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The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves

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Summary

1. Whilst the widespread declines in breeding grassland waders in many parts of Europe have been associated with changes in agriculture, there is concern that predation may compromise recovery of wader populations, even in situations where habitat is suitable, such as nature reserves managed for breeding waders.
2. An 8-year cross-over experiment was used to examine the effect of red fox *Vulpes vulpes* and carrion crow *Corvus corone* control on breeding performance and population trends of lapwing *Vanellus vanellus* on 11 lowland wet grasslands.
3. Predator densities in the absence of control measures were highly variable among sites, and consequently the numbers of predators removed were similarly variable. Overall, predator control measures resulted in a 40% decline in adult fox numbers and a 56% reduction in territorial crows.
4. There was no overall effect of predator control on the failure rate of 3139 lapwing nests. However, the effect of predator control varied significantly among sites, reflecting the variation in predator densities. Predator control measures were more likely to result in increased nest survival at sites where predator densities were high.
5. Nest-temperature loggers deployed at seven sites indicated that 88% of nest predations occurred during darkness, suggesting nocturnal mammalian predators.
6. At seven sites predator control had no overall effect on chick survival, monitored by radio-tracking 459 chicks, but there were differences in the effect of predator control among sites. Densities of predators were low during years without predator control measures at the majority of these sites.
7. At six further sites breeding success, assessed from the proportion of adults accompanied by young late in the season, was twice as high in years when predators were controlled.
8. There was no overall effect of predator control on lapwing population trends across the experimental sites.
9. *Synthesis and applications*. This study highlights the need for information on predator densities and the impact of predators on nest and chick survival, before embarking on predator control measures at a particular site. A decision tree for determining the circumstances in which fox and/or crow control may be both necessary and effective is recommended.

Key-words: breeding lapwing, chick survival, crow, fox, nest success, predation, predator control

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Introduction

The loss and degradation of many important bird habitats in lowland Britain has resulted in population declines and range contractions in a number of species (Gibbons *et al*. 1993; Fuller *et al*. 1995; Chamberlain *et al*. 2000). For example, four breeding wader species have undergone severe declines on lowland wet grassland habitats during the last few decades (lapwing, snipe *Gallinago gallinago*, curlew *Numenius arquata* and redshank *Tringa totanus*, Wilson *et al*. 2005). In lowland wet grassland habitats, these species are now

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primarily restricted to nature reserves and sites managed for birds within agri-environment schemes (Ausden & Hirons 2002). Although the timing of these declines coincides with a period of increase in a number of their avian predators, such as carrion crows *Corax corone* and magpies *Pica pica* (Gregory & Marchant 1996), declines in wader populations are considered to be driven primarily by changes in agricultural grassland management in the UK, particularly improved drainage and increased use of fertilizers (Baines 1988, 1989; Chamberlain *et al*. 2000; Wilson *et al*. 2001). These diminished populations might be more vulnerable to predation than previously, and predation may be restricting breeding densities possibly leading to further declines and local extinction. For example, some studies have shown that the nests of lapwing breeding as isolated pairs or at low densities are more likely to suffer predation compared with those breeding at high densities or in large colonies (Elliot 1985; Berg *et al*. 1992; Seymour *et al*. 2003). However, this is not a universal finding (see Galbraith 1988) and is likely to depend on the predator species involved. Conservation management of wet grassland outside nature reserves, through agri-environment schemes such as the Environmentally Sensitive Areas and Countryside Stewardship, has so far failed to reverse population declines in the UK (Ausden & Hirons 2002; Wilson *et al*. 2005). In this context, predator control may be necessary as a short-term measure, to enable populations of prey species to increase.

To date, most experimental studies of the role of predators in determining bird densities and productivity have been restricted to gamebirds and waterfowl (Newton 1993; Côté & Sutherland 1997). In these cases, the objective of predator control is usually to produce a 'harvestable surplus' of birds in the autumn and winter for sport shooting. Whilst predator control for game management can be effective in increasing the size of the postbreeding population of target species such as grey partridge *Perdix perdix* and may also lead to an increase in the size of the breeding population (Tapper *et al*. 1996; Reynolds & Tapper 1996), the role of predators in avian population limitation generally, is less clear (Newton 1993, 1998; Côté & Sutherland 1997; Evans 2004). Comparatively few studies have examined the effect of predation on the population dynamics of wader species (Hill 1988; Parr 1993; Byrd *et al*. 1994), although there is evidence to suggest that in some areas nest predation rates of species such as curlew are sufficient to account for the observed population decline and would certainly prevent recovery (Grant *et al*. 1999). A review by Newton (1993) found that predator removal resulted in improved nest survival in 23 of 27 studies, increased postbreeding population size in 12 of 17 studies, and increased breeding numbers in 10 of 17 studies. A meta-analysis of 20 predator control studies published up to 1995 (Coté & Sutherland 1997), including many included in the earlier review by Newton (1993), concluded that whilst predator control generally resulted in significant increases in nest survival and postbreeding population size of the prey species, the increase in the size of the subsequent breeding population did not attain statistical significance. Whilst predator control may consistently increase annual breeding performance, the effect on populations is less uniform.

