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Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England

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Summary

1. Agricultural management of grassland in lowland Britain has changed fundamentally in the last 50 years, resulting in spatial and structural uniformity within the pastoral landscape. The full extent to which these changes may have reduced the suitability of grassland as foraging habitat for birds is unknown. This study investigated the mechanisms by which these changes have impacted on birds and their food supplies.
2. We quantified field use by birds in summer and winter in two grassland areas of lowland England (Devon and Buckinghamshire) over 3 years, relating bird occurrence to the management, sward structure and seed and invertebrate food resources of individual fields. Management intensity was defined in terms of annual nitrogen input.
3. There was no consistent effect of management intensity on total seed head production, although those of grasses generally increased with inputs while forbs were rare throughout.
4. Relationships between management intensity and abundance of soil and epigeal invertebrates were complex. Soil beetle larvae were consistently lower in abundance, and surface-active beetle larvae counts consistently higher, in intensively managed fields. Foliar invertebrates showed more consistent negatively relationships with management intensity.
5. Most bird species occurred at low densities. There were consistent relationships across regions and years between the occurrence of birds and measures of field management. In winter, there was a tendency towards higher occupancy of intensively managed fields by species feeding on soil invertebrates. In summer, there were few such relationships, although many species avoided fields with tall swards.
6. Use of fields by birds was generally not related to measures of seed or invertebrate food abundance. While granivorous species were perhaps too rare to detect a relationship, in insectivores the strong negative relationships (in summer) with sward height suggested that access to food may be the critical factor.
7. While it appears that intensification of grassland management has been deleterious to the summer food resources of insectivorous birds that use insects living within the grass sward, intensification may have been beneficial to several species in winter through the enhancement of soil invertebrates.
8. *Synthesis and applications*. We suggest that attempts to restore habitat quality for birds in grassland landscapes need to create a range of management intensities and sward structures at the field and farm scales. A greater understanding of methods to enhance prey accessibility, as well as abundance, for insectivorous birds is required.

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Introduction

The management and productivity of lowland grassland in Britain has changed profoundly over the last 50 years, with increases in fertilizer inputs, changes in stocking practices, increases in silage production, a greater emphasis on optimizing yields of nutrients rather than dry matter *per se*, and development of new harvesting techniques (Chamberlain *et al*. 2000; Fuller 2000; Vickery *et al*. 2001). Although there is growing evidence to link changes in farm management practices to widespread declines of many farmland birds (Fuller *et al*. 1995; Siriwardena *et al*. 1998; Aebischer *et al*. 2000), most relevant research has focused on arable farming systems (Aebischer *et al*. 2000; Fox 2004). Several correlative studies suggest that increasing management intensity in grassland may affect bird populations (Green 1986; Pain, Hill & McCracken 1997; Chamberlain & Fuller 2000; Siriwardena *et al*. 2000) but the underlying mechanisms remain poorly understood (Vickery *et al*. 2001).

In Britain, grassland accounts for *c*. 12·4 million ha, representing more than 65% of the agricultural land (Defra 2002). Most of this grassland is agriculturally improved or semi-improved (Price 2003). A range of birds depend exclusively or partly on grassland, including several rare and declining species (e.g. song thrush *Turdus philomelos* (Brehm), starling *Sturnus vulgaris* (L.) and lapwing *Vanellus vanellus* L.; Perkins *et al*. 2000; Vickery *et al*. 2001; Atkinson, Fuller & Vickery 2002). Indeed, many grassland species are listed as Birds of Conservation Concern or form part of the government's Farmland Bird Index (Vickery *et al*. 2004).

In arable systems there is good evidence that food abundance is the main driver in determining use of fields by birds (Robinson & Sutherland 1999; Brickle *et al*. 2000; Moorcroft *et al*. 2002; Stephens *et al*. 2003). However, food accessibility has also been shown to be an important factor in determining the use of crops (Morris *et al*. 2004, 2001) and set-aside/fallows (Henderson *et al*. 2001). Relatively little research has focused on birds and their food resources in dry lowland agricultural grassland systems. Management, sward structure and composition and the abundance and availability of plant (mainly seed) and invertebrate food resources for birds are inextricably linked (Vickery *et al*. 2001; Atkinson, Buckingham & Morris 2004; McCracken & Tallowin 2004). Understanding the mechanisms and general principles by which grassland management affects field use by birds is vital to the development of sustainable agricultural systems that integrate economically viable farming and bird conservation in grassland habitats (Norris 2004).

In this paper, we present the results of a 4-year study of grassland field use by birds in summer and winter, carried out in two areas in lowland England. The study aimed to identify relationships between field use by birds, agricultural management practices and the abundance of potential food resources. In addition to providing insights into factors that have driven bird declines in landscapes dominated by agricultural grassland, we considered possible management approaches that might be used to stem and reverse this decline. With the exception of Tucker (1992), we are not aware of any previous studies that have examined grassland birds and their food resources, although others have described relationships between bird usage of grassland in lowland England and habitat attributes (Perkins *et al*. 2000; Barnett *et al*. 2004).

