong relationship between nest predation rate and Lapwing nest density. This finding concurs with those of several other studies (Berg et al. 1992; O'Brien 2001; Seymour et al. 2003), although it has not been replicated universally (Galbraith 1988; Sharpe 2006). Our finding could be explained by two separate causal mechanisms. First, Lapwings may be able to deter nest predators by aggressive mobbing behaviour when nesting at high densities. The major predators of ground nesting birds have often been assumed to be avian, because diurnal predation is more frequently observed, from misleading results arising from artificial nest studies (Moore and Robinson 2004), and from observations of mobbing behaviour against birds (which is also diurnally biased) (Elliot 1982; Green et al. 1990; Berg et al. 1992; Sasvári and Hegyi 2000). Avian predators are certainly potential threats to nests, and are probably important as chick predators (Teunissen et al. 2005), which would justify mobbing behaviour. However, based on the assumption that mobbing against other birds is successful (at least sometimes), and that mobbing mammals is rarely successful, a relationship between nest density and predation

rates has been used as at least supporting evidence that avian predation predominates (Elliot 1982; Seymour et al. 2003), even where the identity of predators has not been quantified.

Recent use of nest cameras and temperature data loggers at several European wet grassland (or similar) sites, including those of the current study, have shown that nocturnal/mammalian predation of wader nests is currently more important than diurnal/avian predation (Blühdorn 2002; Olsen 2002; Boschert 2005; Smart 2005; Teunissen et al. 2005; Junker et al. 2006; Bolton et al. 2007). Our finding raises the intriguing possibility that Lapwings nesting in colonies may be better able to defend their nests against predation by mammals, such as foxes, than is commonly supposed. Some studies and anecdotal evidence have indeed revealed that Lapwings will actively mob and/or distract nocturnal predators (D. Isaksson, personal communication; Hodson 1962; Seymour 1999), and they may be more effective than previously thought.

The second explanation of the observed relationship between nest density and predation rate is that Lapwings can identify areas of low predation pressure, and settle in such areas at high densities. There is some evidence to support this hypothesis, since Lapwing breeding densities have been shown to increase from one year to the next in response to the onset of predator control measures (Bolton et al. 2007), which appears to be a behavioural response by Lapwing settling to breed at higher densities as predator densities decline. These two hypotheses are not mutually exclusive: Lapwings may select areas of low predation pressure *and* be more successful at excluding nest predators from such sites. Based on current analysis, it is not possible to differentiate between these alternatives, since no data on predator densities at a field-scale are currently available. However, at a site-scale we found no relationship between annual average Lapwing nesting density (number of nests within 100 m) and fox density (averaged over the wader breeding season, $F_{1,32} = 0.01$; $P = 0.91$). There was a positive relationship between average Lapwing nesting density and Carrion Crow density ($F_{1,34} = 7.98$; $P = 0.0078$, Fig. 4). The latter may reflect nesting decisions by both species relating to invertebrate prey abundance. These analyses at the site level, with predator densities averaged over the entire wader breeding season, are probably not at a suitable spatial or temporal scale to test settling decisions by Lapwings which are made early in the year and probably at the field scale. We recommend that future research focus on measuring predator activity at finer spatial and temporal scales. Nevertheless, based on the data currently available, there is no indication that Lapwings settle at higher densities in sites of low predator abundance.
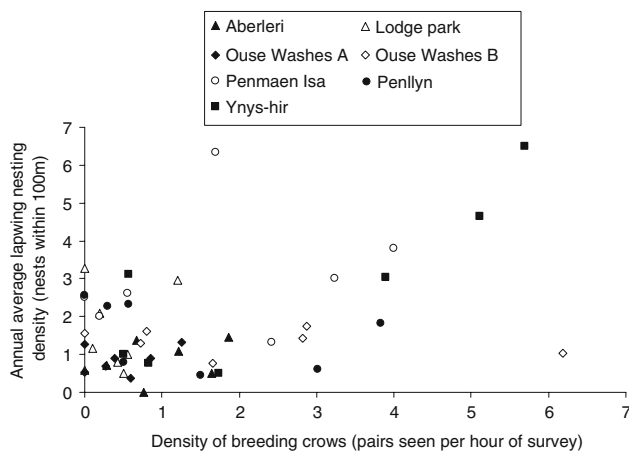
Fig. 4 Relationship between the annual average density of Lapwing nests and breeding Carrion Crows at seven study sites between 1996 and 2003