The aim of this study was to assess the impact of fox and crow control on the productivity and population size of breeding lapwing *Vanellus vanellus*. Of the common breeding waders of wet grassland, the lapwing was selected for this work because its breeding ecology has been well studied and lapwing nests are placed in sparse vegetation which makes them both vulnerable to predators and relatively simple to locate and monitor for research purposes. In common with other wet grassland wader species, the lapwing has suffered a considerable decline in recent decades in response to changes in agricultural practice (Wilson *et al*. 2001). Between 1987 and 1998, the declines have been most severe in Wales (77%) and south-west England (64%, Wilson *et al*. 2001), and the species is currently on the Amber list of Birds of Conservation Concern (Gregory *et al*. 2002). In many areas in the west and south-west of Britain, lapwing breeding populations are highly fragmented and vulnerable to local extinction (Gates & Donald 2000). In England and Wales, the highest breeding concentrations generally occur within nature reserves that are managed specifically for breeding waders (Ausden & Hirons 2002), and this study was carried out in the context of nature conservation management of lowland wet grassland reserves in the UK. However, even in such situations, losses of clutches and young to predators may be considerable, and populations may be prevented from increasing due to high losses to predators. In consequence, control of predator species has been proposed as a reserve management tool to enable populations of waders such as lapwing to increase and/or provide a source of fledged young to recruit into surrounding areas.

Predator control focused on foxes and carrion crows since these species are known to be important predators of wader nests and young (Green *et al*. 1987; Cotgreave 1995). Neither stoat *Mustela erminea* nor weasel *Mustela nivalis* were included in the experiment due to the difficulties involved in trapping these species on grassland and the risk of killing water voles *Arvicola terrestris* in traps located along ditches. This study does not therefore address the general issue of lapwing population limitation by all its predators, but examines the practical conservation benefit, at a site-scale, of levels of predator control that would be achievable on nature reserves in the UK, using legal and humane methods.

Methods

STUDY SITES

In order to test the general applicability of predator control measures as widely as possible, a large number of lowland wet grassland sites in the UK were selected for study, covering a wide geographical area (see Fig. S1 in Supplementary material). They differed in the range of predator species present and predator densities held. In keeping with the overall nature conservation aims of the study sites, routine habitat management was carried out over the course of the 8-year experiment according to the site-specific management plans, to produce the sward structure and hydrological conditions appropriate for breeding lapwing. This investigation constitutes an evaluation of predator control measures in the context of the suite of ongoing habitat management practices that characterize the operation of lowland wet grassland reserves managed for breeding waders in the UK.

Experimental protocol

Experimental control of foxes and carrion crows was carried out over an 8-year period (1996–2003) at 11 sites in England and Wales (Ouse Washes, southern section (TL466845); Aberleri (SN612916); Penmaen Isa (SN678981); Penllyn (SN588989); Ynys-hir (SN679964); West Sedgemoor (ST361258); Pulborough Brooks (TQ054170); Old Hall Marshes (TL975125); Elmley Marshes (TQ965675); Malltraeth Marsh (SH452718) and Berney Marshes (TG466055). At each site predator control was implemented for four consecutive years, and matched with four consecutive years without predator control. The order of presentation of these two treatments was allocated among sites such that five sites (Aberleri, Berney Marshes, Penmaen Isa, Pulborough Brooks and West Sedgemoor) underwent 4 years (1996–99) of predator control followed by 4 years (2000–03) without, whilst the reverse applied to six sites (Elmley, Malltraeth, Old Hall Marshes, Ouse Washes (southern section), Penllyn and Ynys-hir). Treatments were assigned at random within England and Wales. At two further sites (Lodge Park (SN652939) and Ouse Washes (northern section) (TL515910), predator control was carried out for the entire 8 years of the study. The northern section of the Ouse Washes was separated by a 2-km buffer zone from the southern section. Data on lapwing nest survival were also collected from an additional 11 lowland wet grassland sites where experimental predator control was not carried out, in order to obtain information on the range of nest survival values experienced across a large number of reserves and its annual variation. The reserves were: Cantley Marshes TG372035, Buckenham Marshes TG353050, Dungeness TR067185, Exeminster marshes SX960870, Inner Marsh Farm SJ270770, Marshside SD355203, Minsmere TM474672, Nene Washes TL294995, North Warren TM460590, Northward Hill TQ781763, and Otmoor SP563138.

Project management

For a study of this scope, a large number of people were necessarily involved in collection and collation of data. In order to standardize field procedures, data collection and reporting, a detailed manual was produced before the onset of fieldwork, describing the field methods to be adopted and including standard reporting forms. A meeting of all staff was held after each field season to provide an opportunity to verify the adequacy of the field protocols and ensure standardization of their application across all study sites.

Predator control methods and data collection

In England and Wales foxes can be controlled at any time of year by legally approved methods. For all sites except one (Pulborough Brooks) a local professional gamekeeper was contracted to carry out this work to ensure the highest standards of marksmanship. Control was carried out at night from a vehicle in strict accordance with all legal and welfare requirements. A spotlight was used to locate foxes, which were shot with a high-powered rifle. Control was carried out from the beginning of the year to the end of June, with most activity between February and April. It has been suggested (Reynolds 2002) that effort invested in fox control early in the winter is largely wasted since a large proportion of the animals killed at this time of year are itinerant individuals, many of which either will not survive to the following spring or will move on to another area. By conducting fox control at the beginning of the year we aimed to optimize its impact and remove animals likely to be resident in the area. The aim was to reduce the number of foxes on each site during the critical lapwing nesting and chick-rearing period (mid-March to mid-July), rather than reduce the level of the fox population year-round. The number of fox control sessions and the number of foxes killed each year on each site were recorded. Every 2 weeks, an independent assessment of the number and age (adult or cubs) of foxes at each site was made (by reserve or research staff) at night from a vehicle using a high-powered spotlight.