Study sites

The study was carried out in England on 15 lowland grassland farms in east Devon (an area of *c*. 14 × 15 km centred on National Grid reference ST 290070) and 13 in north Buckinghamshire (an area of *c*. 15 × 13 km centred on SP 635210, referred to hereafter as Bucks). These two discrete areas were *c*. 200 km apart (see Fig. S1). In each region, livestock farms were categorized as highly intensive (referred to as intensive), with average annual nitrogen (N) inputs of > 200 kg N ha^{-1}, moderately intensive (referred to as moderate), with inputs of 50–200 kg N ha^{-1}, and extensive, with inputs of < 50 kg N ha^{-1}. In these farms, 16 fields in each management category were selected in each region, making a total of 48 target fields per region, divided equally, as far as possible, between cut and grazed.

The study extended over a 4-year period between 1999 and 2002, but was severely disrupted by foot and mouth disease in summer 2001. Data were collected from all Devon fields in 1999 and 2000, half the Bucks fields in 2000 and all the Bucks fields in 2002. The sampling regimes for the various taxa are summarized in Appendix 1.

Methods

FIELD USE BY BIRDS

In each of the three winters, a minimum of four visits was made to each of the 48 target fields, spread as evenly as possible between early November and the end of February. On each field visit, three types of counts were made to maximize the probability of detecting all birds: (i) two point counts (1 min each) at opposite sides of the field to record birds within the field centre;

(ii) perimeter walks around the entire field edge, recording birds at the field edge and in the boundary; and (iii) transect counts, on which birds were recorded within 10 m of two straight transects, 50 m apart, across the centre of the field, starting and finishing 20 m from the boundary, mainly to detect skylarks *Alauda arvensis* (L.) and meadow pipits *Anthus pratensis* (L.). On each visit, the following environmental variables were recorded: sward structure (patchy, bare ground comprising > 50% of field area; tussocky, tussocks common throughout the field; or uniform), sward height (to the nearest 10 cm), presence of grazing animals, number of molehills (winter only, an absolute count used as an indicator of earthworm abundance; Whittingham, Percival & Brown 2000), proportion of bare ground (winter only) and, once per year, boundary characteristics (hedge width and height to nearest metre for individual boundary units of similar type) and a count of dead and live trees (> 5 m tall) per field boundary.

In summer, timed feeding counts were carried out to provide systematic information on the frequency with which different species foraged in the target fields. These were made along 100-m stretches of field boundary, typically four per field. Birds were recorded over a 5-min period in six distance bands from the field edge up to 100 m from the boundary. At least four sets of timed feeding counts were made for each field spread across the breeding season in three summers (1999, 2000 and 2002).

PLANT AND INVERTEBRATE FOOD RESOURCES

An extensive programme of sampling was carried out to quantify the level of seed and invertebrate food resources in all study fields and each sampling year.

Soil invertebrates were sampled from nine soil cores (10 cm diameter, 10 cm depth) in the spring and autumn. Surface-active (epigeal) invertebrates were sampled using nine pitfall traps in each field, set for 1 week in early spring (except 2001). Invertebrates associated with foliage were sampled in early summer and autumn using a Vortis suction sampler (Burkard Manufacturing Ltd, Rickmansworth, Herts, UK). Full details of sampling procedures are given in Fuller *et al*. (2003).

A measure of the seed resources available for birds was obtained by counting all seed heads present within two 1 × 10-m transects positioned in each of three zones (0–6 m of the field edge, mid-way from the edge to the centre and in the centre of the field) in mid–late autumn.

STATISTICAL ANALYSIS

Management variables

A two-step multivariate approach was used to produce a management index for each field. In step 1, seven nominal management variables for each field in Devon 1999–2000 and Bucks 2000–2002 were summarized by correspondence analysis (CA) using the statistical package CANOCO (ter Braak & Smilauer 1998) for each year separately and all years combined. The nominal variables were: grazed only, cut once, cut twice, hay cut, silage cut, farmyard manure (FYM) applied and slurry applied. The resulting ordinations explained a large proportion of variation in management in the first two axes (58–71%), with axis 1 (termed NOM1) representing a cutting/grazing gradient and axis 2 (termed NOM2) a hay/silage cut gradient. In step 2, the scores of the fields along these CA axes were used together with N inputs, a continuous variable, in a principal components analysis (PCA). The scores from this PCA were used as surrogates for detailed management information. Mean values of PC1 (a gradient of total N application) were taken for all relevant years for each field (referred to as N gradient) and used in subsequent analyses. PC2 (a grazing to cutting gradient) tended to have a nominal response, i.e. cut and aftermath grazed, cut once or cut twice, and annual values were used (as opposed to a mean for all years) because these management variables varied between years. All field boundary features were entered into a PCA and major gradients were identified in the boundary characteristics of fields (Table 1).

