Sensitivities to land use change by breeding Short-eared Owl (*Asio flammeus*) in Britain

Sensibilidade da coruja-do-nabal (*Asio flammeus*) às alterações dos usos do

solo na Grã-Bretanha

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ABSTRACT

Although widespread, populations of Short-eared Owls (Asio flammeus) are declining in most parts of their range. We present aspects of land use relevant to these owls in Britain. Potential environmental determinants of distribution and change were identified by review of the species' known ecology including published literature and ongoing telemetry studies of habitat use. Generalised Additive Models were then used to assess associations of environmental variables with the recent distribution and change over the preceding two decades. Variables identified for inclusion in the models were: semi-natural habitats, temperature, rainfall, elevation, slope, woodland cover, young growth stage forests, vole occurrence and measures of predator occurrence. Threats to their current status included forest expansion and changes in moorland management. Mechanisms for the negative association with forest expansion will be the replacement of preferred semi-natural open moorland and grassland habitats. Mechanisms associated with moorland management are likely associated with changes in predation risk. The latter also has potential implications for the introduction of predators onto islands. Opportunities for restoring breeding populations include restoring areas where predator densities are naturally low, increasing areas where densities of ground predators are maintained at low levels and adapting forest management plans to include open habitat specialists. Although limitations for breeding Shorteared Owls undoubtedly included the distribution of their favoured prey, voles, detection of their significance in models was limited by data on vole distribution and abundance.

Keywords: Asio flammeus, Britain, Conservation framework, Moorland, Predictive models



RESUMO

Apesar da sua distribuição generalizada, as populações de corujas-do-nabal (Asio flammeus) estão em declínio na maioria da sua área de ocorrência. Apresentamos aspetos do uso do solo relevantes para a espécie na Grã-Bretanha. Os potenciais determinantes ambientais da distribuição e alterações foram identificados através da revisão da ecologia conhecida da espécie, incluindo literatura publicada e estudos de telemetria em curso sobre uso do habitat. Foram utilizados modelos aditivos generalizados para avaliar associações de variáveis ambientais com a recente distribuição e alterações decorridas nas duas décadas anteriores. As variáveis identificadas para inclusão nos modelos foram: habitats semi-naturais, temperatura, precipitação, elevação, declive, cobertura florestal, florestas jovens em estágio de crescimento, ocorrência de micromamíferos e medidas de ocorrência de predadores. As ameaças ao seu estatuto atual incluíam a expansão da floresta e alterações na gestão das áreas de matos. Os mecanismos para a associação negativa com a expansão da floresta poderão passar pela substituição de habitats preferenciais de matos semi-naturais abertos e prados. Os mecanismos associados à gestão das áreas de matos provavelmente estão ligados a alterações no risco de predação. Este último tem ainda potenciais implicações na introdução de predadores nas ilhas. As oportunidades para restaurar populações reprodutoras incluem restaurar áreas onde as densidades de predadores são naturalmente baixas, aumentar áreas onde as densidades de predadores terrestres são mantidas em níveis baixos e adaptar planos de gestão florestal para incluir especialistas em habitat aberto. Embora as limitações da população reprodutora de coruja-do-nabal incluam, sem dúvida, a distribuição das suas presas preferenciais, micromamíferos da subfamília Arvicolinae, a deteção da sua significância nos modelos foi limitada pela escassez de dados sobre distribuição e abundância das presas.

Palavras-chave: Asio flammeus, estratégia de conservação, Grã-Bretanha, matos, modelos preditivos

Introduction

The relationships between a species' distribution and population trends with environmental variables can provide key information to conservation planners. 'Habitat Suitability Models' (e.g. Brambilla et al. 2009, Maleki et al. 2016) can be used to identify areas of suitable habitat for a species and therefore be a useful tool when designating protected areas or reserves (Akcakaya 2000, Tinoco et al. 2009, Yost et al. 2008, Kassara et al. 2014) or to highlight areas where new planning developments would have an adverse effect (e.g. Bright et al. 2008). Such approaches can also provide information on how a species is likely to

respond to changes in different aspects of the environment which can then inform conservation and policy and decision makers (e.g. Border et al. 2017).