Carrion crows were trapped from March until June with Larsen cage traps (Anonymous 1994), which use a decoy crow to attract other birds to enter a cage through a trap door. Since Larsen trapping of crows is only really effective for territorial birds, it can only be used from March onwards, once crows have become territorial. Traps were operated in strict accordance with legal welfare requirements, especially in relation to the well-being of the decoy bird. Carrion crows were also shot but the total killed this way was small, amounting to less than 3·5% of the total. The number of Larsen trap-days operated in each season was recorded for each site, together with the total number of birds trapped and shot. The number of crows on each site was assessed by counting the number seen from a fixed transect each fortnight. Since Larsen traps target territorial crows, survey workers differentiated between observations of territorial pairs and non-breeding groups of carrion crows. Survey duration was recorded so that crow numbers could be analysed in terms of the numbers seen per hour.

LAPWING BREEDING SUCCESS DATA COLLECTION

Nest survival

At all 24 sites data were collected on survival rates and causes of failure of lapwing nests. Nests were located by observing lapwing behaviour from a distance, usually from a vehicle, using binoculars and/or telescope. When observed lapwing behaviour 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 recorded and, for sites in Wales and on the Ouse Washes, weighed and measured to determine the likely hatching date (Green 1984; Galbraith & Green 1985) to facilitate subsequent ringing and radio-tagging chicks (see below). The fate of each clutch was monitored every 3–4 days, recording the number of eggs present and the number of chicks hatched. Clutch fate and the cause of nest failure (predation, flooding, trampling or desertion) were determined by reference to a set of standard criteria contained in the manual of methods provided to all fieldworkers. Nests were considered successful if at least one egg hatched. Hatching success (the proportion of nests surviving the 31 days from clutch initiation to hatching, Galbraith 1988) was calculated from Mayfield estimates of daily survival rate (Mayfield 1961, 1975). In dealing with nests of uncertain fate, 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. At the five sites in mid-Wales and the two areas of the Ouse Washes, the timing of nest predation was recorded at a sample of nests using thermistor probes inserted into lapwing nest cups. The thermistors recorded nest-temperature every 5 min to a data logger (Gemini Data Loggers (UK) Ltd, Chichester, '*Tiny-Talk logger*') buried in the ground approximately 0·5 m from each nest cup. The time of day at which the predation event occurred was determined from the nest temperature profile, which showed the final cessation of ongoing incubation routines as the nest contents deviated substantially and irreversibly from normal incubation temperature. Data on the time of day at which nest predation events occurred were used to infer the type of predator involved (mammalian or avian) since no common avian lapwing nest predator is active at these sites during darkness.

Chick survival

At the five sites in mid-Wales and the two areas of the Ouse Washes, the daily survival rate of chicks was assessed by radio-tracking. Since chick survival rates were likely to be age-dependent, it was important to collect data over the entire period up to fledging. Weight constraints on the size of tag that could be attached to newly hatched chicks resulted in a tag life shorter than the duration of the fledging period. It was therefore necessary to tag part-grown chicks as well as hatchlings. The majority of chicks were ringed on hatching and were of known age. A small number (18/459) of chicks that were tagged part-way through the fledging period had not been ringed on hatching, so age was estimated from the regression of age on bill length of known-age chicks. Radio-tags were backpack mounted (Kenward 1987), under licence, using rubber-solution glue and a lint pad. The location and status of radio-tagged chicks was verified every 2–3 days using a handheld Yagi antenna (Biotrack Ltd, Wareham, UK) and Telonics TR4 or ATS R2000 scanning receiver (Telonics, Inc. Arizona, USA).

Lapwing population size and breeding success

At all sites where experimental predator control was carried out, the size of the lapwing breeding population was determined each year using a standard survey technique (O'Brien & Smith 1992). For those sites where chicks were not radio-tracked, breeding success was assessed from the number of adult lapwing with broods late in the breeding season. Since the behaviour of breeding lapwing changes markedly when they have hatched young (Cramp & Simmons 1983), the number of adults accompanied by broods can be readily determined. The number of adult lapwings with young was expressed relative to the size of the breeding population to provide an index of breeding success per female.

DATA ANALYSIS

The analysis of nest and chick survival data follow the principles outlined by Aebischer (1999). Except where otherwise stated, a generalized linear mixed model (GLMM), implemented using the GLIMMIX macro of the SAS® (v. 8·2) statistical package (Littell *et al.* 1996), was used to investigate the effect of predator control measures, selecting the most appropriate error distribution and link function in each case. Details of individual models are given below. Predator control treatment was considered as a categorical variable (0,1) and fox and crow numbers were aggregated at the site-year level for analysis of the impact of control measures. The terms *site* and *site*treatment* were specified as random effects. Significance testing of fixed effects was derived from Wald's F, examining the P-value associated with each term, when included in the null model containing only significant terms. The significance of the site*treatment effect was accomplished by examining the change in –2 log-likelihood between the two models that incorporated all other significant variables and differed only in this random term. The significance of the change in –2 log likelihood was assessed by the chi-squared statistic with one degree of freedom (Littell *et al.* 1996). The potential non-independence of data from the cluster of five study sites around the Dyfi estuary in mid-Wales and the two areas of the Ouse Washes was addressed by the incorporation of a blocking factor into all models. In most cases the block effect was non-significant, indicating independence of data from clustered sites, but was retained in all analyses.

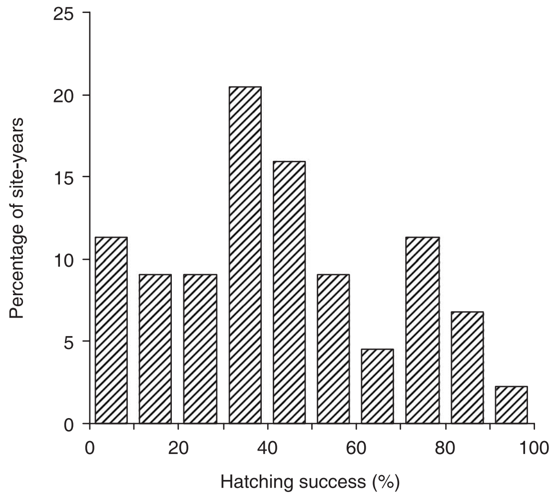

Fig. 1. Frequency distribution of lapwing hatching success (percentage of nests surviving to hatching) at 11 sites that did not undergo predator control measures during 1996–2003. Hatching success was calculated for each site-year.

