

Ecography 35: 134–145, 2012

doi: 10.1111/j.1600-0587.2011.07040.x

© 2011 The Authors. Ecography © 2012 Nordic Society Oikos

Subject Editor: Thorsten Wiegand. Accepted 5 April 2011

Multiple habitat associations: the role of offsite habitat in determining onsite avian density and species richness

Martin Dallimer, Andrew M. J. Skinner, Zoe G. Davies, Paul R. Armsworth and Kevin J. Gaston

M. Dallimer (*m.dallimer@sheffield.ac.uk*), A. M. Skinner, Z. G. Davies, P. R. Armsworth and K. J. Gaston, *Biodiversity and Macroecology Group, Dept of Animal and Plant Sciences, Univ. of Sheffield, Sheffield S10 2TN, UK. Present address of ZGD: Durrell Inst. for Conservation Ecology, Univ. of Kent, Canterbury CT2 7NR, UK. Present address of PRA: Dept of Ecology and Evolutionary Biology, 569 Dabney Hall, Univ. of Tennessee, Knoxville, TN 37996-1610, USA.*

Many animal populations continue to decline despite occurring in protected areas or on sympathetically managed sites. Frequently, this is because a specific habitat patch may not fulfil all the niche requirements of a threatened species. For instance, species often move between, and make use of, multiple habitat types for breeding, roosting and feeding within the same landscape. These cross-habitat interactions present a challenge for conservation. Here we quantify how the habitat associations of individual species and assemblages occurring within two distinct but adjacent habitat types (moorland and farmland) determine a suite of density and richness indicators, using the bird community of the English uplands as a case study. There was a clear association between onsite avian density and richness and offsite habitat structure (e.g. vegetation height, percent cover of dominant plant species, land management practices). Although such effects are not universal across all species and assemblages, where present (for five farmland and three moorland indicators) the increase in explanatory power offered by including offsite habitat structure can be large. By constructing scenarios of possible changes to management practice on both moorland and farmland, we demonstrate a real conservation benefit can be obtained by altering management in offsite habitats. For example, reducing burning intensity on moorland can result in a five-fold increase in snipe *Gallinago gallinago* density on farmland, without an alteration in farmland habitat. For one species (Eurasian curlew *Numenius arquata*), we demonstrate the frequency with which birds move between and utilise farmland and moorland during the breeding season, and therefore the importance of both habitat types to maintaining population densities. The multiple habitat dependency phenomenon quantified here is common and not restricted to birds. The successful conservation of many threatened species will thus depend on coordinated cross-habitat management.

Habitat management, often through the establishment of protected areas, is a cornerstone of biodiversity conservation (Gaston et al. 2008). Nonetheless, many species continue to decline even within existing protected area networks (Sim et al. 2005, Moritz et al. 2008, Newmark 2008), and local population extinctions can occur without apparent changes in habitat quality (Beever et al. 2003). This may be the result of external factors such as diffuse pollution (Lee 1998), climate change (Thomas et al. 2004), invasive species (Coote and Loeve 2003), small population sizes and stochastic events, or, indeed, a combination of these (Benning et al. 2002, Crowl et al. 2008). However, it may also be due to conservation policy and management largely overlooking the importance of habitat quality within the matrix surrounding a protected area (Franklin and Lindenmayer 2009).

There are many circumstances in which animals use different habitat types on a localised and frequent basis. For example, a species may breed or roost in one habitat but use another for feeding (Weiss et al. 1988, Whittingham et al. 2000, Robson et al. 2002, Mackie and Racey 2007), meaning that individuals require different resources from a number of distinct habitat types ('landscape complementation';

Dunning et al. 1992). In such cases, maintaining a persistent breeding population relies on the condition of multiple habitat types within the same landscape. These spatial interactions can represent a conservation challenge, especially where protected area designation focuses on a single habitat to the exclusion of the adjacent matrix (e.g. Special Protection Areas (SPA) in the European Union are designated based on breeding sites and therefore can exclude important matrix, such as for UK moorland, where SPAs do not encompass neighbouring agricultural areas), and/or if the establishment of a protected area leads to unforeseen negative impacts on the surrounding habitats (e.g. 'leakage'; Armsworth et al. 2006, McDonald et al. 2007).

In attempting to understand such spatial relationships, two main approaches have been taken. First, from a behavioural perspective, radio-tracking techniques have been extensively employed to explore how individuals use resources distributed across a landscape (Şekercioğlu et al. 2007, Barbaro et al. 2008, Finlayson et al. 2008). While these investigations allow for a detailed appraisal of movements and habitat preferences, their conclusions are frequently limited to a small number of individuals from a handful of target

species. Second, previous landscape-scale research has shown that the extent of different land-uses within the matrix buffering focal habitat patches can play a role in determining species richness and abundance (Baillie et al. 2000, Feldman and Krannitz 2004, Wethered and Lawes 2005, Martin et al. 2006, Ghilain and B elisle 2008). However, such studies rarely assess habitat structure (e.g. vegetation height, percent cover of dominant plant species, intensity of management practices) of both on and offsite areas for maintaining population sizes and often focus solely on extent of habitat. Here we take a new approach, determining and quantifying how species associations with habitat structure across multiple habitat types within the same landscape influence population densities across the entire community, using the birds of the English uplands as a case study. This region consists of two distinct abutting habitats, comprising moorland intermixed with areas of pastoral farmland. While the moorland has been regionally and internationally recognised as important for biodiversity conservation (Thompson et al. 1995), the adjacent farmland has seldom been included in protected areas designated for their biodiversity interest. The two habitats therefore receive radically different management.

Despite the divergent management and levels of protection, the avian communities on moorland and farmland share several species, some of which use both habitats through their breeding season (Ratcliffe 1990, Whittingham et al. 2000, Robson et al. 2002). In common with lowland birds, agricultural intensification is a major cause of upland bird declines (Henderson et al. 2004, Sim et al. 2005) but, for many species characteristic of the moorland–farmland interface, the precise reasons for the substantial losses remains uncertain (Fuller et al. 2002, Woodhouse et al. 2005). The English uplands therefore offer a particularly appropriate study system for examining the contribution that associations with habitat structure across multiple land-uses play in maintaining populations, of both individual species and overall avian density and richness.

In this paper, we first test the prediction that species density and in one habitat type (e.g. farmland) will be influenced by the characteristics of both habitats that make up the landscape, and hence by the characteristics of the nearby habitat (e.g. moorland). Second, by building scenarios of land management (and hence habitat) change that could be expected under intensification or extensification of upland agriculture, we examine whether multiple habitat dependency could have repercussions for avian biodiversity conservation in the UK uplands. Third, we determine whether these patterns could be driven by direct movements of birds between habitat types by following individual Eurasian curlew *Numenius arquata*. If distinct habitat types do provide separate resources, we would expect individuals to allocate varying amounts of time to different activities within the two habitat types and to move frequently across habitat boundaries.

Methods

Study system

This study centres on the Peak District in northern England (Fig. 1), which is a region of hills characterised by heather



Figure. 1. The Peak District National Park in northern England. Striped area indicates the extent of moorland and all farm sites were within 2 km of this. Inset shows location of the Peak District in Britain.

