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Close to the edge: predation risks for two declining farmland passerines

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Data on the breeding success of two crop-nesting passerines, Skylark *Alauda arvensis* and Yellow Wagtail *Motacilla flava*, were collected in relation to linear features within and surrounding arable crops. Both species were found to experience high rates of nest predation with increased proximity to field boundaries, although the exact nature of the relationship differed with species and, in the case of Skylark, with boundary type. Most nest losses were attributable to predation. During 2006 video cameras deployed on Skylark nests showed that all recorded predation was by mammals of various species, and that these were most active in or around grass margins. The results suggest that further research is needed into ways of minimizing negative impacts of predation on Skylarks. Possible solutions discussed include concentrating Skylark Plots in the field centres away from grass margins and promoting Skylark Plots in fields without grass margins in future agri-environmental schemes.

Keywords: Alauda arvensis, arable, grass margin, Motacilla flava, Skylark, tramline, Yellow Wagtail.

Both Skylark Alauda arvensis and Yellow Wagtail Motacilla flava are red listed as species in rapid population decline in the UK, with the long-term Common Bird Census/Breeding Bird Survey trends in England between 1970 and 2005 being -53% and -65%, respectively (Eaton et al. 2007). A substantial proportion of the remaining populations of both species are now concentrated on arable farmland. For Skylark, research has shown that a variety of changes in farming are likely to have contributed to population decline (Donald 2004). This is particularly true in regions dominated by cereal crops, where a switch from spring to winter sowing results in the rapid development of tall, dense swards that, from late May onwards, restrict both nesting opportunities (Donald 2004) and access to food (Morris et al. 2004). Yellow Wagtail has been less well studied, although recent work has revealed that limitations to the number of breeding attempts may also have a bearing on their decline, as territories in winter-sown cereal fields tend to be abandoned during the latter part of the breeding season (Gilroy 2007). As the Yellow Wagtail is a long-distance migrant, factors

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along the migratory route or on the wintering grounds (e.g. desertification restricting feeding opportunities and/or extending flight distances) may also be contributory (Newton 2004), whilst changes in grassland management (e.g. drainage and increased fertilizer use) have undoubtedly fostered declines in populations breeding in pastoral regions (Wilson & Vickery 2005).

In response to these declines, the UK government now regards birds as a primary quality-of-life indicator, with a suite of 19 farmland species (including both Skylark and Yellow Wagtail) contributing to the indicator. The Department for Environment, Food and Rural Affairs (Defra) has a public service agreement to reverse the long-term decline of farmland bird species by 2020 (Gregory *et al.* 2004). To achieve this, the constituent countries of the UK have introduced a number of agri-environment schemes (AES), co-financed by government and European Union Common Agricultural Policy funds, containing measures designed to benefit farmland biodiversity. For the two species considered in this paper, potentially beneficial measures include:

(1) Small, uncropped areas in winter-sown cereals (option EF8 – Skylark Plots – in Entry Level Stewardship in England), designed to provide foraging and nestsites with enhanced access and low predation risk.

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(2) Sown grass margins (buffer strips) in a variety of AES (e.g. option EE3 – 6-m-wide grass buffer strips – in Entry Level Stewardship in England) provide reservoirs from which invertebrates important in chick diet can disperse into the crop. These may also provide foraging or nest-sites in situations were they are situated away from tall boundary structures. Defra is committed to a Biodiversity Action Plan target to increase the area of cereal field margin under conservation management to 15 000 ha by 2010, a figure that has already been exceeded.

No studies have reported predation as a major driver of population decline for either species. However, it is known that switching to intensive winter cropping can influence Skylark nest predation rates. From late May onwards, as the crop canopy closes, many pairs in winter-sown cereals shift towards nesting in more open areas next to tramlines. the parallel tracks created by tractors moving through the crop. These tramlines also provide predators with access routes through dense crops, with the result that there is an approximate halving of the nest success rate next to these linear features (Donald et al. 2002). With 38% of the British Skylark population occurring in cereals (Browne et al. 2000), it is conceivable that high rates of nest predation in such habitats may have been a contributory factor in driving population declines. As such, nest predation may be an issue worthy of consideration in the design of measures to aid the recovery of this and similar species.