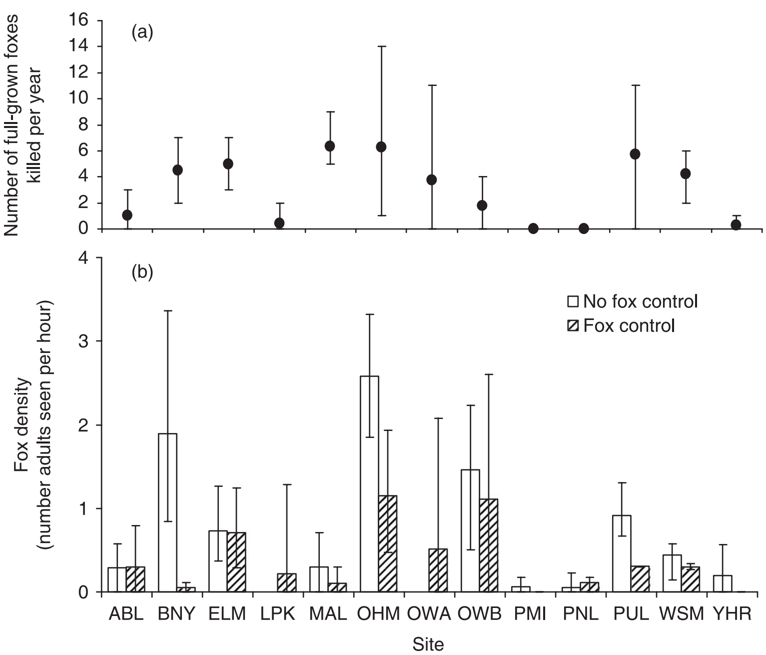

Fig. 2. (a) Number of full-grown foxes killed each season (mean of four seasons ± range over four seasons). (b) Number of adult foxes seen per hour of survey, during years with and without predator control for each study site (mean of four annual survey means, error bars indicate minimum and maximum annual means). Note that predator control was maintained throughout the 8-year study period at Lodge Park and Ouse Washes northern section. Study site codes: Aberleri ABL; Berney BNY; Elmley ELM; Lodge Park Farm LPK; Malltraeth MAL; Old Hall Marshes OHM; Ouse Washes northern section OWA; Ouse Washes southern section OWB; Penmaen Isa PMI; Penllyn PNL; Pulborough Brooks PUL; West Sedgemoor WSM; Ynys-hir YHR.

Results

VARIATION IN NEST SURVIVAL AMONG SITES AND YEARS

In total, 1304 nests were monitored on the 11 sites where no experimental predator control measures were undertaken between 1996 and 2003. Mayfield estimates of the pecentage of nests surviving to hatching for each site-year indicate a wide variation in nest survival to hatching among site-years (Fig. 1). A Type 3, fixed effects binomial errors GLM indicated significant differences among sites and years in daily nest failure rates and significant interaction ($\chi^2_{10} = 77{\cdot}47$ $P < 0{\cdot}0001$, $\chi^2_7 = 61{\cdot}93$ $P < 0{\cdot}0001$, $\chi^2_{26} = 111{\cdot}31$ $P < 0{\cdot}0001$, respectively). Nest failure rates were significantly higher in 1998 and 2000 than in all other years: these two years were associated with high spring flood levels at some sites.

PREDATOR CONTROL: EFFORT AND EFFICACY

The numbers of foxes and crows killed each year and the effect of this level of predator removal on fox and crow numbers is shown for each site in Figs 2–5. The impact of predator control on the number of adults foxes seen per hour varied across sites ($\chi^2_1 = 12{\cdot}32$ $P < 0{\cdot}001$) with a 40% overall reduction in numbers (Fig. 2, $F_{1,9{\cdot}46} = 5{\cdot}14$, $P = 0{\cdot}048$). Although fox control was not usually initiated until February, there was a clear reduction in fox numbers by the beginning of March (Fig. 3).

The reduction in territorial crow numbers, which averaged 56%, was consistent over all sites (site*treatment interaction non-significant $\chi^2_1 = 1{\cdot}48$ $P = 0{\cdot}45$), and highly significant ($F_{1,87{\cdot}8} = 36{\cdot}52$, $P < 0{\cdot}0001$, Poisson error structure, log link, log survey duration included as an offset). Conversely, crow control measures did not result in a significant reduction in total crow numbers ($F_{1,85{\cdot}5} = 0{\cdot}16$, $P = 0{\cdot}69$), indicating a compensatory influx of birds replacing those removed.

There was evidence of a cumulative effect of predator control over the four years on fox densities: the number of adult foxes seen per hour of survey declined significantly with the number of consecutive years of predator

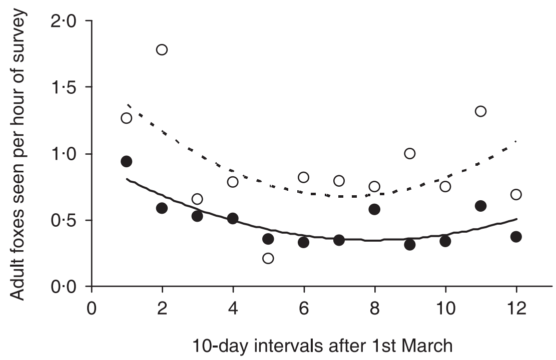

Fig. 3. Seasonal reduction in fox numbers resulting from fox control (filled circles). For details on the timing of fox control operations see Methods. The quadratic regressions are shown.