Table 1. Spearman rank correlation coefficients between field boundary variables and boundary PCA axes 1 and 2 scores. $*P < 0.05$, $**P < 0.001$

	Boundary PCA axis 1	Boundary PCA axis 2
Bank	−0·02	0
Fence/wall	0·34**	−0·1
Wood	0·13	0·18
Hedge with trees	0	0·05
Hedge without trees	−0·3**	0·11
Treeline	0·01	0·04
Ditch	−0·1	−0·09
Stream, river or pond	−0·24*	0·26*
Other	0·15	0·08
Total hedge volume	−0·09	0·13
Mean height	−0·02	0·17
Total boundary length	−0·22*	0·07
Number of alive trees	0·37**	0·03
Number of dead trees	−0·03	0·1

Stepwise multiple regression techniques were used to analyse invertebrate data. Two separate regression analyses were conducted because several management and vegetation variables were intercorrelated. First, invertebrate abundance was regressed against N input (kg ha^{-1}) and the scores of NOM1 (cutting to grazing gradient) and NOM2 (hay or cut once to silage or twice cut gradient). Secondly, regressions with vegetation measurements were performed, which used up to three independent variables (dependent on time of sampling): plant species richness, sward height and sward height variance.

Bird occurrence on fields

Zero counts were obtained for individual bird species on the majority of fields surveyed. Modelling abundance or density using generalized linear model-type analyses was not possible, as the error distribution did not conform to normal or Poisson distributions. Therefore, repeated-measures logistic regression (to take account of non-independence of different visits to the same field in the same year) with the field as the sampling unit was used to examine species–environment relationships, including direct relationships with invertebrate abundance, for all species recorded on more than 5% of occasions. Probability of occurrence was modelled as a function of field area and the independent variable of interest, separately for each species, region and year. In winter, a bird was regarded as present if it was seen on any of the point, perimeter or transect counts, and in summer, if it was seen during any of the timed feeding counts. The full range of independent variables considered is listed in Appendices 2 and 3 for winter and summer, respectively. To test for non-linear relationships, quadratic terms were included in all models, except those for the grazing–cutting principal component score, boundary features and invertebrates. Statistically significant relationships (see Appendices 2 and 3) were those that remained when effects of field area had been accounted for.

Analyses that related birds to invertebrate groups adopted specific rules for defining potential food resources, based on the timing of sampling and the likely food items that would be taken by birds (Wilson *et al*. 1999). Potential winter foods were assessed in autumn and early spring, i.e. immediately before or after winter. For large invertebrate feeders these were from autumn soil cores and Vortis samples (although the latter were not regarded as food for corvids) and from spring soil cores and pitfalls. Potential winter foods for small invertebrate feeders were beetle larvae from soil cores and all taxa from Vortis samples in the autumn, and beetle larvae from spring soil cores and all taxa, except large ground beetles, from spring pitfalls. In summer, food resources for large invertebrate feeders were regarded as all taxa from spring soil cores, pitfalls and the early Vortis samples (individuals > 2 mm). For small invertebrate feeders, potential resources were beetle and fly larvae from spring soil cores, all taxa except large ground beetles from pitfalls, and all taxa from early Vortis samples. Aerial feeding birds were not matched to invertebrate groups. Seed densities were only matched to species that eat significant quantities of seed (see Appendices 2 and 3; Wilson *et al*. 1999).

Results

SEED RESOURCES FOR BIRDS

The autumn seed head count data were examined for field zone effects. A significant effect ($P < 0{\cdot}05$) was found in Bucks in 2002 only, with a greater number of grass seed heads in the centre of the field than elsewhere. Field zone was therefore considered not to be a general factor determining availability of seed resources.

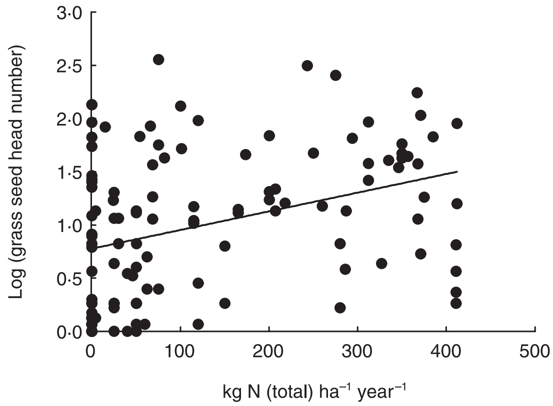

Fig. 1. Relationship between log of grass seed head number per 10 m^2 against total N input for 96 study fields. Each point represents a study field. The regression coefficients are shown against the fitted response, $y = 0{\cdot}0017\ (\pm\ 0{\cdot}00043)x + 0{\cdot}78$ ($\pm\ 0{\cdot}082$), $r^2 = 0{\cdot}12$ (combined data from Devon in 2000 and Bucks in 2000 and 2002).