This paper examines the role of linear habitat features in determining nest predation rates for both Skylarks and Yellow Wagtails in arable fields. In particular, we consider whether field boundary habitats (such as the ditches, hedges and grass margins that surround virtually every field) have an influence on nest predation rates. In addition, we examine the role of tramlines in determining nest success for Yellow Wagtails. We also consider predator identity, activity patterns and discuss potential mitigation of the effects of predation on the population productivity of our study species.

METHODS

Study sites

Yellow Wagtail data were collected during 2003 and 2005 from six arable farms, covering 33 km² of north Cambridgeshire and south Lincolnshire. Crops on these sites were not experimentally manipulated

 Table 1. The four experimental treatments on the SAFFIE sites.

 See Morris (2007) for details of establishment and management methods.

Treatment	Abbreviation
Experimental control – conventionally managed winter wheat without Skylark Plots or grass margins	CONV
Winter wheat with 6-m-wide grass margins + Skylark Plots	PLOMAR
Winter wheat with 6-m-wide grass margins only Winter wheat with Skylark Plots only	MAR PLOT

(Gilroy 2007). Skylark data were collected during April–August 2004–06 from 19 sites (five in Lincolnshire, four in Herefordshire, four in Suffolk, two each in Cambridgeshire and Essex, and one each in Norfolk and Northamptonshire) cropped with winter-sown wheat that formed part of the Sustainable Arable Farming for an Improved Environment (SAFFIE) project. Each site contained four treatments, on which benefits for biodiversity, including nesting and foraging birds, were assessed (Table 1).

Nest monitoring

For both species, two visits per month were made to each study area, during which breeding pairs were located using territory-mapping methodology (Marchant *et al.* 1990). Nests were found either through direct observation of returning adults or systematic searches of the area of focal activity. Nest positions were mapped and marked with small pieces of coloured tape on nearby wheat plants to aid relocation. They were then revisited every 2–4 days to provide data on nest productivity and outcome and nestling body-condition, as outlined in Morris *et al.* (2004) for Skylark and Gilroy (2007) for Yellow Wagtail.

During 2006 on a subset of nine sites, 10 custombuilt video camera units, based on a black-and white camera (PH86 T; Maplin, Barnsley, UK) and a Memocam DVR image storage unit (Video Domain Technologies Ltd, Petah Tikva, Israel), were deployed on 29 Skylark nests (all the nests located during April–July for which spare camera units were available during the egg or chick stages) to identify nest predators and to determine whether they varied with proximity to field edge and the type of boundary features. A passive-infrared sensor awakened the system from standby mode to record three images at 0.3-s intervals every time movement was detected in a set field of view around the nest. Further details of the cameras are given in Bolton *et al.* (2007). When the cameras were not deployed on nests, they were used to monitor movement of potential predators and prey along linear features, such as margins and tramlines.

Statistical analyses

Generalized linear models were used to identify those predictors explaining significant variation in nest survival rates (Welham 1993). The AIC-based multi-model comparison approach (Whittingham et al. 2005) was not used as this experiment tested specific hypotheses about the effects of a small number of predictor variables on a multi-centre trial (Stephens et al. 2007). Significance of predictors was tested using a backwards deletion process, where the least significant variables were sequentially removed until a Minimum Adequate Model (MAM) was reached in which all variables were retained at $P \le 0.05$. For Skylark models, site and a site \times field interaction term were included as random effects in mixed models (using the GLIMMIX macro in SAS Enterprise Guide 3), to account for unmeasured spatial variation (the interaction term accounts for homogeneity of management practice being greater within rather than between individual farms). For Yellow Wagtail models, however, this treatment was inappropriate, as the restricted number of site levels (six), all situated in the same geographical area, meant that the data violated the assumption of normality in level means required for random effects models (Brown & Prescott 2005). Consequently, site effects in Yellow Wagtail models were treated as fixed effects (using PROC GENMOD in SAS).