Calluna vulgaris dominated moorland, principally managed for livestock farming and red grouse *Lagopus lagopus* shooting. The Peak District forms the focus of many types of protected area designation; for instance, the region as a whole is subject to planning restrictions that are the basis of its National Park status, while the moorland is specifically covered by the Southern Pennine Moors SPA (Stroud et al. 2001) which is intended to protect the region's breeding bird interests.

Bird surveys

We surveyed 37 paired sites, each comprising an area of moorland and an area of farmland habitat which fell within 2 km of moorland (Fig. 1). As property-level factors are important in determining patterns of avian species richness on farms in this landscape (Dallimer et al. 2009), where possible pairs were selected so that the moorland and farmland sites were owned or managed by the same individual (this was not possible in nine cases where the study farm did not manage the nearby moorland). The mean distance between the moorland and farmland sites within a pair was 2.03 km (range 0.65–4.95). The mean distance between moorland

sites was 20.8 km (range 2.9–37.2). Moorland was defined as all unenclosed land, predominantly semi-natural and upland in character, and used primarily for extensive grazing (Defra 2008). Farmland was defined as any land enclosed into fields by walls or fences and dominated by grassland intensively managed by grazing and mowing, which may retain some semi-natural characteristics. Moorland bird surveys were carried out based on standard methodologies (Newson et al. 2005) by a single observer walking, at a constant slow speed, 2 km of parallel transects spaced 500 m apart in a 1 × 1 km square (100 ha). Only birds resident in, or making use of, the surveyed area were counted and those flying over were excluded. Farmland bird surveys covered individual properties. Where needed, parallel transects were placed 400 m apart to ensure full coverage of the property while avoiding double counting the same parts of the farm. This enabling farmed land to be surveyed using a comparable technique to that used on moorland. On average, 95.0 ha (SD 66.7 ha) of farmland were surveyed per property.

During surveys, on encountering a bird, the distance and angle from the observer to the bird was measured using a laser rangefinder (Leica LRF1200) and compass. This enabled the perpendicular distance of the bird from the transect

to be calculated and distance sampling methodology to be employed to estimate abundance (Thomas et al. 2010). Bird surveys were carried out between one and three hours after sunrise, on two separate visits at least six weeks apart between 28 March and 5 July 2007.

When bird numbers are converted to density estimates, detectability must be taken into account. This can be influenced by the structural characteristics of the habitat being surveyed and the cue that was used to locate the bird (i.e. whether the individual was only heard or was seen as well as heard). We took into account heterogeneity in detectability arising from habitat type (moorland or farmland) and cue type (seen or heard) by including these as factor covariates when calculating the detection functions. Species-specific functions were estimated for 33 species with 60 or more registrations, with and without both factor covariates. For the remaining less common species, a detection function was estimated using registrations for a group of similar species (Supplementary material Appendix 1). Subsequently, candidate models of the detection function were chosen and tested against the data. Model selection was based on minimum Akaike information criteria (AIC) and χ^2 goodness of fit tests. The selected best supported detection

Table 1. Definitions, median and range, of variable used in the analysis of the patterns of avian density across paired farmland and moorland sites in the Peak District, northern England.

Farmland habitat variable	Median	Interquartile range	Description
Intensive grass	0.87	0.72–0.93	The proportion of surveyed fields that were improved (following the Phase 1 Habitat Survey definition; JNCC 2007). High values equate to more intensive agricultural management.
Mowed land	0.31	0.05–0.48	The proportion of surveyed fields that were cut for hay or silage as opposed to solely being used for grazing. Higher values equate to more intensive agricultural management.
Vegetated boundaries	0.08	0.03–0.15	The proportion of field boundaries that were vegetated (hedges, woods). Lower values are expected with intensive agricultural management.
Trees	158	58–375	The total number of trees within surveyed fields. Lower values are expected with intensive agricultural management.
Rush cover	0.03	0.01–0.06	The proportion of surveyed fields with rush (mainly <i>Juncus effusus</i>) cover. Lower values are expected with intensive agricultural management.
Wet features	0.14	0.06–0.34	The proportion of surveyed fields with wet features (ditches, ponds, streams). Lower values are expected with intensive agricultural management.
Moorland habitat variable	Median	Lower – upper quartile	Description
Heather cover	0.45	0.22–0.56	The median proportion of all surveyed quadrats on a site that was covered by heather <i>Calluna vulgaris</i> . Lower values are expected with intensive management.
Grass cover	0.19	0–0.81	The median proportion of all surveyed quadrats on a site that was covered by grass. Higher values are expected with intensive management.
Sedge cover	0.08	0–0.40	The median proportion of all surveyed quadrats on a site that was covered by sedge, including <i>Eriophorum</i> species. Lower values are expected with intensive management.
Gorse cover	0.04	0–0.27	The median proportion of all surveyed quadrats covered by gorse <i>Ulex europaeus</i> . Lower values are expected with intensive management.
Burning	0.47	0–1.69	The intensity of any managed burning carried out on the site, assessed on a scale from 0 (very recent burns with still-charred vegetation present) to 5 (no evidence of burning). Low values equate to an intensive burning management regime.
Vegetation height	42.42 cm	32.49–52.47 cm	The maximum height of vegetation. Lower values are expected with intensive management.

function model (Supplementary material Appendix 1) was then applied to the number of encounters on each transect to give a species-specific estimate of the density of individuals. Distance data were analysed using Distance 5.0 release 2 (Thomas et al. 2006).

We generated a suite of avian density and richness indicators based on survey data. The density of seven individual species of conservation concern (snipe *Gallinago gallinago*; Eurasian curlew *Numenius arquata*; meadow pipit *Anthus pratensis*; willow warbler *Phylloscopus trochilus*; linnnet *Carduelis cannabina*; reed bunting *Emberiza schoeniclus* and skylark *Alauda arvensis*) that occurred sufficiently often on both habitats to allow analysis, was calculated for each moorland and farmland site. In addition the density and species richness of all birds (Total), and of two assemblages of greater conservation relevance, namely upland specialists (Upland specialists), and species of conservation concern (Conservation concern; Supplementary material Appendix 2), were compiled for each farm or moor site.

Habitat surveys

Within farmland, habitat surveys assessed those variables that have been shown to influence avian abundance or breeding success in the UK uplands (Robson et al. 2002, Pearce-Higgins and Yalden 2003) and for farmland birds in general (Atkinson et al. 2005, Whittingham et al. 2005, Dallimer et al. 2009; Table 1). Each surveyed field was characterised according to whether it was improved grassland (following the Phase 1 Habitat Survey definition; JNCC 2007), cut for silage or hay in the year of the survey, the proportion of the field boundaries that were vegetated with hedges or woodlands (as opposed to unvegetated fences and walls), the number of trees present in the surveyed fields, the proportion of rush cover and the proportion of fields with wet features. Moorland sites covered the full range of habitats typical of the unenclosed extensive grazing in the region, including *Calluna*-dominated sites as well as areas of gorse *Ulex europaeus* and bracken *Pteridium aquilinum*. To assess moorland habitat structure, quadrats (50 × 50 cm) were placed every 100 m along four parallel transects 200 m apart (44 per survey square). In each quadrat, vegetation height, vegetation cover and whether or not managed burning had been conducted, were recorded. Mean values were calculated for each site.