Habitat variables and predation rates

The second, weaker relationship with nest predation rate was the distance of nests from the field boundary. The finding that nests further from the field edge suffered lower predation rates is common to previous studies of Lapwings nesting in arable habitats (Sheldon 2002; Sharpe 2006), although several studies of wader (including Lapwing) nest predation have not found a relationship with distance to habitat edge and/or linear features (Berg 1996; Seymour 1999; Ottvall et al. 2005). Our finding is probably related to the preferential use of field margins by several predator species for navigation through the landscape and as foraging areas (e.g. foxes hunt voles in rank vegetation commonly associated with field margins), and the use of fences and boundary trees as vantage points. Foxes have been observed following habitat edges and linear features (including bunds, vehicle tracks and the edges of *Glyceria* beds) in wet grassland in Britain (Seymour 1999) and along wetland edges on the Great Plains of North America (Phillips et al. 2004). Chance encounters with nests close to the field edge are therefore likely to be higher than for nests away from the field boundary. The lack of any significant interaction between either fox or crow density and distance from field boundary, indicates that the effect is related to predation by several predator species.

There was some evidence for effects of nest crypsis and distance from predator vantage point on predation rate in smaller subsets of data that did not encompass all site-years. A relationship with distance to vantage points has been found in some previous studies for both Lapwing (Berg et al. 1992; Sheldon 2002) and Black-tailed Godwit *Limosa limosa* (Johansson 2001), though more commonly, researchers have failed to find such an effect (e.g. Valkama et al. 1999; Seymour et al. 2003; Ottvall 2005; Sharpe

2006). The influence of vantage points may also vary according to the densities of predators that use such features (corvids). The majority of sites included in the current analysis were managed primarily for breeding waders, and predator vantage points would have been removed as far as possible as part of the reserve management plan, so the lack of such relationships in the current dataset is not altogether unexpected. Waders tend to select micro-habitat that provides greater concealment than that generally available, but there is often no relationship between nest concealment and predation rates (Grant et al. 1999; Thyen and Exo 2005). The effect of nest concealment may vary with the predator community: concealment is important where visual (avian) predators are most important, but is relatively ineffective against aural/olfactory (mammalian) predators (Colwell 1992). Alternatively, nest concealment may be ineffective if predation is incidental (Vickery et al. 1992). The interaction effects are counter-intuitive (that nest concealment/distance from vantage points becomes less important as crow density increases), and offer no simple biological explanation.

Conclusions and management implications

The findings of the current study have implications for land managers who wish to improve productivity of Lapwings. If Lapwings can deter both avian and mammalian predators when nesting at high densities, nest predation rates could potentially be reduced by habitat management measures to ensure high local nesting density (such as creating limited areas of habitat suitable for nesting at individual sites). Additionally or alternatively, habitat manipulations may be employed to reduce predator densities in areas where Lapwings are encouraged to nest. This may be achieved by reducing the availablility of suitable den/nesting sites. Such habitat management could include the removal of nesting trees or scrub for corvids, removal of den sites (e.g. wooded copses, earth banks) for foxes and predator-proof fences. However, in order to determine the most effective habitat management to reduce predator impacts, more work is needed to establish the factors limiting the densities of key predators. We recommend further data collection, to examine the relationships between local predator density, nesting density and nest predation rate, to determine which of the two hypotheses drives the relationship observed in the current study and elsewhere, or whether both operate.

In addition to the management suggested above, our findings suggest that management of the centres of the largest field to create nesting habitat as far from the field boundary as possible would further minimise nest predation rates. Our inconsistent findings regarding nest concealment, combined with the knowledge that avian

predation is relatively unimportant at these sites, suggests that, while management to reduce availability of vantage points may have some benefits for Lapwing nest success, it has less potential than management that increases Lapwing nesting density.

Zusammenfassung

Prädation von Nestern des Kiebitz (Vanellus vanellus) in feuchtem Grastiefland in England und Wales: Effekte von Nestdichte, Habitat und Prädatorabundanz