Binomial models were constructed for analysis of differences in daily mortality rates (DMRs) of nests. Given that both species are multi-brooded, there was a risk of non-independence in our nest data, as multiple nests may have been recorded from the same individual pairs. For both species considered in our study, it was not possible to identify and follow the movements of individual birds nor pairs of birds, which for Skylarks at least are believed to stay together throughout the breeding season (Donald 2004). However, in both species, pairs are known to shift nest-sites and territory locations between breeding attempts, owing to seasonal changes in habitat structure (Donald et al. 2002; J. Gilroy unpubl. data). This implies that predation rates will vary independently with each sequential nesting attempt, to maximize our power to resolve relationships between habitat and predation rates, we modelled each nest as an independent datum. For Yellow Wagtail nests, separate models were used to measure nest mortality with proximity to tramlines, as a two-level factor ('on', < 20 cm, and 'away from', \geq 20 cm, tramlines; the 20-cm threshold represented an approximate distance for which all mammalian predators recorded in our study could easily have reached the contents of a nest from the tramline without entering the crop), and to the field edge, which was modelled in two ways: (1) as a continuous variable and (2) grouped into five distance bands, to test for differences in predation rates between the bands. For Skylarks, models were constructed separately for distance to field edges (continuous variables) with and without grass margins. For both species, the response variable, DMR, was calculated according to the following equation: DMR = Outcome for each nest (where Failure = 1 and Success = 0)/the number of days the nest was exposed to predators. As nests were not visited every day, the mid-point of time between penultimate and final visits was used to determine the binomial denominator. Thus, model outputs were akin to the Mayfield DMR outlined in Johnson (1979) but, as we were primarily interested in losses due to predation and not nests failing for other reasons (abandonment, starvation, accidental destruction by agricultural machinery), the models presented here did not include nests lost to causes other than predation. As most losses in our study were attributable to predation, the DMR presented here is very similar to the 'true' Mayfield DMR (Johnson 1979), and only the former is presented in this paper. Similar binomial models were also constructed to examine Skylark DMR in the four SAFFIE experimental treatments (Table 1). For Figures 1-3, the outputs from the DMR models were also used to calculate the Mayfield-adjusted values for the proportion of nests (predated and successful) lost to predators over the average duration of a successful nest (i.e. between the first egg-laying date and the date when young left the nest: 22 days for Skylark and 27 days for Yellow Wagtail in these

minimizing the risk of pseudoreplication. In order

Skylark and $1 - [(1 - DMR)^{27}]$ for Yellow Wagtail. Other predictors tested as fixed effects (along with interaction terms) were 'year' (two- or three-level factor) in all models; crop (three-level factor) in Yellow Wagtail models; and 'treatment' (four-level factor – or as a simplified two-level margins versus

studies) using the formulae: $1 - [(1 - DMR)^{22}]$ for

Table 2. Summary of Yellow Wagtail and Skylark nest data,
showing year of data collection, crop types, the total number of
nests located and outcome (numbers of nests and percentages
of the original samples sizes).

	Yellow Wagtail	Skylark		
Year	2003, 2005	2004–2006		
No. of nests	111 (63 winter wheat, 48 potatoes)	183 (winter wheat)		
No. successful	74 (67%)	109 (60%)		
No. of failures	37 (33%)	74 (40%)		
No. predated	31 (28%)	61 (33%)		

non-margin contrast) in the Skylark models. In contrasts between SAFFIE experimental treatments, continuous variables describing characteristics of 'boundary' (adapted from Wilson *et al.* 1997) and 'adjacent habitat' surrounding the treatments were also included.

As camera data on nest predators came from a single year and usually involved small sample sizes, no attempt has been made to analyse them using formal statistical methods and the data presented are tabulated sums of the raw data.

RESULTS

For both species, details of sample sizes, crop type and success rates are given in Table 2. From remains left at the nest, most nest failures were attributed to predation.