Species–habitat relationships

We modelled the relationship between the avian density/richness indicators and habitat characteristics using linear regression. To meet the assumptions of the modelling process, densities of individual species were square-root transformed prior to analyses and a Poisson error structure, corrected for over-dispersion (analogous to a negative binomial distribution) where necessary (Crawley 2007), was used to model the response of assemblage-level richness. All possible model combinations were constructed for the predictor variables, using AICc comparisons to identify the most parsimonious model (Burnham and Anderson 2002). For each indicator, we determined: 1) model weights for candidate models, 2) the relative importance of each variable in explaining avian density/richness, by calculating w_i , the Akaike weight, and 3) model explanatory power. In addition, poor predictor variables can still have high w_i . A single randomly generated variable was therefore added to the existing data (Whittingham et al. 2005). Five hundred model sets were generated, and the w_i for the random variable was calculated. Variables that offer poor predictive power fall within the confidence intervals of this random variable. All calculations were carried out in R 2.10.1 (R Development Core Team 2009).

The above modelling procedure was initially followed for onsite only habitat variables (i.e. farmland habitat for farmland avian density/richness indicators and moorland habitat for moorland avian density/richness). We also wished to understand the importance of offsite habitat associations (i.e. moorland habitat structure for farmland birds and farmland habitat structure for moorland birds). This was assessed by combining on and offsite habitat variables in the following way. First we built two sets of models using onsite only habitat variables for farmland and moorland sites respectively. For each avian density/richness indicator, we selected variables from these two model sets with a w_i that was greater than the 80% confidence interval of the random variable in each for combination in a final model. These combined models therefore included predictors with the highest relative importance from both habitat types, and may thus contain offsite measures (e.g. moorland and farmland habitat variables predicting moorland curlew densities). If no variable had a w_i greater than the 80% confidence interval of the random variable for either model set, then combined models were not constructed.

Table 2. Mean bird density estimates for moorland and farmland sites and correlation coefficients (significant relationships highlighted in bold) for the association between species density on moorland and farmland habitat types in the Peak District, northern England.

	Farm density (mean birds ha ⁻¹ /range)	Moor density (mean birds ha ⁻¹ /range)	Correlation coefficient	p
Total	2.10 (0.77–3.56)	2.19 (1.21–3.80)	–0.05	0.80
Upland	0.50 (0–2.23)	1.73 (0.92–3.08)	–0.11	0.57
Cons concern	0.97 (0.14–2.80)	1.94 (1.16–3.44)	–0.26	0.15
Eurasian curlew	0.04 (0–0.18)	0.04 (0–0.18)	0.32	0.08
Meadow pipit	0.34 (0–1.21)	1.34 (0.59–2.71)	0.04	0.84
Snipe	0.06 (0–0.48)	0.02 (0–0.27)	0.37	0.04
Skylark	0.08 (0–0.57)	0.09 (0–0.29)	–0.08	0.65
Linnnet	0.07 (0–0.40)	0.05 (0–0.46)	0.11	0.56
Willow warbler	0.05 (0–0.16)	0.03 (0–0.22)	–0.03	0.85
Reed bunting	0.01 (0–0.10)	0.02 (0–0.15)	0.12	0.51

Combined models were weighted by the inverse of the distance between the paired sites to account for any spatial autocorrelation. We used AICc comparisons to determine whether the combined models offered a better explanation for onsite avian density/richness indicators than onsite habitat variables alone.

A statistically important link between onsite density/richness and offsite habitat variables may not translate into meaningful conservation management recommendations. Therefore where the combined on and offsite habitat models offered the most parsimonious explanation for variations in avian density/richness, we constructed scenarios to illustrate the likely impact of land management changes, representing either an intensification or extensification of agricultural practices, leading to alterations to current habitat characteristics. Scenarios were based on the range of variation in land management practices and habitat structure recorded in the study; specifically, scenarios assumed that management actions would result in the habitat variables with the highest relative importance (w_i) for each habitat type (farmland and moorland) to change from their current median to either the 1st or 3rd quartile.

Management could take place entirely on farmland, moorland, or on both habitats in parallel, resulting in a matrix of nine possible scenarios (1st quartile, median and 3rd quartile for the farmland habitat variable cross-factored with the 1st quartile, median and 3rd quartile for the moorland habitat variable). This allows a direct comparison of when offsite habitat management (either alone or in parallel with onsite management) leads to a greater change in avian density or richness.

Curlew movements and behaviour

Direct causal evidence of the role that both habitat types could play in determining species densities can be gathered by observations of individuals moving between the two habitat types. To quantify these effects, vantage-point watches of focal Eurasian curlew individuals were carried out at five locations covering the eastern edge of the Peak District, noting movements and behaviour. Individual behaviour was recorded every minute for a minimum of ten minutes or for as long as the bird remained in view. Behaviour was

Table 3. Akaike weights (w_i) for each explanatory variable included in the regression models exploring the relationship between avian density/richness indicators and onsite habitat characteristics for: (a) farmland; and (b) moorland. Threshold gives the 80% CI for the random variable in each model. N is the number of variables (highlighted in bold) for which $w_i >$ threshold, r^2 gives the explanatory power of a model including these variables (e.g. Curlew density = intensive grass + vegetated boundaries + wet features). Where no variable had a $w_i >$ threshold for moorland or farmland (meadow pipit, linnet and upland density), combined models were not constructed.

(a)

Avian density (birds ha ⁻¹)/richness	Intensive grass	Mowed land	Vegetated boundaries	Trees	Rush cover	Wet features	Threshold	N	r ²
Curlew	0.735	0.199	0.628	0.497	0.342	0.818	0.535	3	0.45
Snipe	0.281	0.309	0.200	0.222	0.972	0.314	0.394	1	0.42
Meadow pipit	0.946	0.281	0.202	0.726	0.653	0.340	0.373	3	0.48
Willow warbler	0.210	0.199	0.243	0.948	0.623	0.233	0.348	2	0.30
Linnet	0.265	0.243	0.234	0.212	0.226	0.226	0.399	0	0.00
Reed bunting	0.394	0.226	0.194	0.493	0.685	0.474	0.440	3	0.32
Skylark	0.290	0.258	0.237	0.962	0.607	0.244	0.361	2	0.36
Total	0.230	0.207	0.212	0.501	0.260	0.244	0.419	1	0.08
Cons concern	0.671	0.224	0.402	0.304	0.694	0.333	0.392	3	0.35
Upland	0.948	0.193	0.288	0.417	0.800	0.433	0.425	3	0.51
Total richness	0.202	0.704	0.201	0.534	0.222	0.273	0.400	2	0.18
Cons concern richness	0.419	0.467	0.279	0.205	0.219	0.216	0.297	2	0.20
Upland richness	0.335	0.487	0.489	0.202	0.298	0.318	0.322	3	0.27

(b)