The relationships between total seed-head number and management intensity were variable. In Devon in 1999, a reduction ($P < 0{\cdot}001$) in total seed-head number was found with increased N input, but not in 2000. However, in Bucks in 2000 there was a linear increase ($P < 0{\cdot}01$) in total seed head numbers with N input, because of an increase in grass seed head abundance at high N input. In 2002, there was no such relationship. An overall significant ($P < 0{\cdot}001$) positive response in grass seed head number with increased N input was found for both Devon and Bucks (Fig. 1). Where high grass seed head numbers were found in late summer on fields receiving high N inputs, they were predominantly *Lolium perenne* and *Lolium multiflorum*. On low input fields, a wider range of grass species contributed to seed resources.

Forb seed head abundance was low regardless of N inputs and there were no significant effects of N input. In Devon, 22% of the study fields had no forb seed heads and 47% had less than five seed heads 10 m^{-2}. In Bucks, 52% of the study fields had no forb seed heads and 86% had less than five seed heads 10 m^{-2}.

INVERTEBRATE FOOD RESOURCES FOR BIRDS

Detailed results of analyses of the relationships between invertebrates and management variables are presented elsewhere (Fuller *et al*. 2003) and summarized in Table 2. Within the three broad groups of invertebrates (soil, epigeal and foliar sward dwelling), some showed consistent associations with management variables whilst others varied in different years/regions. Among the soil-dwelling invertebrates, beetle larvae were less abundant in intensively managed fields. Earthworm numbers were higher in these fields in Devon in spring 1999 and in Bucks in autumn 2000.

Among the epigeal taxa, associations between invertebrate counts and management variables varied between years and regions. However, significantly

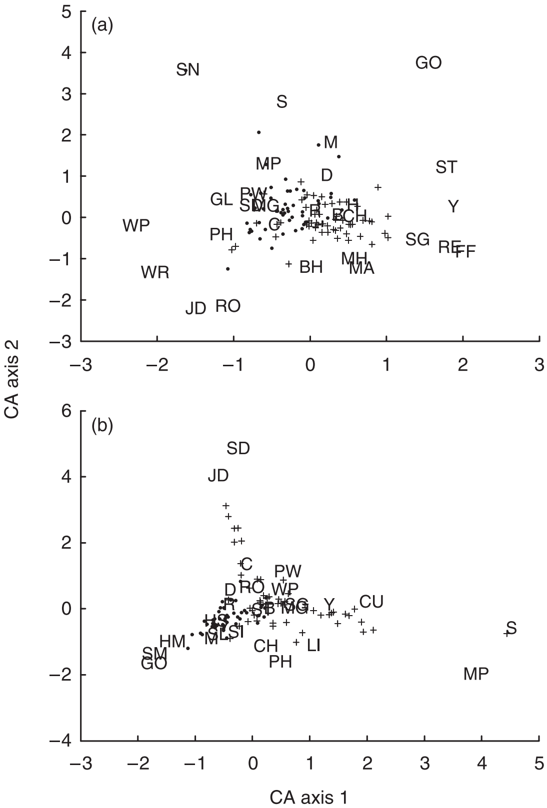

Fig. 2. CA of (a) winter bird assemblages in 48 target fields in each of Bucks and Devon, based on the presence or absence of species recorded in individual fields during point counts/ perimeter walks/transects, and (b) summer bird assemblages on the same target fields based on the presence or absence of species recorded in individual fields during the timed counts. Each point represents the axis score, averaged across years, for individual fields. Only species occurring in > 1% of fields were included in the analyses. Plus signs, Bucks fields; circles, Devon fields. Species symbols in alphabetical order: B, blackbird *Turdus merula* L.; BH, black-headed gull *Larus ridibundus* L.; C, carrion crow *Corvus corone* L.; CH, chaffinch *Fringilla coelebs* L.; CU, curlew *Numenius arquata* L.; D, dunnock *Prunella modularis* L.; FF, fieldfare *Turdus pilaris* L.; GL, grey wagtail *Motacilla cinerea* Tunstall; GO, goldfinch *Carduelis carduelis* L.; H, grey heron *Ardea cinerea* L.; HM, house martin *Delichon urbica* L.; HS, house sparrow *Passer domesticus* L.; JD, jackdaw *Corvus monedula* L.; LI, linnet *Carduelis cannabina* L.; M, mistle thrush *Turdus viscivorus* L.; MA, mallard *Anas platyrhynchos* L.; MG, magpie *Pica pica* L.; MH, moorhen *Gallinula chloropus* L.; MP, meadow pipit *Anthus pratensis* L.; PH, pheasant *Phasianus colchicus* L.; PW, pied wagtail *Motacilla alba* L.; R, robin *Erithacus rubecula* L.; RE, redwing *Turdus iliacus* L.; RO, rook *Corvus frugilegus* L.; S, skylark *Alauda arvensis* L.; SD, stock dove *Columba oenas* L.; SG, starling *Sturnus vulgaris* L.; SI, swift *Apus apus* L.; SL, swallow *Hirundo rustica* L.; SM, sand martin *Riparia riparia* L.; SN, snipe *Gallinago gallinago* L.; ST, song thrush *Turdus philomelos* Brehm; WP, wood pigeon *Columba palumbus* L.; WR, wren *Troglodytes troglodytes* L.; Y, yellowhammer *Emberiza citrinella* L.).