Yellow Wagtail

There was a significant difference in nest survival rates between nests situated on the tramlines and nests situated further away ($\chi_1^2 = 4.82$, P = 0.028) in winter wheat crops (Fig. 1). This relationship was not significant in potato crops ($\chi_1^2 = 2.07$, P = 0.150). Modelled as a continuous variable, there was a significant negative relationship ($\chi_1^2 = 7.31, P = 0.007$) with distance to the field edge, which applied to all crop types (Fig. 2). When these nests were grouped into five distance bands radiating out from the crop edge (band 1 = 0-50 m; band 2 = 51-79 m; band 3 = 80-109 m; band 4 = 110-139 m; band $5 \ge$ 140 m), in all but one comparison the proportion of nests predated decreased between successive bands. Nests in the furthest distance band (≥ 140 m) from the crop edge had significantly lower failure rates than those in the two distance bands less than



Figure 1. Differences in Mayfield adjusted values for the proportion of Yellow Wagtail nests (predated and successful) in winter wheat crops lost to predators in relation to proximity to tramlines. Estimates and 95% confidence intervals are derived from the back-transformed Least Squares Means output from GLM.



Figure 2. The predicted relationship between the Mayfieldadjusted values for the proportion of Yellow Wagtail nests (predated and successful) in winter wheat and potato crops lost to predators in relation to proximity to crop edges. Estimates are derived from the back-transformed Least Squares Means output from GLM.

80 m from the edge, but differences between the other bands were not significant (Table 3). Owing to limited sample sizes, the relative influence of different field boundary types on nest predation rate was not analysed.

Skylark

Data were analysed separately for: (1) fields with 6-m-wide grass margins around the edge and (2) non-margin fields, where the crop edge comprised hedges, tracks, ditches, etc. In model (1), the proportion of nests predated showed a pronounced quadratic relationship with distance from the nearest grass margin (Fig. 3), with both the linear ($F_{1,78} = 6.96$, P = 0.01) and the squared ($F_{1,78} = 6.51$, P = 0.013) terms being significant. Further investigation showed that there were significant differences in DMRs when the SAFFIE data were analysed including a four-level treatment predictor ($F_{3,47} = 3.51$, P = 0.0225).

Table 3. Results of analyses of pairwise comparisons of differences of least squares means in DMR of (1) Yellow Wagtail in relation to a five-level distance band from crop edge and (2) Skylark nests in relation to a four-level factor crop treatment.

Yellow Wagtail									
Distance Band†	2	3	4	5					
1 2 3 4 5	+ ns	+ ns + ns	+ ns + ns – ns	+ * + * + ns + ns					
Skylark Treatment‡ CONV PLOMAR MAR PLOT	PLOMAR - *	MAR – ns + ns	PLOT - ns + * + ns						

+Yellow Wagtail: distance bands are as follows: band 1 = 0-50 m, band 2 = 51-79 m, band 3 = 80-109 m, band 4 = 110-139 m, band $5 = \ge 140$ m from crop edge.

‡Skylark: See Table 1 for treatment codes.

+ indicates greater predation in the 'row' category relative to the 'column' category; - indicates less predation in the 'row' category relative to the 'column' category. ns = non-significant; * significant at P < 0.05.



Figure 3. Mayfield-adjusted values for the predicted proportion of Skylark nests (predated and successful) in winter wheat lost to predators from two separate models: (1) in relation to distance from the nearest grass margin (broken line) and (2) in relation to distance from the nearest crop edge without a grass margin (solid line). In (1) there was a significant quadratic relationship. In (2) there was a non-significant relationship. Estimates are derived from back-transformed Least Squares Means output from GLMM.

Predation was significantly greater on PLOMAR than on CONV and PLOT and non-significantly greater than on MAR. There were no significant differences between the other factor levels (Table 3). Over the 22 days from first egg-laying until the young left the nest, the overall proportion of Skylark nests predated was 46% in CONV, 89% in PLOMAR, **Table 4.** Measures of nesting success and productivity for a subsample of 150 Skylark nesting attempts in winter wheat fields during 2004–06 for which the outcome was either 'success' (0) or 'predation' (1) and for which the data allowed accurate calculation of DMR. Chicks/nesting attempt is the mean number of Skylark chicks leaving the nest per nesting attempt and Chicks/10 ha is the cumulative total of chicks produced per 10 ha throughout the breeding season. Treatments shown are the four included in the SAFFIE experimental design (Table 1) and two subsets of the PLOMAR treatment (PLOMAR > 50, PLOMAR > 75) that included crop-centre nests > 50 m and > 75 m from the field boundary, respectively, rather than from the whole PLOMAR treatment area.