Avian density (birds ha ⁻¹)/richness	Heather cover	Grass cover	Sedge cover	Gorse cover	Burning	Vegetation height	Threshold	N	R ²
Curlew	0.252	0.303	0.294	0.216	0.418	0.441	0.342	2	0.12
Snipe	0.235	0.922	0.287	0.197	0.530	0.344	0.386	2	0.31
Meadow pipit	0.249	0.218	0.293	0.210	0.234	0.394	0.398	0	0.00
Willow warbler	0.564	0.300	0.451	0.466	0.555	0.244	0.462	3	0.27
Linnet	0.304	0.219	0.343	0.300	0.380	0.753	0.384	1	0.22
Reed bunting	0.223	0.245	0.276	0.591	0.212	0.560	0.375	2	0.18
Skylark	0.396	0.480	0.289	0.205	0.308	0.707	0.378	3	0.27
Total	0.224	0.216	0.442	0.348	0.230	0.579	0.399	2	0.19
Cons concern	0.221	0.239	0.284	0.235	0.215	0.494	0.406	1	0.09
Upland	0.220	0.299	0.253	0.221	0.226	0.241	0.381	0	0.00
Total richness	0.776	0.262	0.321	0.879	0.214	0.217	0.374	2	0.35
Cons concern richness	0.460	0.228	0.363	0.544	0.601	0.250	0.390	3	0.42
Upland richness	0.259	0.267	0.338	0.230	0.854	0.223	0.283	2	0.50

classified as foraging, vigilance, loafing, reproductive or other. For each movement (any flight or directional walk that did not involve foraging), the location of the start and end points was recorded on a 1:10 000 scale map, either by reference to physical features, or by calculation in relation to the vantage point using a laser rangefinder and compass. Movement length was calculated from these points and habitat type noted. Although curlews are present in the study area from mid-February, we restricted our observations to the breeding season which we defined as starting when territory establishment began and ending when all adult curlews had left the study area (2 April–15 July 2008).

We acknowledge that the resulting movement and behavioural data are not strictly independent as we were unable to identify focal individuals between visits. Radiotracking or colour marking birds could have overcome this difficulty. However, we were interested in adult behaviour throughout their breeding season, and adult curlew cannot be safely trapped on upland breeding grounds until the end of the incubation period due to a high risk of nest desertion (Robson 1998).

Results

Species–habitat relationships

Across both habitat types, 90 species were encountered. Of these, 83 occurred on farmland, 50 on moorland and just under half (43) were shared between the two habitat types. Our results for Total, Upland specialist and Conservation concern density refer to these shared species (Supplementary material Appendix 2). The mean density of Upland specialists and species of Conservation concern was notably higher on moorland compared to farmland; however Total density was broadly similar (Table 2).

Of the seven individual species examined, the meadow pipit was the most abundant, occurring at densities of up to 2.71 birds ha⁻¹ on moorland sites. The correlation coefficients between bird densities on the paired moorland and farmland sites ranged from -0.26 for Conservation concern species to 0.37 for the snipe, with only the latter relationship significant (Table 2). There is, therefore, little evidence for a direct correlation in density between habitat

Table 4. Combined models using onsite and offsite habitat variables for avian density/richness indicators. For each indicator, where the combined model is more parsimonious (lower AICc) than the onsite only model (Table 3), the proportional change in r^2 is given. Habitat variable names in bold were the most important predictors with the highest w_i and were used for scenario building. For example for willow warbler density, the onsite only model for farmland was the most parsimonious and therefore no details of the combined model are presented. In contrast, there was a 29% improvement in r^2 for willow warbler density on moorland when offsite habitat characteristics were included. Scenarios examining the conservation management relevance of offsite variables were therefore built including farmland Rush cover and moorland Heather cover (Table 5, Fig. 2).

Avian density (birds ha ⁻¹)/richness	Onsite habitat	Onsite model		Combined model		Proportional r^2 change	Farmland variables (w_i)	Moorland variables (w_i)
		r^2	AICc	r^2	AICc			
Curlew	Farmland	0.45	-51.73	0.52	-52.83	0.15	Wet features (0.72) , Intensive grass (0.68), Vegetated boundaries (0.50)	Burning (0.69)
	Moorland	Null	Null	Null	Null			
Snipe	Farmland	0.42	-21.66	0.51	-24.31	0.21	Rush cover (1.00)	Burning (0.82)
	Moorland	0.31	-44.34	0.35	-42.99			
Willow warbler	Farmland	0.30	-50.62	0.32	-48.69			
	Moorland	0.27	-34.24	0.34	-34.73	0.29	Rush cover (0.52)	Heather cover (0.68) , Burning (0.56), Gorse cover (0.55)
Reed bunting	Farmland	0.29	-60.06	0.30	-60.49	0.03	Wet features (0.57)	Vegetation height (0.56)
Skylark	Moorland	0.12	-38.71	0.17	-38.09			
	Farmland	0.36	-20.16	0.38	-18.50			
Total	Moorland	0.25	-19.50	0.27	-17.30			
	Farmland	0.08	72.55	0.31	65.85	3.04	Trees (0.23)	Vegetation height (0.91) , Sedge cover (0.90)
Cons concern	Moorland	0.15	63.87	0.15	66.35			
	Farmland	0.31	4.80	0.36	5.24			
Total richness	Moorland	0.09	-7.83	0.19	-9.13	1.18	Intensive grass (0.67)	Vegetation height (0.48)
	Farmland	0.18	216.50	0.19	218.96			
Cons concern richness	Moorland	0.35	177.82	0.44	176.20	0.25	Mowed land (0.73)	Heather cover (0.95) , Gorse cover (0.84)
	Farmland	0.20	167.41	0.27	165.84	0.34	Mowed land (0.44)	Burning (0.60)
Upland richness	Moorland	0.35	151.97	0.45	151.98			
	Farmland	0.22	138.57	0.16	140.81			
	Moorland	0.40	130.58	0.44	132.52			

types. However, this does not preclude the possibility that the characteristics of one habitat type influence the densities of birds in another.

For farmland avian indicators, the explanatory power of onsite variables ranged from an r^2 of 0.00 (linnet) to 0.51 (Upland specialists density; Table 3a). Similarly, for moorland avian indicators, models containing onsite only variables had an explanatory power of between 0.00 (meadow pipit and Upland specialist densities) and 0.50 (Upland specialist richness; Table 3b). Combined models (Table 4) were built for all avian density/richness indicators where at least one habitat variable from both farmland and moorland had a w_i greater than the random variable 80% confidence interval threshold value (Table 3). In the majority of cases, onsite habitat models remained more parsimonious, indicating that offsite habitat was not an important consideration. Nevertheless, for eight indicators (out of a total of 18), the combined model was more parsimonious. The proportional increase in explanatory power gained by including offsite habitat characteristics ranged from a 3% (reed bunting on farmland) to 304% (Total density on farmland) improvement compared to onsite habitat alone. We therefore constructed scenarios to examine the conservation management relevance of these offsite relationships (Table 5, Fig. 2a–h).

In all cases where combined models were constructed, changing land management on both farmland and moorland in parallel delivered greater improvements to the avian density/richness indicators than interventions on a single habitat (Fig. 2). For all individual species, management scenarios focussed just onsite led to better conservation outcomes than if management were changed for offsite habitat only. However, for three of the assemblage-level indicators (Total richness on moorland, Conservation concern richness on farmland and Total density on farmland), the offsite management scenarios resulted in greater improvements. In the case of Total avian richness on moorland, reducing mowed land coverage on farms led to an extra 2.55 species on moorland in comparison to reducing heather cover onsite.