more surface-active beetle larvae were trapped in intensively managed fields in both regions. However, spiders were inversely correlated with N input in Bucks in 2000 and 2002.

Foliar invertebrates tended to be more abundant in less intensively managed, more species rich, grassland. Leafhopper (Auchenorrhyncha) abundance increased with plant species richness in 75%, and with sward height at 50%, of the sites and dates. The abundance of the most common groups (adult beetles, beetle larvae and spiders) increased with sward height on several sites and dates. There was evidence that the abundance of several of the groups with lower average density and patchier distributions (caterpillars, true bugs and sawfly larvae) was also influenced by management intensity. In particular, greater numbers of sawfly larvae were present in less intensively managed, taller and more botanically diverse swards.

WINTER BIRD COMMUNITIES

In winter, the bird communities associated with fields in the two regions differed in their species composition. The majority of species showing regional differences were more frequently recorded in Bucks. CA showed that redwing *Turdus iliacus* (L.), fieldfare *Turdus pilaris* (L.), song thrush, starling and yellowhammer *Emberiza citrinella* (L.) were more strongly associated with fields in this region (Fig. 2a).

The majority of bird species occurred on a low proportion of fields, reflecting generally low densities. Only seven species (blackbird *Turdus merula* (L.), carrion crow *Corvus corone* (L.), starling, redwing, fieldfare, magpie *Pica pica* (L.) and meadow pipit) were recorded on more than 20% of field visits. Eleven of the 26 most frequently recorded species were present on < 10% of field visits.

Results of logistic regression analyses are summarized in Table 3a for the 16 most frequently occurring species (see Appendix 2). Overall, there were few consistent relationships between the presence of bird species and aspects of field management across the two regions; many relationships were only evident in one year and region. The following account emphasizes the main patterns and strongest associations.

Nine of the 16 species showed relationships with N input (eight positive), although relationships were generally evident in just one year–region combination. Carrion crow was an exception because it was more frequently recorded on highly intensive fields in four of the six data sets. There were very few associations with grazing or cutting management, but nine species showed relationships with the presence of grazing animals, with corvids generally associating with them but thrushes avoiding them. Sward height was negatively associated with field use for four large invertebrate feeders in Bucks (rook *Corvus frugilegus* (L.), jackdaw *Corvus monedula* (L.), magpie and starling). In contrast, one small insectivore, meadow pipit, was recorded consistently more frequently in tall swards in Devon. Boundary variables generally had little effect on field usage (see Appendix 2). In Bucks, four species were positively related to abundance of molehills (Table 3a, see Appendix 2) and three to the amount of bare ground.

Relationships with abundance of food resources were surprisingly few in number and generally weak (see

Table 2. Associations between counts of soil, epigeal and foliar invertebrates, the vegetation and management variables. Data are summarized across sites and years. Positive relationships are indicated by ++ (significant positive relationships on 50% or more of all sampling occasions) and + (significant positive relationships on < 50% of all sampling occasions). Negative relationships are indicated by – – (50% or more occasions) and – (< 50%). Calculations take account of instances where contrasting associations were observed at different sites/dates. ND, no data

	Sward height	Plant diversity	N input	Cutting (–) to grazing (+) gradient	Hay (–) to silage (+) gradient
Soil invertebrates					
Earthworms	ND	–	+	+	
Fly larvae	ND	+	–	+	–
Beetle larvae	ND	++	– –		–
Epigeal invertebrates					
All beetles	ND		+		–
Ground beetles	ND	–		– –	
Beetle larvae	ND	– –	++		+
Spiders	ND	++	– –	+	
Foliar invertebrates					
Adult beetles	++	+	–	+	–
Beetle larvae	+		–	++	
Spiders	+				–
Leaf hoppers	+	++	– –	–	–
True bugs	+		+	–	–
Caterpillars		+	–	–	–
Sawfly larvae	++	++	–	–	– –