Treatment (sub-treatment)	No. of nests	Overall success rate (%)	DMR	Chicks/ nesting attempt	Chicks/ 10 ha
CONV	29	72	0.029	1.61	2.04
PLOMAR	51	45	0.107	0.29	0.79
MAR	33	61	0.062	0.71	0.96
PLOT	37	76	0.032	1.54	2.82
(PLOMAR > 50)	36	47	0.063	0.80	2.19
(PLOMAR > 75)	27	52	0.052	0.99	2.72

73% in MAR and 50% in PLOT. No other predictors significantly affected DMR.

A comparison between PLOMAR (whole field area) with subsets of the PLOMAR data [the crop centre at two distances from the margin (1) > 50 m (PLOMAR > 50) and (2) > 75 m (PLOMAR > 75)], and PLOT, revealed that DMRs of nests in PLO-MAR as a whole were 1.7 times higher than in PLOMAR > 50 and double those in PLOMAR > 75. DMRs in PLOMAR > 50 and PLOMAR > 75 were nearly double and 1.6 times higher, respectively, than in PLOT. However, the numbers of chicks leaving the nest per unit area in PLOMAR > 75 were nearly equal to PLOT, owing to a greater density of nests per 10 ha (2.75 vs. 1.88) and a slightly greater mean brood size (3.67 vs. 3.19) in PLOMAR. For PLOMAR > 50, the number of chicks leaving the nest per unit area was 0.6 less than PLOT, although it was slightly greater than for CONV (Table 4).

Nest cameras

Twenty-nine Skylark nests were under surveillance for a total of 5589 h. Fifteen fledged successfully, three lost complete broods to starvation during cold, wet weather, three clutches of eggs were abandoned (also during poor weather) and eight were predated (Table 5). Half of the predations occurred in PLOMAR. All nest predators were mammals: five

 Table 5.
 Summary of Skylark nest predation events captured by video surveillance.

Nest Predator stage		Treatment	Time	Distance from boundary (m)		
Badger	Egg	CONV	03:30	100		
Badger	Egg	CONV	24:30	50		
Badger	Egg	PLOMAR	22:10	120		
Badger	Egg	PLOMAR	00:05	0 (in margin)		
Badger	Chick	MAR	21:58	90		
Stoat	Chick	PLOMAR	19:48	10		
Weasel	Chick	PLOMAR	19:01	2.5 (in margin)		
Brown Rat	Chick	PLOT	04:38	80		

Badgers Melus melus, and single Weasel Mustela nivalis, Stoat Mustela erminea and Brown Rat Rattus norvegicus. Badgers were active both on treatments with and without margins and throughout the field. predating nests from the edge up to 120 m into the crop (Table 5). At night, mice Mus spp. and rats were filmed in close vicinity to several incubating or brooding Skylarks, but in no case did the female leave the nest or show agitation and the rodents made no attempt to predate the nest contents. However, in two cases, mice nibbled cold eggs in abandoned nests and a rat predated a brood of nestlings from an unattended nest. The two instances of predation by small mustelids were within 10 m of the field boundary in treatments with grass margins. Predation was divided equally between nests at the egg and chick stages (Table 5). A total of 1010 h of camera deployment on tramlines and grass margins (potential predator access routes) recorded (on multiple occasions in descending order of frequency) Badgers, mice and Brown Rats and (on single occasions) Red Fox Vulpes vulpes, Domestic Dog Canis lupus familiaris, Magpie Pica pica and Carrion Crow Corvus corone. Badgers, mice and Brown Rats were recorded in tramlines over 50 m from the crop edge (Table 6).