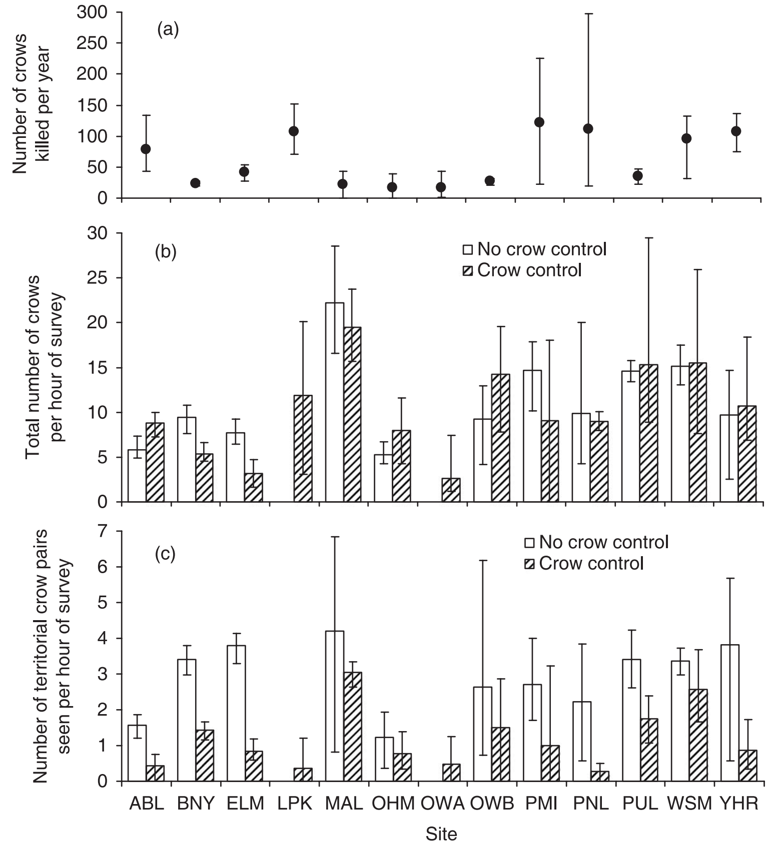

Fig. 4. (a) Number of crows killed each year (mean ± range over 4 years) for each study site. (b) Total number of crows seen per hour of survey, during years with and without predator control for each study site (mean of four annual survey means, error bars indicate minimum and maximum annual means). (c) Number of territorial pairs of crows seen per hour of survey, during years with and without predator control for each study site (mean of four annual survey means, error bars indicate minimum and maximum annual means). Site codes as Fig. 2.

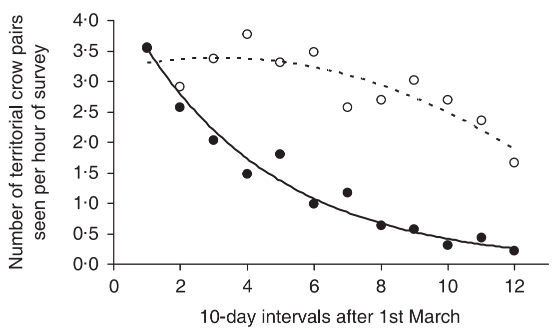

Fig. 5. Seasonal reduction in territorial crow pairs resulting from crow control (filled circles). For details on the timing of crow control operations see Methods. The quadratic regressions are shown.

control ($F_{1,33\cdot8} = 12\cdot80$, $P = 0\cdot001$). Whilst the number of territorial crows seen per hour of survey also declined over the course of the four years of control, the effect was not significant ($F_{1,36\cdot3} = 2\cdot67$, $P = 0\cdot11$, Poisson errors, log survey duration as offset for both models).

In view of the high degree of variation among sites in the number of foxes killed during the control operations, we examined the factors potentially determining the number of full-grown animals killed per season. The yearly total of full-grown foxes killed at each site was more closely related to the number of spotlight fox control sessions ($F_{1,30\cdot3} = 25\cdot09$, $P < 0\cdot0001$) than the number of foxes seen per hour of survey ($F_{1,48\cdot7} = 3\cdot84$, $P = 0\cdot056$). Intriguingly, the number of crows trapped per season was not related to the density of territorial birds $F_{1,34\cdot4} = 0\cdot70$, $P = 0\cdot41$, or trapping effort (trap-days per season, $F_{1,40\cdot4} = 2\cdot64$, $P = 0\cdot11$), but rather to the density of non-territorial birds ($F_{1,50\cdot4} = 7\cdot49$, $P = 0\cdot009$). The relationship with non-territorial birds may result from a greater tendency for breeding birds to challenge decoy birds in Larsen traps in situations where frequent territory defence is required, due to high densities of non-territory holders.