Table 3. Responses of birds in (a) winter and (b) summer to sward structure and management variables for individual fields. Relationships were tested separately for each season and region. Where significant positive and negative relationships occurred, these were scored +1 and –1, respectively, and summed to give an overall score that was used to assess the generality of the relationships. Positive relationships are indicated by ++ (total score is equal to 50% or more of all possible occasions), + (< 50% of the possible occasions). Negative relationships are indicated by – – (50% or more occasions) and – (< 50%). *n*, number of possible site–year combinations. Bare ground and molehills were not recorded in summer

Species	Sward height	Hay (–) to silage (+) gradient	N input	Presence of livestock	Proportion of bare ground	Number of molehills
(a) **Winter**	$n = 4$	$n = 4$	$n = 6$	$n = 6$	$n = 4$	$n = 6$
Carrion crow			++	+	+	
Rook	–		+	+		
Jackdaw	–		+			
Magpie	–		–	+		–
Blackbird				–		
Fieldfare		–		– –		+
Redwing				–		+
Starling	–		+			
Song thrush				–		
Robin		+	+			
Pied wagtail			+		+	
Meadow pipit	++		+	+	+	+
Skylark						+
Chaffinch						
Snipe				–		
Woodpigeon			+			
(b) **Summer**	$n = 4$	$n = 4$	$n = 4$	$n = 4$		
Carrion crow	– –	+	+	+		
Rook	–	–	+	+		
Jackdaw	–			+		
Magpie	– –					
Blackbird	–		+			
Starling	–					
Swift						
Swallow				–		
House martin	–	–	–			
Robin						
Skylark			–	–		
Woodpigeon	– –		+			

Appendix 2). The strongest positive relationships ($P < 0.01$) were for meadow pipit with seeds in Bucks (2001) and pied wagtail *Motacilla alba* (L.) with autumn spiders in Devon (1999). Only eight of the 976 relationships were significant (six positive and two negative relationships) and may well have represented chance effects.

SUMMER BIRD COMMUNITIES

As in winter, there were marked differences between regions in the summer feeding assemblages. In general, bird communities in Bucks were more diverse and there was more variation between individual fields than in Devon (Fig. 2b). Also, most species occurred on a low proportion of the fields. Ten species occurred on > 20% of occasions (swallow *Hirundo rustica* (L.), house martin *Delichon urbica* (L.), woodpigeon *Columba palumbus* (L.), carrion crow, rook, jackdaw, magpie, blackbird, starling and skylark) and 13 on less than 10% of occasions. Of species occurring on at least 1% of occasions, many of the ground invertebrate feeders and several of the smaller passerines occurred more frequently in Bucks. However, aerial feeders and several thrush species occurred more frequently in Devon.

Relationships between summer bird assemblages, management and other attributes of fields are summarized in Table 3b (see also Appendix 3). There were no consistent relationships with N input or with the hay to silage gradient. Corvids showed positive relationships with the presence of livestock in Bucks. The most striking relationships were with sward height, with eight out of 12 species showing negative relationships. In six cases this occurred in both regions. There were no relationships with boundary features (see Appendix 3) except that in Bucks skylarks avoided fields that had large hedges.

As in winter, there were few relationships with food resources in the summer. Of 480 possible relationships, only 29 were significant (23 negative, six positive). There were no consistent patterns for individual bird species or groups of invertebrates (see Appendix 3).

Discussion

This study aimed to gain a greater understanding of the mechanisms by which agricultural management affects grassland birds and, based on the results, to identify possible management practices that might be used to improve bird diversity and abundance on grassland farms.

The study, in two regions of lowland England, found generally low densities of birds in grass fields in both winter and summer, with most species only being recorded in a small proportion of fields.

RELATIONSHIPS BETWEEN BIRDS AND GRASSLAND MANAGEMENT

The bird communities of the two regions showed considerable overlap in species composition, but there were also some clear differences. In summer and winter, the diversity and abundance of birds tended to be higher in Bucks than Devon, possibly related to the amount of arable and fallow land. Arable cropland and fallow accounted for only 17% of the agricultural land in east Devon, whereas in north Bucks these categories comprised 41% of the agricultural land (Fuller *et al*. 2003). The nature of the surrounding landscape, particularly the presence and extent of arable land, is known to influence grassland bird communities (Robinson, Wilson & Crick 2001; Atkinson, Fuller & Vickery 2002). Alternatively, the low numbers in Devon may be an edge of range effect for several species (Gibbons, Reid & Chapman 1993; Chamberlain & Fuller 2001; Atkinson, Fuller & Vickery 2002).