DISCUSSION

Field boundary habitats are known to be extremely important in providing both foraging and nesting habitats for many species of farmland bird, as well as other taxa (Perkins et al. 2002, Vickery et al. 2002). However, for both species considered in our study. nest proximity to field boundaries had a significant negative influence on productivity, with nests placed closer to boundaries experiencing higher rates of nest predation (Figs 2 & 3). Yellow Wagtail nests located in close proximity to tramlines were also associated with increased rates of nest predation (Fig. 1), echoing results from previous work on Skylarks (Donald et al. 2002, Donald 2004). Surveillance of Skylark nests revealed that a suite of mammalian predators were responsible for all recorded predation events (Table 5), a finding similar to that of a study on predation of artificial ground nests in Sweden (Söderström et al. 1998). It seems likely that linear habitat features act to concentrate the activities of mammalian predators within arable field environments, either by providing refugia or simply by presenting easy access routes through the landscape (Tryjanowski et al. 2002). Hence, although field boundary habitats provide many benefits to farmland biodiversity, they may also have possible detrimental effects for some species.

The significant negative relationship between Yellow Wagtail nest predation rate and proximity to tramlines in winter wheat crops (Fig. 1) is very similar to the relationship previously described for Skylark (Donald *et al.* 2002, Donald 2004). It seems that in both cases, tramlines are favoured for nest placement as the opening in crop canopy allows access to the ground, which may be limited in the otherwise dense and tall sward of a winter-sown cereal field (Wilson *et al.* 2005). Similarly, tramlines may act as concourses for land mammals unable to

 Table 6.
 Summary of potential nest predators recorded during over 1000 h of remote sensor camera deployment on linear features (grass margins and tramlines) in wheat fields. Observations are summed in distance bands measured from the field boundary.

Treatment	Dist band (m)	Camera deployment (h)	Badger	Fox	Stoat	Mouse spp	Rat	Dog	Magpie	Crow	Total potential predators	Encounter rate (predators/100 h)
Margin	within margin (< 6)	689.28	6	1	1	6	2	1	1	1	19	2.76
-	50–99	103.58	0	0	0	2	1	0	0	0	3	2.90
	100–149	47.33	1	0	0	0	0	0	0	0	1	2.11
Non-Margin	< 50	54	1	0	0	0	0	0	0	0	1	1.85
	50–99	116.25	0	0	0	0	0	0	0	0	0	0.00

move through the crop itself, increasing local predator activity, and hence the likelihood that nests will be encountered. In potato crops, there was no significant relationship between tramline proximity and nest predation rate for Yellow Wagtails, probably reflecting the fact that tramlines are generally less well defined in this crop, and therefore less attractive to mammals. It is uncertain how important nest predation in tramlines is as a limiting factor for Yellow Wagtail populations. As the dominant crop in UK arable agriculture and a favoured nesting habitat, winter-sown cereals are likely to support a relatively large proportion of Yellow Wagtail populations in arable regions (Gilroy 2007). Predation rates in tramlines could therefore influence breeding productivity on a large scale, although the magnitude of this impact on population maintenance is unknown. For Skylark, the indications are that predation is less important than the limitation of the number of breeding attempts caused by the switch to winter sowing of cereals (N. Ratcliffe unpubl. data). Nevertheless, designing agri-environment options that shift the focus of nesting activity away from tramlines is likely to have some benefit.

Our results suggest that proximity to field boundary habitats may be an important determinant of nest predation rates. For Yellow Wagtail, nest predation rates gradually decreased away from field edges in both potato and wheat, but 100 m into the crop, predation rate was still 50% (Fig. 2). It was not possible to explore the relative influence of different boundary types specifically. For Skylarks, the highest nest predation rates occurred in cereal fields with experimental 6-m grass margins, with predation rates peaking within 50 m of these margins (Fig. 3). In fields without grass margins, the relationship between predation rate and field edge was not significant. Within grass margins themselves, nest survival was relatively high, probably due to most nests being well concealed under dense, creeping vegetation. The highest rates of nest predation were associated with the combination of Skylark Plots and grass margins (Table 4). A possible explanation could relate to the high density of territorial birds associated with the combination of Skylark Plots and margins (Cook et al. 2007). However, despite the high nest density, low productivity, due to increased nest predation, poses a potential ecological trap, as outlined by Battin (2004).