EFFECT OF PREDATOR REMOVAL ON LAPWING NEST SURVIVAL

During the course of the 8-year experiment, a total of 3139 nests were monitored at the 13 sites where predator control was conducted. The effect of predator removal on nest survival was highly variable among sites (Fig. 6). Whilst some sites showed increases in the proportion of nests surviving to hatching during years of predator control (e.g. Berney and Elmley), others showed reductions in hatching success of a similar magnitude during years of predator control (e.g. Aberleri and Pulborough). To further investigate lapwing response to predator control, we tested the hypothesis that the differential response among sites might be due to variation in predator densities in the absence of predator control measures ('background' predator densities). Some reserves had very low background densities of predators (especially foxes), and at such sites, very few predators were removed, so lapwing nests would be exposed to similar, low densities of these predators under both experimental treatments. To test this hypothesis, a Type 3 binomial errors mixed model of nest survival was developed, using a logit link and the number of days each nest was observed as the binomial denominator. The following explanatory variables were included: year; treatment; blocking factor, background fox density; background territorial crow density; background fox density*treatment and background territorial crow density*treatment, with site and site*treatment as random factors. The model indicated that the effect of predator control measures on nest failure rates was a function of the background densities of both adult foxes and territorial crows (background fox density*treatment $F_{1,6\cdot74} = 8\cdot73$, $P = 0\cdot022$; background territorial crow density*treatment $F_{1,5\cdot61} = 10\cdot99$, $P = 0\cdot018$) and that when these effects were controlled for, there was a significant overall improvement in daily nest survival rate in relation to predator control (Fig. 7, $F_{1,8\cdot30} = 13\cdot24$, $P = 0\cdot006$). There was significant variation among sites in the magnitude of the effect of predator control on nest survival (site*treatment interaction

χ^2_1 = 14·10, P < 0·001) but no consistent variation among years in nest failure rates ($F_{7,47}$ = 1·09, P = 0·39), and the blocking factor accounting for the aggregation of sites in Wales was not significant, although it was retained in the final model ($F_{1,6\cdot79}$ = 0·08, P = 0·79).

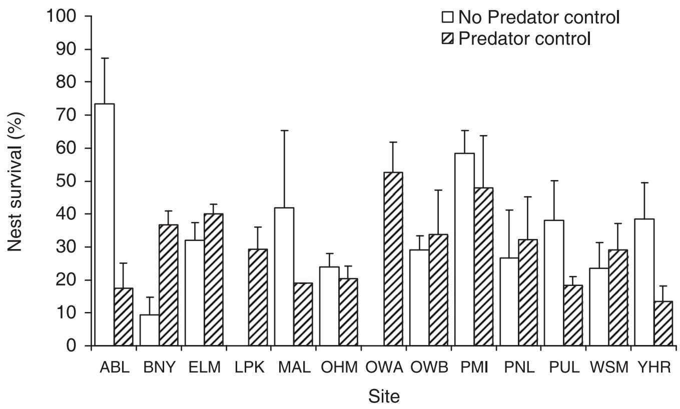

Fig. 6. Effect of fox and crow control on lapwing nest survival on lowland wet grassland reserves. Bar heights are the means of annual values +1 SE. Site codes as Fig. 2.

IDENTITY OF PREDATORS OF LAPWING NESTS

Significantly more nest predation occurred during the hours of darkness (indicative of mammalian predator species) than during daylight (Table 1, χ^2_1 = 28·27, P < 0·0001), but there were no differences in the proportion of nocturnal predation events occurring on the Ouse Washes, compared with the sites in Wales (χ^2_1 = 0·58, P = 0·44).

EFFECT OF PREDATOR REMOVAL ON LAPWING CHICK SURVIVAL

A mixed model of daily chick mortality rates (chick identity as a random factor, site modelled as a fixed effect) showed a significant negative relationship with chick age ($F_{1,4295}$ = 4310·08, P < 0·0001) and consistent differences among years ($F_{7,337}$ = 6·73, P < 0·0001). There were differences in chick survival rates among sites ($F_{6,336}$ = 3·81, P = 0·0011) and significant variation in the effect of predator control among sites (site*treatment interaction $F_{4,337}$ = 6·36, P < 0·0001, but there was no consistent effect of predator control measures on daily chick mortality ($F_{1,336}$ = 1·61, P = 0·20). It was not possible to incorporate the blocking term in this model, but a second model, fitting the blocking factor in place of site, produced the same main effects detailed above. The lack of any overall effect of predator control may have been a result of the choice of sites. Most of the sites chosen for chick survival monitoring tended to have low densities of both predator species even in the absence of control measures (Figs 2 & 4).

Data on breeding success, based on the number of lapwing with young, were available for the six sites where radio-tracking was not carried out. A fixed effects model showed that among these sites there were no consistent differences in breeding success according to year (χ^2_7 = 8·80, P = 0·27) but the proportion of adults accompanied by young was doubled in years when predator control measures were carried out (model least-squares means (± SE): 0·343 ± 0·040 and 0·155 ± 0·036, χ^2_1 = 13·03, P = 0·0003), an effect which was consistent across all sites studied (site*treatment χ^2_4 = 5·90, P = 0·21).

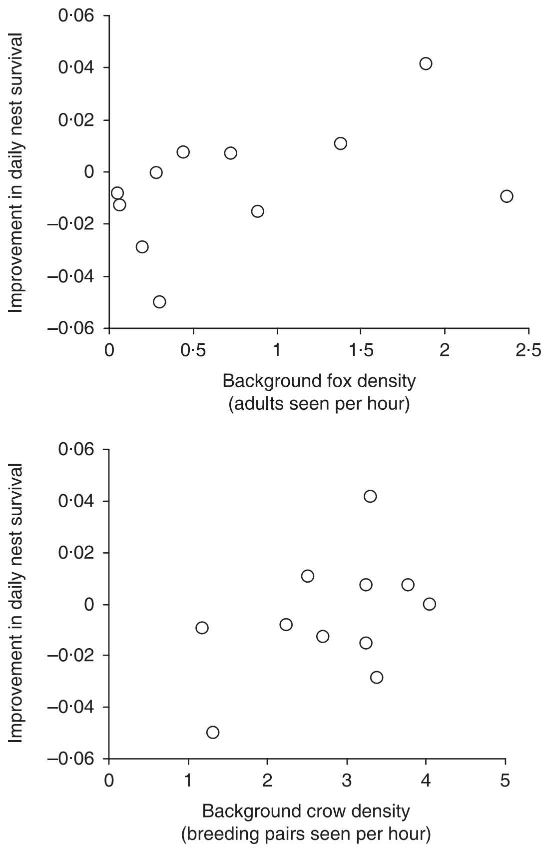

Fig. 7. Improvement in daily lapwing nest survival probability in response to predator control, as a function of fox and crow densities in years without predator control. The improvement in nest survival is calculated as the difference in daily survival rate over four years with and without predator control for each site. Negative values indicate a deterioration in nest survival in years of predator control.