In winter, there was an overall tendency for intensively managed fields to be used more frequently by birds, particularly large soil invertebrate feeders such as carrion crow and jackdaw. A study of wintering birds in central England also found generalist insectivores were more numerous on fertilized and grazed improved grassland than on unfertilized, cut and grazed, unimproved grasslands (Barnett *et al*. 2004). Studies by Scullion & Ramshaw (1987) and Tucker (1992) indicate that moderate use of organic fertilizer (farmyard manure) may benefit grassland birds by increasing the abundance of soil-dwelling invertebrates (Marshall 1977; Edwards & Lofty 1982; Standen 1984; Unwin & Lewis 1986) or their accessibility by bringing them closer to the surface. In the present study, there was some evidence that soil invertebrates were more abundant in the intensive than extensively managed fields of Devon, corroborating the suggestion that the larger species of soil invertebrate feeders have not been disadvantaged by the intensification of grassland management over the last 50 years.

Few consistent patterns of winter bird occurrence were found that related to particular management intensity/environmental variables. However, there were some significant relationships in at least one year or one region. Rook, jackdaw, magpie and starling showed a negative association with increasing sward height, whereas meadow pipit showed a positive relationship. Perkins *et al*. (2000) also found significant responses to sward height, although the effect differed among species. In the present study, negative relationships were found between the presence of grazing animals in winter and the occurrence of blackbird, redwing, fieldfare and song thrush, whereas crow, rook, magpie and meadow pipit were positively associated with grazing. Tucker (1992) found positive relationships with presence of livestock and field use by magpie and jackdaw [as well as lapwing and golden plover *Pluvialis apricaria* (L.)], but no species were significantly negatively associated with this factor. In agreement with Perkins *et al*. (2000), the presence of bare ground appeared to be important in influencing field use by several species in winter, including crow, pied wagtail and meadow pipit.

In summer, there were also very few relationships between field use by birds and management intensity, and no consistent relationships with the hay to silage gradient or with boundary features. However, sward height was important in influencing field use by several species, fields with shorter swards being used more consistently in both regions by many ground invertebrate feeders.

Several species of passerine birds depend on foliar invertebrates for feeding their nestlings, for example buntings, skylark, whinchat *Saxicola rubetra* (L.) and red-backed shrike *Lanius collurio* (L.). The strong negative relationships between these invertebrates and management intensity (silage cutting and N input), and positive relationships with plant diversity (which has decreased with intensification), suggest that food resources will have declined for these bird species during the breeding season in recent decades. This is probably an important mechanism underlying bird declines in grass-dominated areas.

RELATIONSHIPS BETWEEN BIRDS AND FOOD RESOURCES

Granivorous finches and buntings were particularly rare in both regions, a fact highlighted in previous studies (Chamberlain & Fuller 2001), which may have influenced results. However, as Barnett *et al*. (2004) found, the only species for which seed head abundance was a factor influencing field use was meadow pipit (Bucks 2001), which was also the most abundant species to have a significant seed component in its diet. Wilson *et al*. (1999) found that although grass seeds, and in particular seeds of *Poa* spp., were eaten by a number of farmland birds in winter, seeds of broad-leaved weeds were far more important as food. Seeds of broad-leaved species were rare in the grasslands studied, rendering them unsuitable for seed-eating species. Lack of arable crops in grassland-dominated landscapes, as exemplified by the Devon region, severely limits the foraging opportunities for seed-eating birds in winter (Atkinson, Fuller & Vickery 2002) and could also influence local breeding densities (Robinson, Wilson & Crick 2001; Gillings *et al*. 2005).

Perhaps our most unexpected result was the lack of any clear relationships between invertebrate food abundance and field use by birds. It is possible that the timing of sampling for invertebrates did not give an adequate index of food abundance in winter, although this could not have been a problem in summer when bird and invertebrate sampling were carried out at similar times (Fuller *et al*. 2003). It is also possible that birds were feeding in areas or on invertebrates that were not sampled, such as localized 'hot spots' of high invertebrate abundance, or that size classes selected by birds did not match those adopted in our model (> 2 mm). However, a sampling mismatch between the spatial or temporal pattern of food abundance and bird occurrence seems unlikely to explain the overwhelming absence of a clear relationship.

Failure to find a link between field use and food abundance, coupled with the strong negative relationships with sward height, suggests that access to food supplies, rather than food abundance *per se*, could be the critical factor in determining field use. This is supported by the observation that, while field use by birds was generally negatively related to sward height, the opposite was true for sward-dwelling invertebrates (Table 2).

Several recent studies on granivorous species have highlighted the importance of food accessibility as well as abundance in determining intake rates of birds and habitat selection (Moorcroft *et al*. 2002; Whittingham & Markland 2002), and the same is probably true for invertebrate feeders (Perkins *et al*. 2000). The selection of short swards may also reflect the increased ability to detect avian predators (Whittingham & Evans 2004). Invertebrate abundance and richness tends to increase as the structural complexity of swards increases. However, many birds prefer to forage in short swards, including several passerines such as skylark and starling (Feare 1984; Cramp 1988; Cramp & Perrins 1994; Wilson *et al*. 1997; Schön 1999; Deveraux *et al*. 2004). Thus, areas of short sward or bare earth, where prey is accessible to birds, next to patches of structurally complex swards, where prey is relatively abundant, may increase the suitability of grassland as foraging habitat.