The high nest predation rates experienced in fields with both experimental grass margins and Skylark Plots (Table 4) are perhaps most probably a function of increased predator attraction to these sites, which are likely to offer enhanced foraging opportunities to most generalist predators. In treatments with grass margins, the higher encounter rates (the number of predators filmed per 100 h of camera deployment) of potential nest predators in the crop as well as within the margins supports the conclusions that predators may be more numerous or active in such environments (Table 6). Although mammal populations were not directly monitored during the experiments, SAFFIE revealed that abundance of both birds and invertebrates increased in the crop adjacent to experimental margins (Clarke et al. 2007). Other studies have shown that the presence of grass margins can greatly increase the abundance of small mammals (Shore et al. 2005). Mammalian predators may be attracted by this increased food abundance (invertebrates, small mammals or birds). and may then occur at higher densities within the adjacent crop, resulting in increased incidental nest predation (Vickery et al. 1992). In our study, both Badgers and rodents were recorded foraging more than 50 m into the crop in experimental fields (Tables 5 & 6). Opportunistic foragers, such as Foxes and Badgers, are known to concentrate their efforts in response to the availability of food resources (Lucherini & Crema 1995). Although both species can rely heavily on earthworms, this food source is dependent on environmental conditions, and alternative foods and foraging habitats (e.g. crops in dry weather, such as experienced during summer 2006) are readily utilized (Cavallini & Lovari 1991). Additionally, high Skylark nest densities in fields with both Skylark Plots and margins could lead to increased nest encounter rates by predators, possibly allowing individuals to develop a search image for nests and thus inducing a density-dependent functional response (Roos 2002).

Although birds, including various corvids and raptors, are known to predate Skylark nests (Donald 2004), cameras in our study confirmed that mammals were the main predators. As sample sizes from the nest cameras were relatively small and originated from a single year, it was not possible to draw robust conclusions on predator activity from this study. On camera, the greatest range and encounter rate of mammalian predators occurred in, or close to, the margins (Table 6). Faeces, tracks and routeways found near margins further supported this pattern. It has been shown that the introduction of 6-m margins into arable fields increased the small mammal biomass at the field edge by up to three times compared with standard field edges (Shore et al. 2005), but the present study recorded only one predation by a rodent (Table 5). At night, rodents were also recorded visiting deserted nests with abandoned eggs and empty nests that had previously been predated, but when they encountered nests with incubating females, no attempts were made to predate the nests, suggesting that parent birds are often capable of repelling small mammals. This study found that larger predatory mammals, which may be tracking dispersing invertebrates or small mammal populations, caused the majority of nest predations (Table 5). Stoat, Weasel and Red Fox, the last not recorded predating nests in our study, but a known predator of Skylark nests elsewhere (Tryjanowski 2000), were filmed only in close proximity to the margins (Table 6). In contrast, Badgers, the main predating species in our study, were active on treatments with and without margins and throughout the field, predating nests from the edge up to 120 m into the crop (Tables 5 & 6). Larger mammals were recorded moving along the interface between margin and crop, particularly as the margins became more overgrown. From here, they would be able easily to access the network of tramlines running across the field centre.

Mitigation of predation through AES

These findings have improved the understanding of relationships between habitat features and nest predation rates for our study species. Understanding such relationships may be useful in the design of AES aimed at reversing their declines within arable farmland. Rigorous testing of Skylark Plots in SAF-FIE has shown that they enhance Skylark densities and can be beneficial to breeding success (Morris et al. 2004, 2007, Donald & Morris 2005). Grass margins also benefit a range of taxa including, under certain circumstances, nesting and foraging Skylarks (Edwards et al. 2001, Wilson 2001). SAFFIE has demonstrated synergistic effects of combining the two management practices in the same field (Cook et al. 2007). For many species the effect was positive, but Skylarks suffered very high rates of nest predation, resulting in productivity per unit area falling below even the low level found in conventional wheat crops. If the level of predation observed in SAFFIE were repeated, wide-scale implementation of the same combination of options side by side in the same field has the potential to impact Skylark populations negatively. Both Skylark Plots (option EF8) and 6-m grass buffer strips (option EE3), which differ only slightly from the SAFFIE grass margins, are now available throughout England as options in Entry Level Stewardship, which is designed to benefit widespread but declining species such as the Skylark.