Curlew movements and behaviour

For the Eurasian curlew we established that one possible mechanism for relationships between onsite avian density and offsite habitat structure is direct movements of individuals between habitats. We identified 25 breeding pairs, either by locating nests (five were found, all of which were on moorland) or observing simultaneous display flights and territorial behaviour. In total, 652 movements were recorded; 24.2% (158) of these were between habitat types, but the proportion of between-habitat movements varied among locations (range 7–56%). At all locations, continuous blocks of both moorland and farmland were large (their areas extending to several thousand hectares), so there is no a priori reason why the length of movements should differ when birds cross habitat boundaries. Nevertheless, movement length ranged from 4 to 1400 m (mean = $247.7 \pm \text{SD } 207.4$ m), and was significantly longer ($F_{1,650} = 66.25, p < 0.000$) between habitat types (359.2 ± 232.8 m) than within (212.1 ± 185.2 m; Table 6a, Fig. 3). Between-habitat movements remained significantly longer when we took into account the effect

Table 5. Parameter estimates (SE) from regression models exploring the relationship between avian density/richness indicators and both onsite and offsite habitat characteristics to be used for scenario building (determined in Table 4).

Avian density (birds ha ⁻¹)/richness	Habitat	Farmland habitat characteristic					Moorland habitat characteristic			
		Intensive grass	Mowed land	Trees	Rush cover	Wet features	Heather cover	Burning	Vegetation height	
Curlew	Farmland	0.066 (0.031)						0.044 (0.019)		
Snipe	Farmland	-0.034 (0.042)			2.288 (0.470)	0.315 (0.078)		0.067 (0.029)		
Willow warbler	Moorland	0.053 (0.049)			-0.662 (0.419)					
Reed bunting	Farmland	0.134 (0.060)				0.237 (0.071)	0.176 (0.106)		-0.003 (0.001)	
Total	Farmland	2.667 (0.536)		0.001 (0.000)					-0.016 (0.011)	
Cons concern	Moorland	0.883 (0.190)							0.005 (0.003)	
Total richness	Moorland	3.533 (0.068)	-0.310 (0.145)							
Cons concern richness	Farmland	2.514 (0.096)	-0.388 (0.230)					0.095 (0.055)		

of site and individual bird in a mixed modelling framework ($F_{1,284} = 88.24$, $p < 0.000$). The median number of movement segments recorded from each focal individual over a given survey visit was one (range 1–16; Table 6b).

Behavioural observations covered 112.7 h (6761 min) on 216 separate occasions. The proportions of time spent carrying out the four major activities varied between habitat types ($\chi^2 = 678.93$, $DF = 4$, $p < 0.001$), but were consistent across locations ($\chi^2 = 19.83$, $DF = 4$, $p = 0.210$, ns). Using a binomial proportions test, on a behaviour-by-behaviour basis, a greater proportion of time was spent foraging on farmland than moorland (63 compared to 33%; $\chi^2 = 587.57$, $p < 0.001$). On moorland, curlew spent a greater proportion of time loafing (29 compared to 16% on farmland; $\chi^2 = 132.39$, $p < 0.001$), being vigilant (19 compared to 15%, $\chi^2 = 17.54$, $p < 0.001$) and carrying out reproductive behaviour (5 and 3%; $\chi^2 = 13.03$, $p < 0.001$).

Discussion

The habitat associations of the UK upland bird assemblage are, in many cases, relatively well understood

(Buchanan et al. 2005, Pearce-Higgins and Grant 2006). Management actions, usually associated with agricultural production or estate management, both on moorland (e.g. burning – Yallop et al. 2006; predator control – Fletcher et al. 2010; grazing – Evans et al. 2006) and farmland (agricultural intensification – Fuller and Gough 1999, Fuller et al. 2002, Henderson et al. 2004; agri-environment scheme implementation – Dallimer et al. 2010a; farm business configuration – Dallimer et al. 2009) are known to influence both upland habitats and the biodiversity that they support. Despite this knowledge many avian populations in the moorland/farmland fringe continue to decline (Henderson et al. 2004, Sim et al. 2005) without clear reasons (Fuller et al. 2002, Woodhouse et al. 2005).

Previous landscape-scale research has demonstrated that land use in the matrix surrounding a focal habitat patch can affect avian richness and abundance (Devictor and Jiguet 2000, Heikkinen et al. 2004). Indeed, in the Peak District, richness and community composition of moorland birds is influenced both by local habitat and surrounding land cover (Dallimer et al. 2010b). Here we take this approach a step further and demonstrate associations between onsite avian density/richness indicators and offsite habitat structure