APPROACHES TO IMPROVING HABITAT QUALITY FOR GRASSLAND BIRDS

Most agri-environment schemes for grassland have focused on reducing overall levels of management intensity through reductions in N inputs and grazing levels. Low input, extensive livestock systems have historically created and maintained the ecological diversity of unimproved grasslands in Europe, and a relatively low intensity of management is likely to be central to any attempts to restore grassland biodiversity (Vickery *et al*. 2001). Restoring habitat quality for birds in grassland landscapes will require the creation of microhabitat diversity at the scale of individual fields and whole farms to increase prey abundance and accessibility. At the whole-farm scale, this should involve the integration of extensive and intensive management in different fields, possibly by rotating late hay cutting and low-moderate grazing intensity and/or by creating diverse sward structures through adopting different grazing intensities (and different N input) (Buckingham, Atkinson & Rook 2004).

At the within-field scale, management could be directed at margins (Haysom, McCracken & Foster 1999; Haysom *et al*. 2000, 2004; Vickery, Carter & Fuller 2002) or field centres (analogous to 'skylark scrapes' in arable systems; Morris *et al*. 2004). For example, in silage systems an uncut and/or unfertilized field margin may provide a reservoir of invertebrates able to recolonize the grass sward after cutting, thereby offering enhanced feeding opportunities for bird species that prefer to forage close to the field boundary, such as yellowhammer and blackbird. In livestock systems, this could be achieved by fencing margins or field corners on intensively grazed land. Provision of such 'refugia' would need to take account of the seasonal movements and differing mobility of invertebrates. Although there have been few studies of the spatial dynamics of invertebrates in grass fields, large fields may require special measures analogous to beetle banks in arable fields (Thomas, Wratten & Sotherton 1991). Soil invertebrate abundance may also be enhanced by the use of farmyard manure (Scullion & Ramshaw 1987; Tucker 1992) but the role of soil moisture on soil invertebrate abundance requires further investigation.

The establishment of low-input field margin strips will eventually create botanically and structurally diverse swards rich in seeds as well as invertebrates. On intensive livestock farms, the abundance of grass seed heads could be increased by fencing off field margins after mid-summer grazing (or cutting) and avoiding late summer/early autumn grazing. The cultivation and fallowing of field margin strips could also be beneficial, particularly where the seed bank of *Poa annua* is high, while direct sowing of different seed mixtures would broaden the range of seed resources. At the field scale, an increase in number of hay meadows prior to aftermath grazing would provide foraging habitat for granivorous passerines (Barnett *et al*. 2004), although over a very short period in autumn. Increasing bird diversity through management to enhance food resources for granivorous species is most likely to be achieved by incorporating arable cropping into grassland farming systems, i.e. re-establishing more mixed farming in grass-dominated landscapes (Evans 1997; Atkinson, Fuller & Vickery 2002; Benton, Vickery & Wilson 2003).

Smaller-scale measures aimed at increasing food accessibility could also play a role at the local scale. The challenge is to create habitat patches that will enhance food/prey accessibility for birds throughout the year without causing major management problems for the farmer. Appropriate management prescriptions must be packaged into an agri-environment scheme that provides demonstrably beneficial effects to farmland birds (Kleijn & Sutherland 2003). Specific examples are the provision of tall vegetation and bare ground within otherwise intensively managed short swards, or bare ground within fields closed for a silage or hay cut. Feeding patches should have a large edge-to-area ratio, such as long narrow or irregular shaped patches, to enhance the interface between patch and crop. Patches of bare soil within grassland can be created using herbicides or mechanical disturbance such as rotavation, or by using salt licks to promote a localized poaching. In paddock grazing systems, electric fencing could create an ungrazed strip between paddocks.

CONCLUSION

We have demonstrated that the relationships between birds and their plant and invertebrate food supplies in grassland, and how these are affected by management practices, are extremely complex and species-specific. Developing broad plans for managing grassland more sensitively for birds is likely to be extremely difficult. The creation of swards rich in plant species and supporting diverse, abundant invertebrate communities may not necessarily create optimal conditions for grassland birds. The accessibility of prey is a key issue for birds in grassland systems. There is a need to create microhabitat diversity at the scale of individual fields and whole farms, not only to increase invertebrate abundance but also, and crucially, to improve the accessibility of prey to foraging birds. Experimental studies that manipulate grassland microstructure at a range of scales, whilst linking foraging behaviour to subsequent breeding success, are much needed.

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Supplementary material

The following supplementary material is available for this article online:

Fig. S1. Map of study areas.

Appendix 1. Sampling regime.

Appendix 2. Relationship between birds and food abundance and environmental variables in winter.

Appendix 3. Relationship between birds and food abundance and environmental variables in summer.

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