One potential solution to the predation problem would be to advocate that grass strips and Skylark Plots are not placed in same field in Entry Level Stewardship agreements. However, for many other species this would not be desirable, as SAFFIE results suggest that the synergistic effect of combining the two management options is beneficial in the vast majority of cases (Cook et al. 2007). Another possible solution may be a zone of separation between Skylark Plots and grass margins. In SAFFIE, productivity per unit area of nests more than 75 m from the margin was akin to the high levels on fields with Skylark Plots but no margins (Table 4). However, such zones of separation have yet to be tested experimentally and this should be a priority before they can confidently be recommended as a solution. There may also be some possible disadvantages with such a zone of separation. It is possible that it could discourage some hedgerow species (e.g. Linnet Carduelis cannabina and Yellowhammer Emberiza citrinella), which appear to benefit from the combination of Skylark Plots and margins, from foraging in Skylark Plots. However, 75 m is well within the core foraging range of most species. A zone of separation could also reduce colonization of Skylark Plots by invertebrate species: a vital source of food for chicks of Skylarks, Yellow Wagtails and many other bird species. However, the value of Skylark Plots as foraging areas is believed to be due primarily to provision of access to food via the short sparse swards, rather than as centres of food abundance per se (Morris et al. 2004, Clarke et al. 2007). High densities of Skylark Plots could concentrate Skylarks in the crop-centre, potentially attracting higher densities of mobile predators to these areas. Donald (2004) documents such an example in set-aside, although it is doubtful whether winter wheat crops, even with favourable management, would support such high densities of Skylarks. Ultimately, if the numbers of Entry Level Stewardship agreements containing Skylark Plots remain low (currently they are in < 3% of agreements), then there is no prospect of wide-scale synergistic effects, positive or negative, of positioning this combination of options in the same field. However, should a revision of option management, funding or changes in farmer attitude lead to an increase in

Skylark Plot uptake, then a programme of monitoring nest predation and predators should be considered to assess effects at the wider scale and whether the suggested mitigation measures are effective.

For Yellow Wagtails, measures to improve breeding success in arable farmland might focus on attracting nesters away from tramlines in cereal fields. Skylark Plots could theoretically achieve this by providing ground access within the crop itself. Although Yellow Wagtail densities are often greater in fields with Skylark Plots (Cook et al. 2007), there is currently little evidence that Skylark Plots are selected by nesting Wagtails ahead of adjacent tramlines (SAFFIE unpubl. data). Fallow plots for ground-nesting birds, available in the English Higher Level Scheme (options HF13 and HF17), might support a preferred vegetation structure during the breeding season and therefore attract settlers away from cereal fields. although this requires further confirmation (Stevens & Bradbury 2006). As with Skylark Plots, such fallow plots may not be adopted on a large enough scale to bring about recovery of this widespread but scarce species. Yellow Wagtails are known to show a strong preference for potato crops when they are available (Mason & Macdonald 2000, Gilroy 2007), and the vegetation structure of this crop may be highly preferable for nesting. Consequently, the creation of in-field plots supporting a similar vegetation type could be effective in attracting Wagtails away from nesting in tramlines. Further work (commencing 2008) exploring suitable options to provide this vegetation structure may be fruitful. Importantly, the success of any in-field habitat management strategy in providing safe nesting habitat will depend on the proximity of treatment plots to field boundary habitats. Maintaining a minimum distance of 50 m from adjacent boundaries should be considered a priority in any trials.

It is possible that reductions in predation could also be achieved through predator control. However, with data from a limited sample gathered during a single breeding season, it is still uncertain whether the predators identified in our study would necessarily be the same in other years or areas. Future study may elucidate this but even if the range of mammals identified in our study were found to be more widespread predators of nests, current legislation in Great Britain prohibits the killing of Badgers (the chief nest-predator in 2006) unless under special government-issued licences. Others, such as Stoats and Weasels, are difficult to control effectively without substantial and sustained effort by experienced gamekeepers: a resource no longer available to many arable farmers. Given the restrictions and costs involved, it seems likely that the provision of safe and suitable nesting habitat, rather than predator control, is most likely to deliver improved breeding productivity for these declining species.

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