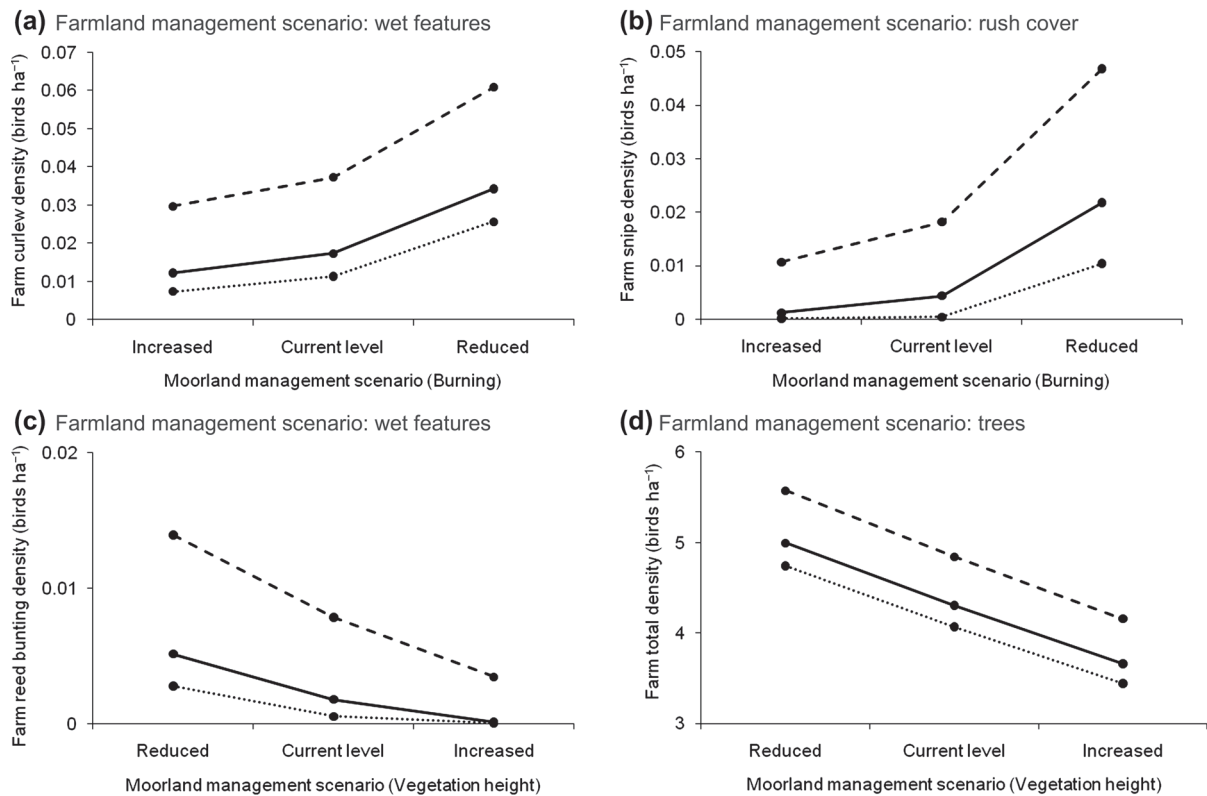


Figure 2. Impact of moorland and farmland management scenarios on avian density/richness. Lines represent the three possible farmland habitat management scenarios: solid line – current level, dotted line – a reduction, dashed line – an increase. Moorland scenarios are given on the x-axis. Avian density/richness indicators for farmland are: (a) curlew density; (b) snipe density; (c) reed bunting density; (d) total density; and (e) conservation concern species richness. Moorland avian indicators are: (f) willow warbler density; (g) conservation concern density; and (h) total species richness. The scenarios can be interpreted as follows: in (a), curlew density on farmland can be raised from 0.017 birds ha⁻¹ (farmland and moorland habitat under current management regimes) to 0.037 birds ha⁻¹ by increasing wet features on farms (farmland, increased; moorland, current management levels). This is greater than the improvement possible by reducing the intensity of burning on moorland, where curlew density would increase to 0.034 birds ha⁻¹ (farmland, current; moorland, reduced management). However, appropriate management on both farmland and moorland (increasing wet features on farmland, increased management; and reducing the burning intensity on moorland; reduced management) would result in the density of curlew on farmland increasing to 0.061 birds ha⁻¹.

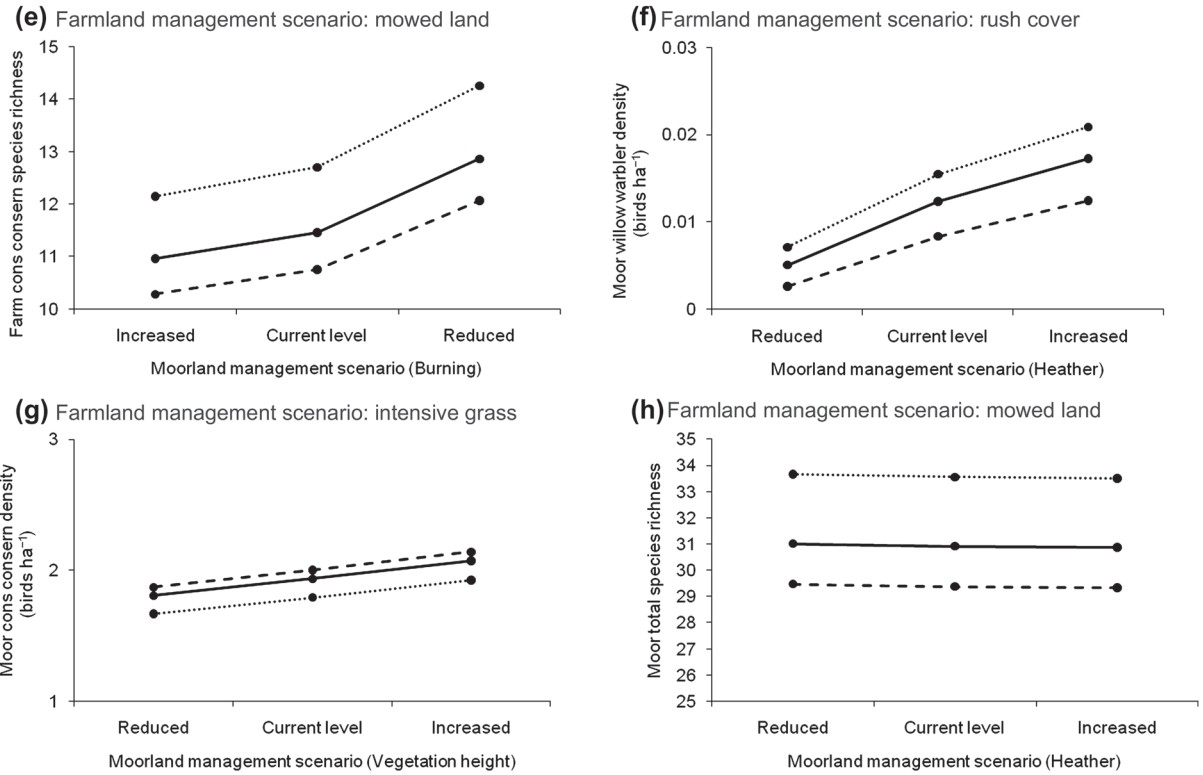


Figure 2. *Continued.*

(e.g. vegetation height, percent cover of dominant plant species etc). Although such effects are not universal, where present (for five farmland and three moorland avian indicators) the increase in explanatory power offered by including offsite habitat structure can be large. For example, reducing the intensity of the burning management regime

on moorland can result in a two-fold increase in farmland Eurasian curlew density (Fig. 2a) without altering current farmland habitat.

One possible mechanism for this is the movement of individuals between habitat types. For example, Eurasian curlews are wide-ranging, travelling as far as 3 km from nesting

Table 6. Curlew movements between and within moorland and farmland habitat types across five study sites in the Peak District, northern England: (a) movement lengths and numbers both between and within habitat types; (b) the number of curlew pairs present on each site, together with the number of times a focal individual was watched, and the number of movements that were recorded (number of segments).

(a)						
Site	Movement length			Number of movements		
	Between (m)	Within (m)	Ratio	Between	Within	Proportion
1	316	238	1.33	10	80	0.11
2	315	184	1.71	35	59	0.37
3	302	204	1.48	80	63	0.56
4	793	304	2.61	7	95	0.07
5	495	168	2.95	26	194	0.12
Overall	359	212	1.69	158	491	0.24

(b)				
Site	Number of pairs	Number of focal individual watches	Number of segments	Number of segments per watch (median/range)
1	6	45	90	1 (1–16)
2	5	47	94	1 (1–8)
3	5	93	143	1 (1–5)
4	4	64	102	1 (1–3)
5	5	135	220	1 (1–7)
Overall	25	384	649	1 (1–16)