Although widespread, populations of Short-eared Owls are declining in many parts of their range (Burfield 2008, Booms et al. 2014). For example, their breeding range in Britain contracted from occupancy of 381 ten-km squares with high levels of evidence of breeding in 1990 to 245 by 2010 (Balmer et al. 2013). Bird Atlases are particularly renowned for the depth and extent of their coverage (Eaton et al. 2013). To date, three atlases of breeding birds in Britain and Ireland

have been completed at 20-year intervals with fieldwork for the first centered around 1970 (Sharrock 1976, Gibbons et al. 1993, Balmer et al. 2013). Through identifying associations between the distribution and abundance of breeding Short-eared Owls in Britain with other environmental data sets, we explore the efficacy of developing a tool that predicts their sensitivity to future potential land use and other changes. The aim was to identify:

Limitations – the topographical or other environmental attributes that limit Shorteared Owl distribution and abundance in Britain but which are unlikely to be changed through land management and the areas where these limitations will have the greatest impact;

Threats – features with which the species' current abundance and distribution appear to have an association, and therefore are likely to be a threat to the species if those conditions change within the current distribution, and where changes in these features will have the greatest impact;

Opportunities – spatial examples of where land-use changes could lead to range expansions or increased abundances of target species.

We suggest that this approach should form the basis of a conservation framework for this declining species and for the habitats on which it relies.

Methods Bird data

Bird data used as dependent variables in predictive models (see below) were sourced from comparable bird atlas fieldwork undertaken in 1988-91 (Gibbons et al. 1993, hereafter *BA1990*) and 2008-11 (Balmer et al. 2013, hereafter *BA2010*). For both atlases, volunteers surveyed a sample of tetrads (2 km 2 km), making two 1-hour visits to each tetrad. In *BA1990* observers simply listed the species encountered, whereas in *BA2010*

they counted the number of individuals encountered which has implications for the calculation of abundance change (see below). Any counts or presence information outside the known breeding range (judged from recorded breeding evidence and distribution maps from the respective atlas) were turned to zeroes/absences in order to remove the presence of known (or almost certainly known) migrants from analyses. As counts were not available for BA1990 we used a 'frequency method' for deriving an index of change in abundance. This is the proportion of surveyed tetrads within each hectad (10 x 10 km) where the species was recorded. It was used in BA1990 to map spatial variation in relative abundance and relies on the assumption that the frequency index is a valid measure of bird abundance. Simulations and pilot fieldwork confirmed that a positive relationship does exist and is only likely to be unrealistic for the most abundant and widespread of species (Balmer et al. 2013). Accordingly, abundance change for Short-eared Owls in each hectad was calculated by subtracting the BA1990 frequency index from the BA2010 frequency index. Hectads where the species was not present in either atlas period were excluded from the change index as it would not be possible to separate stable hectads from ones where the species was never present.

Environmental data

Potential factors to be included in predictive models (see below) included general information on topography and climate and also specific variables identified by a review of literature of the known ecology of Short-eared Owls. These included:

Climate (temperature and precipitation)

Data was sourced from the UK meteorological office at the 5 km resolution (Perry & Hollis 2005). To encompass

conditions when the birds were breeding we used the mean of mean monthly temperatures and the mean of total monthly rainfall from the months April, May, June and July. For winter conditions, the mean of mean winter temperatures and the mean of total rainfall from the months of December, January and February before the breeding season of interest (i.e. December 2007 for 2008 survey) were calculated. The mean of these variables for each 5 km square was then calculated over the relevant years for each period to match the Bird Atlas surveys, 1988–1991 and 2008–2011.