Table 1. Number of lapwing nest predation events recorded during daylight and darkness across seven study sites. Site codes as in Fig. 2

Timing of nest predation	OWA	OWB	ABL	LPK	PMI	PNL	YHR
Daylight	1	3	0	3	0	0	0
Darkness	6	10	2	12	5	8	4

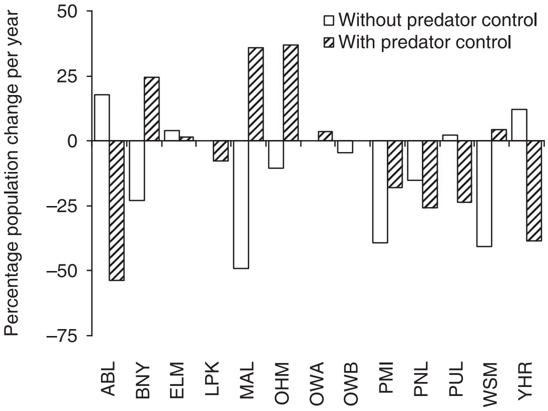

Fig. 8. Annual percentage change in population size of breeding lapwing during years with and without fox and crow control. Site codes as Fig. 2.

EFFECT OF PREDATOR REMOVAL ON LAPWING POPULATION TRENDS

The annual percentage change in lapwing population size was determined for each site from the slopes of the linear regressions of Ln(population size) on year during the periods with and without predator control (Fig. 8). Extensive flooding interrupted nesting on the Ouse Washes in 1998, 2000 and 2001, resulting in no reliable data on population size for the two study areas in those years. Consequently, the population trend could not be reliably computed for the treatment period 2000–03. Most sites exhibited extremely large population changes (increases and decreases of up to 30% per annum were common), which were unlikely to have been simply the result of local productivity and mortality. Population changes of such magnitude almost certainly involve local immigration and emigration. There was no relationship between average nest survival over each 4-year treatment period and the population trend during the same period, across sites (General Linear Model with normal error distribution, including site blocking factor $\chi^2_1 = 1{\cdot}61$, $P = 0{\cdot}20$). Unsurprisingly, therefore, there was no effect of predator control treatment on population trends ($\chi^2_1 = 0{\cdot}84$, $P = 0{\cdot}36$).

We also examined the hypothesis that the background density of foxes and crows (i.e. densities in years without predator control) might influence the impact of predator control measures on population trends (as shown above for nest survival rates). There was evidence that the effect of predator control on lapwing population trend was dependent on the background density of foxes (General Linear Model with normal error distribution, including site blocking factor $\chi^2_1 = 4{\cdot}78$, $P = 0{\cdot}029$) and a suggestion of a similar effect of territorial crows ($\chi^2_1 = 2{\cdot}88$, $P = 0{\cdot}09$). Controlling for these interactions revealed weak evidence of an overall effect of predator control treatment on lapwing population trend ($\chi^2_1 = 3{\cdot}20$, $P = 0{\cdot}074$).

Discussion

The predator control measures employed in this study resulted in a mean 40% reduction in adult fox densities and a mean 56% reduction on territorial crow densities during the course of the lapwing breeding season, across all sites. Reductions in fox numbers were apparent from the beginning of March onwards, whereas for territorial crows numbers were reduced from the beginning of April. The removal of territorial crows resulted in a compensatory influx of non-breeding birds, such that the total densities of crows remained similar between years with and without crow removal. There was evidence for a cumulative effect of predator removal on fox densities over the course of 4 years, indicating that the measures employed in one year had an impact on fox densities the following year. This was an unexpected finding, since we anticipated that the predator control measures would simply reduce fox densities during the breeding season in a local and temporary fashion. We also found that the densities of foxes were extremely variable among sites in years without predator control. On some sites in Wales, low densities of foxes during the lapwing breeding season resulted in the lack of any fox removal in years when predator control measures were operative. As a result, when adopting a simple treatment-based approach to analysis of these data, we found no consistent evidence of reduced lapwing nest or chick mortality during years of predator control. However, when we examined the effect of predator control in relation to background predator densities for each site (i.e. densities in years without predator removal), we found a significant interaction, and controlling for this effect resulted in a significant overall effect of predator control on nest failure rates. Among the six sites where detailed monitoring of chick survival was not carried out (where predator densities were generally higher), there was a significant first-order effect of predator control treatment on the proportion of lapwing with young. The variation in background fox and crow densities on the study sites is likely to be dependent on the surrounding habitat (Webbon *et al*. 2004) and the level of predator control practised by neighbouring land managers.

There was not strong evidence of an overall effect of fox and crow control on population trends across all sites. The magnitude of the mean annual population changes indicated that immigration and emigration occurred among sites and consequently population trends were unrelated to nest survival rates averaged across the 4-year treatment periods. During the settlement period when territory and nest-site selection occurs, lapwing are highly responsive to sward and surface water conditions (Milsom *et al*. 2000, 2002) and the numbers breeding on a particular site in any year will be influenced by the relative suitability of nesting habitat in neighbouring areas.