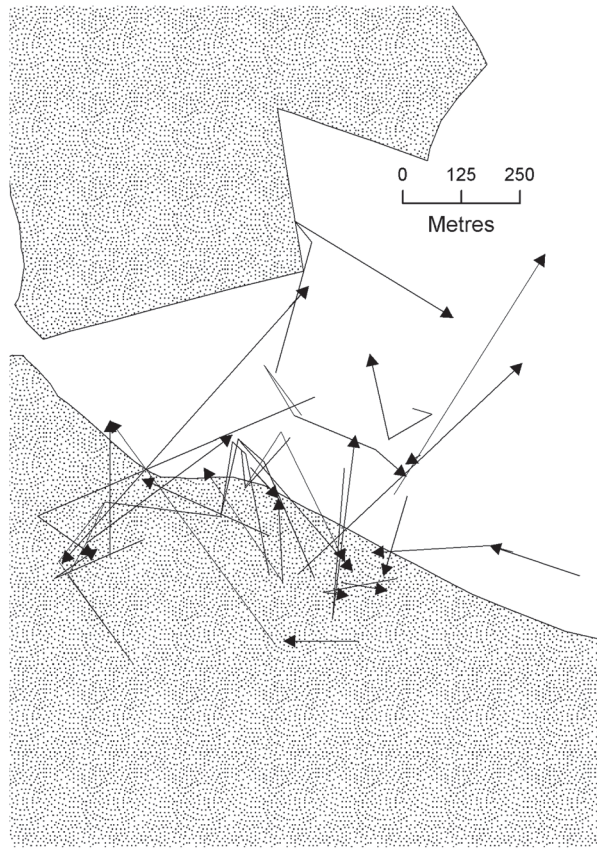


Figure 3. An example of Eurasian curlew *Numenius arquata* moving between moorland (stippled) to neighbouring farmland in the Peak District of northern England. Each arrow shows the length and direction of short movements made by individual birds.

sites to feed (Robson 1998). Our behavioural observations illustrate that they require resources from two different habitat types within a single breeding season (cf. Dunning et al. 1992). Curlews frequently moved between moorland and farmland (a quarter of all movements). Curlews spent more time feeding on farmland than moorland, so much so that over half their time-budget on farmland was used for foraging; while on moorland, where all nests were located, a greater proportion of time was spent on reproductive behaviour. As curlews surveyed on farmland were likely to be foraging, the density of birds observed on a farmland site depended, in part, on the numbers breeding on nearby moorland and hence the habitat characteristics of these areas.

Radiotracking studies in the uplands have shown that golden plovers *Pluvius apricaria*; Whittingham et al. 2000 and curlew (Robson et al. 2002) use multiple habitats, a trait that has also been described for some passerines (Raine et al. 2006) and raptors (Ratcliffe 1990). However, multiple habitat dependency is widespread and not limited to highly mobile birds; for example many amphibians (Becker et al. 2007) and odonates (Remsburg and Turner 2009) require both aquatic and terrestrial habitats to complete their lifecycle, and bats roost and forage in different habitats (Mackie and Racey 2007). Multiple habitat dependencies can also operate at a variety of spatial and temporal scales. For instance, during one year the same vegetation type may provide divergent niche requirements for different generations of bivoltine insects (Roy and Thomas

2003). Many species seasonally migrate over regional or global scales to utilise different habitats (Webster et al. 2002), which can present particular challenges to their management (Martin et al. 2007, Klaasen et al. 2008).

In this study, we have quantified the extent to which avian density and richness in the uplands can be associated with the characteristics of neighbouring habitat types in the same landscape. Although such effects are limited to a subset of the indicators examined here, the potential benefits for the management of upland bird communities are large not least given the recognised conservation importance of the UK uplands in general, and moorland in particular. However, farming in these regions operates at the margins of profitability (Acs et al. 2010) and hence will undergo substantial changes in response to shifts in both policy and commodity prices in the future. The consequences of such changes are likely to manifest themselves across both farmland and moorland avian communities, and we need to understand more fully how individual species use habitats and resources over multiple spatial and temporal scales (Fuller et al. 2004). For example, alterations in the mowing intensity on farmland can decrease the richness of the moorland avian community by around five species (Fig. 2). By way of a contrast, changing the frequency of burning management on moorland has the potential to lead to a five-fold increase in farmland snipe density, irrespective of farm management (Fig. 2). The effective conservation of some upland bird species and communities will therefore require an integrated approach to landscape conservation planning and management. For those species that use more than one habitat type on a local and frequent basis, unforeseen consequences of focussing conservation efforts on a single habitat type could result in population declines.

Acknowledgements – We thank the farmers and landowners of the Peak District, National Farmers Union, Peak District National Park Authority, Moors for the Future, National Trust, RSPB, N. Hanley, S. Acs, P. Robertson and P. Wilson, D. Chamberlain and three anonymous reviewers provided useful comments. The research was funded as part of the UK Research Councils' Rural Economy and Land Use Programme (RELU). RELU is a collaboration between ESRC, NERC and BBSRC with additional funding from Defra and the Scottish Government. KJG holds a Royal Society–Wolfson Research Merit Award.

References

- Acs, S. et al. 2010. The effect of decoupling on marginal agricultural systems: implications for farm incomes, land use and upland ecology. – *Land Use Pol.* 27: 550–563.
- Armsworth, P. R. et al. 2006. Land market feedbacks can undermine biodiversity conservation. – *Proc. Natl Acad. Sci. USA* 103: 5403–5408.
- Atkinson, P. W. et al. 2005. Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. – *J. Appl. Ecol.* 42: 932–942.
- Baillie, S. R. et al. 2000. Consequences of large-scale processes for the conservation of bird populations. – *J. Appl. Ecol.* 37: 88–102.
- Barbaro, L. et al. 2008. Multi-scale habitat selection and foraging ecology of the Eurasian hoopoe (*Upupa epops*) in pine plantations. – *Biodivers. Conserv.* 17: 1073–1087.
- Becker, C. G. et al. 2007. Habitat split and the global decline of amphibians. – *Science* 318: 1775–1777.