Es gibt Bedenken, dass die Prädation von Kiebitznestern zusätzlichen Druck auf die im Rückgang befindlichen Populationen dieser Art in Europa ausüben könnte. An sieben Standorten in England und Wales wurden tägliche Nestprädationsraten für 1390 Nester zu verschiedenen Variablen in Beziehung gesetzt unter Anwendung Generalisierter Linearer Gemischter Modelle. Die stärkste Vorhersagevariable war die Dichte der Kiebitznester (Anzahl Nester innerhalb 100 m): Die Prädationsraten nahmen mit zunehmender Nestdichte ab. Da nachtaktive Arten, wahrscheinlich Säugetiere, als Hauptprädatoren von Kiebitznestern an diesen Standorten identifiziert worden sind, lassen diese Ergebnisse darauf schließen, dass Kiebitze Säugerprädatoren abwehren oder aber in Regionen mit niedrigem Prädationsdruck in hoher Dichte nisten können. Auf Standortebene gab es keinen Zusammenhang zwischen der Dichte von Kiebitznestern und der Fuchsdichte und einen positiven Zusammenhang mit der Dichte von Krähennestern. Es gab einen schwächeren Effekt der Entfernung zur Feldgrenze: Nester, die näher an der Grenze lagen, waren mit höherer Wahrscheinlichkeit von Prädation betroffen. Schwache Interaktionseffekte zwischen Krähendichte und sowohl der Sichtbarkeit der Nester als auch ihrer Entfernung zum Aussichtspunkt wurden in Modellen identifiziert, die nur einen Teil der Nester betrachteten. Diese Interaktionseffekte waren gegen die Intuition, im größeren Datensatz nicht zu finden, und es gibt für sie keine offensichtliche Erklärung. Falls Kiebitze, die in hoher Dichte brüten, in der Lage sind, Prädatoren abzuwehren, hat dies Konsequenzen für das Landmanagement. Kleinere Areale könnten innerhalb potentiellen Bruthabitats gemanagt werden, um Kiebitze dazu zu ermutigen, in dichten Kolonien zu nisten. Die Auswahl größerer Felder für ein solches Management, wo Nester weit entfernt von der Feldgrenze lokalisiert sein können, sollte den Wert solcher Maßnahmen verbessern.

References

Aebischer NJ (1999) Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. Bird Study 46:522–531

Bellebaum J (2001) Breeding success of lapwing Vanellus vanellus at two German wetland reserves: stable numbers in spite of high predation rates. Wader Study Group Bull 96:21

Bellebaum J (2002) Prädation als Gefährdung bodenbrüter Vögel in Deutschland - eine Übersicht (in German with English summary: Predation as a threat to ground-nesting birds in Germany—a review). Ber Vogelsch 39:95–117

Berg Å (1996) Predation on artificial, solitary and aggregated wader nests on farmland. Oecologia 107:343–346

Berg Å, Lindberg T, Kallebrink KG (1992) Hatching success of lapwings on farmland: differences between habitats and colonies of different sizes. J Anim Ecol 61:469–476

Blühdorn I (2002) Bestandsentwicklung und Brutbiologie einer Kiebitzkolonie (Vanellus vanellus) während der Extensivierung ihres Brutgebietes [in German with an English summary]. PhD thesis, Westfälischen Wilhelms-Universitat, Münster

Bolton M, Tyler G, Smith KW, Bamford R (2007) The impact of experimental fox and crow control on lapwing Vanellus vanellus breeding success on wet grassland nature reserves. J Appl Ecol 44:534–544

Boschert M (2005) Analysis of nest losses of the Eurasian Curlew Numenius arquata in the upper Rhine Valley of Baden—a comparison between results from 2000 to 2002 and former periods with focus on predation (in German with an English summary). Vogelwelt 126:321–332

Chamberlain DE, Crick HP (2003) Temporal and spatial associations in aspects of reproductive performance of lapwings Vanellus vanellus in the United Kingdom, 1962–1999. Ardea 91:183–196

Colwell MA (1992) Wilson's phalarope nest success is not influenced by vegetation concealment. Condor 94:767–772

Elliot RD (1982) Nesting dispersion of lapwings in relation to predation and anti-predator defence. PhD thesis, University of Aberdeen

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

Galbraith H (1988) Effects of agriculture on the breeding ecology of lapwings Vanellus vanellus. J Appl Ecol 25:487–503

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

Green RE (1984) Nomograms for estimating the stage of incubation of wader eggs in the field. Wader Study Group Bull 42:36–39

Green RE (1988) Effects of environmental factors on the timing and success of breeding of common snipe Gallinago gallinago (Aves: Scolopacidae). J Appl Ecol 25:79–93

Green RE, Hirons GJ, Kirby JS (1990) The effectiveness of nest defence by black-tailed godwits Limosa limosa. Ardea 78:405–413

Hart JD, Milsom TP, Baxter A, Kelly PF, Parkin WF (2002) The impact of livestock on lapwing *Vanellus vanellus* breeding densities and performance on coastal grazing marsh. Bird Study 49:67–78