Data from nest temperature loggers suggested that non-avian predators were responsible for the great majority of nest predations. This is an intriguing finding since recorded fox densities were generally much lower for the Welsh sites than for the Ouse Washes (Fig. 2) and, taken together with the observation that fox control did not improve nest survival for any of the Welsh sites (indeed, predator control resulted in an increase in nest predation at Aberleri), suggests that mammalian predators other than foxes were principally responsible for nest failures at the Welsh sites.

Our findings support the conclusions of the meta-analysis of Côté & Sutherland (1997) and review of Newton (1993), which found fairly uniform effects of predator removal on components of avian annual productivity, but less consistent effects on breeding population size. Of the 20 studies considered by Côté & Sutherland (1997), 16 were conducted on gamebird or waterfowl species, which are characterized by very large clutch sizes. This reproductive strategy is likely to have evolved in response to intense predator pressure and the breeding success of such species is likely to respond readily to reductions in numbers of their predators. The effects of predator removal on breeding success of waders may therefore be less pronounced than for gamebirds and waterfowl. The single wader species included in the meta-analysis (golden plover *Pluvialis apricaria*) showed no increase in breeding success in response to predator control (Parr 1993).

The fox densities resulting from predator removal during control years were very similar to those reported, using similar survey methods, from a predator control experiment conducted on Salisbury Plain, UK, between 1985 and 1990 for the benefit of grey partridge *Perdix perdix* (Tapper *et al*. 1996; site-means of 0·38 and 0·30 sightings per hour, respectively). This suggests that efficacy of fox control was comparable in the two experiments (assuming similar detectability of foxes in the two studies). Differences in survey methods and analysis preclude direct comparisons of predator control on crow densities. Whilst the current study found significant effects of predator control on components of annual productivity, but not on population growth, Tapper *et al*. (1996) were able to demonstrate population effects of predator control on grey partridge. There are a number of possible reasons for these differences, including the range of potential predator species targeting by control measures, and the degree of philopatry and site-fidelity of the two prey species.

For a locally mobile species such as lapwing, the population-level benefits of improved productivity and recruitment may not be readily identifiable at the specific sites where predator control measures are implemented due to interannual shifts in breeding locality. An important step towards quantifying the consequences at a meta-population level of improvements in nest and chick survival is the development of a demographic model. This will permit an evaluation of the meta-population response to improvement in certain life-history parameters, such as nest and chick survival, that may result from local management measures such as predator control.

The analytical approach developed here should serve as a model for evaluation of predator control issues in other areas and systems. First, there is a need to parameterize the relationships between densities of the main predators and key life-history stages. For lapwing, the principal knowledge gap relates to the impact of different predator species at both the egg- and chick-stage. Remote monitoring of nests using digital recording equipment is currently underway to address this issue.

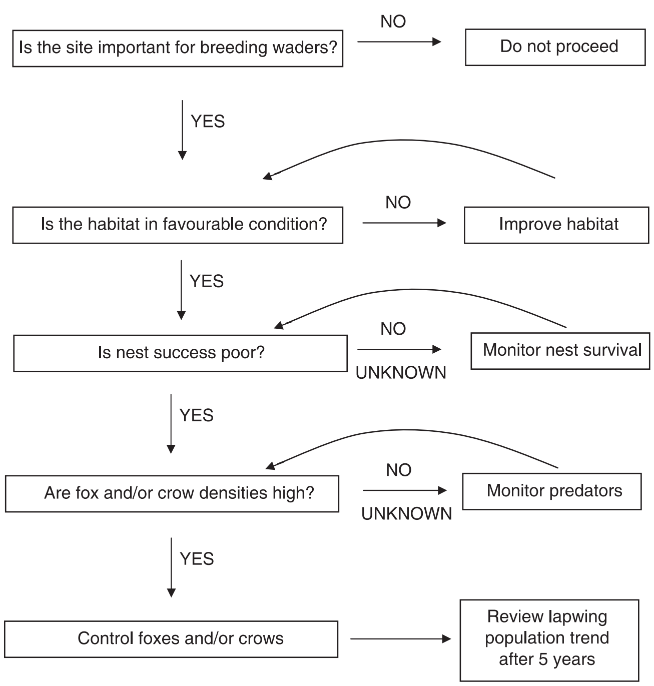

Fig. 9. Decision tree for evaluation of fox and crow control for benefit of breeding lapwing on lowland wet grassland reserves. Parameter thresholds (nest survival, fox and crow densities) derived empirically. Nest survival is taken as surrogate for annual productivity in the absence of a viable method for economically assessing annual productivity for a large number of sites simultaneously.

DECISION RULES FOR ASSESSMENT OF PREDATOR CONTROL ON LOWLAND WET GRASSLAND RESERVES

Since predator control is a time-consuming, costly and controversial activity, especially in a nature conservation context, it cannot be viewed simply as a cost-neutral insurance measure that may yield a benefit. Rather, any potential benefit of predator control needs to be demonstrated and weighed against the benefits of other potential management actions competing for conservation resources. Unless the impact of predators and the need for their control can be demonstrated, resources may be better spent elsewhere. In the light of this, we suggest the use of a decision tree (Fig. 9) to assess the value of fox and/or crow control on a site-by-site basis, rather than a blanket approach. Predator control should only be considered for sites supporting important wader populations, with good habitat conditions and high nest loss to predators. For the nature reserves included in this study, the outcomes of the implementation of this decision tree will be monitored for 5 years from 2005 and the procedure will then be reviewed.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://www.blackwell-synergy.com

Fig. S1. Location and size (ha) of study sites.