- Beever, E. A. et al. 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. – *J. Mammal.* 84: 37–54.
- Benning, T. L. et al. 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. – *Proc. Natl Acad. Sci. USA* 99: 14246–14249.
- Buchanan, G. et al. 2005. Characterization of moorland vegetation and the prediction of bird abundance using remote sensing. – *J. Biogeogr.* 32: 697–707.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodal inference. – Springer.
- Coote, T. and Loeve, E. 2003. From 61 species to five: endemic tree snails of the Society Islands fall prey to an ill-judged biological control programme. – *Oryx* 37: 91–96.
- Crawley, M. 2007. *The R book*. – Wiley.
- Crowl, T. A. et al. 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. – *Front. Ecol. Environ.* 6: 238–246.
- Dallimer, M. et al. 2009. What explains property-level variation in avian diversity? Taking an inter-disciplinary approach. – *J. Appl. Ecol.* 46: 334–343.
- Dallimer, M. et al. 2010a. Field-level bird abundances are enhanced by landscape-scale agri-environment scheme uptake. – *Biol. Lett.* 6: 643–646.
- Dallimer, M. et al. 2010b. Agricultural land-use in the surrounding landscape affects moorland bird diversity. – *Agric. Ecosyst. Environ.* 139: 578–583.
- Defra 2008. Uplands Land Classification. – <www.defra.gov.uk/rural/uplands/land-classification.htm> accessed 24 March 2009.
- Devictor, V. and Jiguet, F. 2000. Community richness and stability in agricultural landscapes: the importance of surrounding habitats. – *Agric. Ecosyst. Environ.* 120: 179–184.
- Dunning, J. B. et al. 1992. Ecological processes that affect populations in complex landscapes. – *Oikos* 65: 169–175.
- Evans, D. M. et al. 2006. Low intensity, mixed livestock grazing improves the breeding abundance of a common insectivorous passerine. – *Biol. Lett.* 2: 636–638.
- Feldman, R. E. and Krannitz, P. G. 2004. Bird composition of oak ecosystem fragments in an urbanized setting: the influence of adjacent coniferous forest fragments. – *Ecoscience* 11: 338–346.
- Finlayson, G. R. et al. 2008. Multi-scale patterns of habitat use by re-introduced mammals: a case study using medium-sized marsupials. – *Biol. Conserv.* 141: 320–331.
- Fletcher, K. et al. 2010. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. – *J. Appl. Ecol.* 47: 263–272.
- Franklin, J. F. and Lindenmayer, D. B. 2009. Importance of matrix habitats in maintaining biological diversity. – *Proc. Natl Acad. Sci. USA* 106: 349–350.
- Fuller, R. J. and Gough, S. J. 1999. Changes in sheep numbers in Britain: implications for bird populations. – *Biol. Conserv.* 91: 73–89.
- Fuller, R. J. et al. 2002. Declines of ground-nesting birds in two areas of upland farmland in the south Pennines of England. – *Bird Study* 49: 146–152.
- Fuller, R. J. et al. 2004. The relevance of non-farmland habitats, uncropped areas and habitat diversity to the conservation of farmland birds. – *Ibis* 146 (Suppl. 2): 22–31.
- Gaston, K. J. et al. 2008. The ecological performance of protected areas. – *Annu. Rev. Ecol. Evol. Syst.* 39: 93–113.
- Ghilain, A. and Bêlisle, M. 2008. Breeding success of tree swallows along a gradient of agricultural intensification. – *Ecol. Appl.* 18: 1140–1154.
- Heikkinen, R. K. et al. 2004. Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural–forest mosaic. – *J. Appl. Ecol.* 41: 824–835.
- Henderson, I. G. et al. 2004. Evidence for declines in populations of grassland-associated birds in marginal upland areas of Britain. – *Bird Study* 51: 12–19.
- JNCC 2007. Handbook for Phase 1 Habitat Survey – a technique for environmental audit, revised reprint 2003, reprinted 2007. – JNCC.
- Klaassen, M. et al. 2008. Optimal management of a goose flyway: migrant management at minimum cost. – *J. Appl. Ecol.* 45: 1446–1452.
- Lee, J. A. 1998. Unintentional experiments with terrestrial ecosystems: ecological effects of sulphur and nitrogen pollutants. – *J. Ecol.* 86: 1–12.
- Mackie, L. J. and Racey, P. A. 2007. Habitat use varies with reproductive state in noctule bats (*Nyctalus noctula*): implications for conservation. – *Biol. Conserv.* 140: 70–77.
- Martin, T. G. et al. 2006. Is landscape context important for riparian conservation? Birds in grassy woodland. – *Biol. Conserv.* 127: 201–214.
- Martin, T. G. et al. 2007. Optimal conservation of migratory species. – *PLoS One* 2: e751.
- McDonald, R. I. et al. 2007. Estimating the effect of protected lands on the development and conservation of their surroundings. – *Conserv. Biol.* 21: 1526–1536.
- Moritz, C. et al. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. – *Science* 322: 261–264.
- Newmark, W. D. 2008. Isolation of African protected areas. – *Front. Ecol. Environ.* 6: 321–328.
- Newson, S. E. et al. 2005. Evaluating the Breeding Bird Survey for producing national population size and density estimates. – *Bird Study* 52: 42–54.
- Pearce-Higgins, J. W. and Yalden, D. W. 2003. Variation in the use of pasture by breeding European golden plovers *Pluvialis apricaria* in relation to prey availability. – *Ibis* 145: 365–381.
- Pearce-Higgins, J. W. and Grant, M. C. 2006. Relationships between bird abundance and the composition and structure of moorland vegetation. – *Bird Study* 53: 112–125.
- R Development Core Team 2009. R: a language and environment for statistical computing. – R Foundation for Statistical Computing.
- Raine, A. F. et al. 2006. Natal philopatry and local movement patterns of twite *Carduelis flavirostris*. – *Ring. Migr.* 23: 89–94.
- Ratcliff, D. A. 1990. *Bird life of mountain and upland*. – Cambridge Univ. Press.
- Reensburg, A. J. and Turner, M. G. 2009. Aquatic and terrestrial drivers of dragonfly (Odonata) assemblages within and among north-temperate lakes. – *J. North Am. Benthol. Soc.* 28: 44–56.
- Robson, G. 1998. The breeding ecology of curlew *Numenius arquata* on North Pennine Moorland. – PhD thesis, Univ. of Sunderland.
- Robson, G. et al. 2002. The use of marginal farmland by curlew *Numenius arquata* breeding on upland moors. – *Aspects Appl. Biol.* 67: 75–84.
- Roy, D. B. and Thomas, J. A. 2003. Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. – *Oecologia* 134: 439–444.
- Şekercioğlu, C. H. et al. 2007. Persistence of forest birds in the Costa Rican agricultural countryside. – *Conserv. Biol.* 21: 482–494.
- Sim, I. M. W. et al. 2005. Recent changes in the abundance of British upland breeding birds. – *Bird Study* 52: 261–275.
- Stroud, D. A. et al. 2001. The UK SPA network: its scope and content. – JNCC.

- Thomas, C. D. et al. 2004. Extinction risk from climate change. – *Nature* 427: 145–148.
- Thomas, L. et al. 2006. Distance 5.0. Release 2. – Univ. of St. Andrews, Research Unit for Wildlife Population Assessment.
- Thomas, L. et al. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. – *J. Appl. Ecol.* 47: 5–14.
- Thompson, D. B. A. et al. 1995. Upland heather moorland in Great Britain – a review of international importance, vegetation change and some objectives for nature conservation. – *Biol. Conserv.* 71: 163–178.
- Webster, M. S. et al. 2002. Links between worlds: unraveling migratory connectivity. – *Trends Ecol. Evol.* 17: 76–83.
- Weiss, S. B. et al. 1988. Sun, slope and butterflies: topographical determinants of habitat quality for *Euphydryas editha*. – *Ecology* 69: 1486–1496.
- Supplementary material (Appendix E7040 at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.
- Wethered, R. and Lawes, M. J. 2005. Nestedness of bird assemblages in fragmented Afriomontane forest: the effect of plantation forestry in the matrix. – *Biol. Conserv.* 123: 125–137.
- Whittingham, M. J. et al. 2000. Time budgets and foraging of breeding golden plover *Pluvialis apricaria*. – *J. Appl. Ecol.* 37: 632–646.
- Whittingham, M. J. et al. 2005. Habitat selection by yellowhammers *Emberiza citrinella* on lowland farmland at two spatial scales: implications for conservation management. – *J. Appl. Ecol.* 42: 270–280.
- Woodhouse, S. P. et al. 2005. Effects of land-use and agricultural management on birds of marginal farmland: a case study in the Llyn peninsula, Wales. – *Agric. Ecosyst. Environ.* 107: 331–340.
- Yallop, A. R. et al. 2006. The extent and intensity of management burning in the English uplands. – *J. Appl. Ecol.* 43: 1138–1148.