Hodson NL (1962) Lapwing's persistent attack on fox. Br Birds 55:590

Johansson T (2001) Habitat selection, nest predation and conservation biology in a black-tailed godwit (*Limosa limosa*) population. PhD thesis, University of Uppsala

Junker S, Düttman H, Ehrnsberger R (2006) Hatching success and chick survival of lapwings (*Vanellus vanellus*) breeding in grasslands with different agricultural management—results of a long-term study in the Stollhammer Wisch (Wesermarsch district, Lower Saxony). Paper presented at *Ökologie und Schutz von Wisenvögeln in Mitteleuropa*, Vechtaer Fachdidaktische Forschungen und Berichte

Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) SAS system for mixed models. SAS Institute, Cary

Manolis JC, Andersen DE, Cuthbert FJ (2000) Uncertain nest fates in songbird studies and variation in Mayfield estimation. Auk 117:615–626

Mayfield H (1961) Nesting success calculated from exposure. Wilson Bull 73:255–261

Mayfield H (1975) Suggestions for calculating nest success. Wilson Bull 87:456–466

Milsom TP (2005) Decline of northern lapwing *Vanellus vanellus* breeding on arable farmland in relation to loss of spring tillage. Bird Study 52:297–306

Moore RP, Robinson WD (2004) Artificial bird nests, external validity, and bias in ecological field studies. Ecology 85:1562–1567

O'Brien MG (2001) Factors affecting breeding wader populations on upland enclosed farmland in northern Britain. Institute of Cell, Animal and Population Biology, University of Edinburgh

Olsen H (2002) Patterns of predation on ground nesting birds. PhD thesis, Royal Veterinarian and Agricultural University, Copenhagen

Ottvall R (2005) Breeding success and adult survival of redshank *Tringa totanus* on coastal meadows in SE Sweden. Ardea 93:225–236

Ottvall R, Larsson K, Smith HG (2005) Nesting success in redshank *Tringa totanus* breeding on coastal meadows and the importance of habitat features used as perches by avian predators. Bird Study 52:289–296

Peach WJ, Thompson PS, Coulson JC (1994) Annual and long-term variation in the survival rates of British lapwings *Vanellus vanellus*. J Anim Ecol 63:60–70

Phillips ML, Clark WR, Nusser SM, Sovada MA, Greenwood RJ (2004) Analysis of predator movement in prairie landscapes with contrasting grassland composition. J Mammal 85:187–195

Sasvári L, Hegyi Z (2000) Avian predators influence the daily time budget of lapwings *Vanellus vanellus*. Folia Zool 49:211–219

Seymour AS (1999) The ecology of nest predation by red foxes *Vulpes vulpes*. PhD thesis, University of Bristol

Seymour AS, Harris S, Ralston C, White PCL (2003) Factors influencing the nesting success of lapwing *Vanellus vanellus* and behaviour of red fox *Vulpes vulpes* in lapwing nesting sites. Bird Study 50:39–46

Sharpe FE (2006) Productivity and population trends of northern lapwing (*Vanellus vanellus*) in Britain. PhD thesis, University of Bath

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

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

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

Stillman RA, MacDonald MA, Bolton MR, Durell SEA, le V dit, Caldow AWG, West AD (2006) Management of wet grassland habitat to reduce the impact of predation on breeding waders: Phase 1. Report to DEFRA. CEH, Winfrith, Dorset

Teunissen W, Schekkerman H, Willems F (2005) Predatie bij weidevogels: Op zoek naar de mogelijke effecten van predatie op de weidevogelstand (in Dutch with an English summary): Sovon Vogelonderzoek Nederland

Thyen S, Exo K-M (2005) Interactive effects of time and vegetation on reproduction of redshanks (*Tringa totanus*) breeding in Wadden Sea salt marshes. J Ornithol 146:215–225

Valkama J, Currie D, Korpimäki E (1999) Differences in the intensity of nest predation in the curlew *Numenius arquata*: a consequence of land use and predator densities? Ecoscience 6:497–504

Vickery PD, Hunter MLJ, Wells JV (1992) Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos 63:281–288

Webbon C, Baker PJ, Harris S (2004) Faecal density counts for monitoring changes in red fox numbers in rural Britain. J Appl Ecol 41:768–779

Whittingham MJ, Evans KL (2004) The effects of habitat structure on predation risk of birds in agricultural landscapes. Ibis 146(Suppl. 2):210–220

Wilson AM, Ausden M, Milsom TP (2004) Changes in breeding wader populations on lowland wet grasslands in England and Wales: causes and potential solutions. Ibis 146(Suppl. 2):32–40