Topography (elevation and slope) - Elevation (in meters above sea level) was extracted from the GGIAR-SRTM 90m raster (Jarvis et al., available at http://srtm.csi.cgiar.org) taking the mean elevation over each hectad (depending on the scale of the analysis). Slope was calculated from elevation in ARCGIS (ESRI 2011). The slope of each elevation raster cell is the maximum rate of change in elevation in one raster cell compared to its eight neighbours. The lower slope values indicate flatter areas, higher values indicate steeper areas. The median slope was taken for each hectad to better represent mostly flat areas.

Habitat - In Britain, the majority of Shorteared Owls breed in upland environments, where they use heather moorland, rough grassland and new plantations (Goddard 1935, Roberts & Bowman 1986, Shaw 1995, Calladine & Morrison 2013), whereas in the lowlands (where they are now very localized) they are mainly found on coastal habitats; salt marshes, dune systems and rough grassland (Taylor et al. 1981, Grainger 2003). Land cover categories from the UK Land Cover Map (Morton et al. 2011) were summarised to create three broad categories of percentage cover within each hectad: (i) semi-natural habitats inclusive of unimproved grasslands, heaths, mires and montane habitats; (ii)

coniferous woodlands and (iii) coastal habitats. Additional information on young age-class plantation forests and percent cover of coniferous forest was sourced from the Forestry Commission's National Forest Inventory for 2011 (https://www.forestry.gov.uk/inventory).

Prey abundance - The presence and abundance of small mammals, especially voles, the species' main prey source in Britain and across much of its range, is one key determinant of their distribution (Village 1987, Korpimäki & Norrdahl 1991). Although widespread across mainland Britain, voles are absent from some islands and archipelagos. In the absence of more reliable data on vole distribution and abundance (and because this can vary temporally), simple presence or absence of voles was included in models based on their known distribution across islands.

Predation risk - Short-eared Owls are ground nesting birds and as such can be particularly vulnerable to ground predators. Three sources of data were used as proxies for predation risk: (a) the distribution of the mammalian predators - Red Fox (Vulpes vulpes), Badger (Meles meles) and Stoat (Mustela ermina) from Arnold (1993); (b) indices of abundance of avian predators from Bird Atlases (Balmer et al. 2013); and (c) indices of Willow Grouse (Lagopus lagopus scotia) abundance from Bird Atlas data. For mammalian predators, simple presence or absence within each hectad was used as a factor in the models. An index of avian predator abundance was derived from Bird Atlases which combined abundances of Carrion Crow (Corvus corone), Hooded Crow (C. cornix), Common Raven (C. corax) and Eurasian Buzzard (Buteo buteo) to provide an index of abundance for generalist avian predators. To accommodate some extremely high values due to large flocks of corvids, counts greater than 50 were set to 50; 99% of count were 50 or below. Willow Grouse abundance was similarly derived from Bird Atlases and was used as a proxy of management specifically for that species; a combination of management for heather (*Calluna vulgaris*) and active control of predators (Tharme et al. 2001, Fletcher *et al.* 2010). To reduce stochasticity and potential bias specifically associated with the Willow Grouse count data, average counts for all tetrads within a hectad were used as the abundance index; preliminary analysis with the Willow Grouse count data showed that this variable worked best.

Predictive models

Generalised Additive Models (GAMs) were used to assess associations of environmental variables with the change in relative abundance of Short-eared Owls as the dependent variables. The model used a Gaussian distribution (the index was approximately normally distributed) and included a 2D spatial smooth of normalized easting and northing (using thin plate regression splines) to account for spatial autocorrelation and variation in sampling intensity. As the aim was to measure the effect of change, ideally we tried to use environmental variables that reflected change between BA1990 and BA2010. For example change in mean winter temperature or change in Willow Grouse count. However where this was not possible, only the data coinciding with BA2010 were used in the model. Selection of variables to include in the full models considered variance inflation factors (VIFs; Zuur et al. 2009). Variables with VIFs > 3 and correlations to other variables > 0.7 were removed. Where two or more variables were strongly correlated, variables with a stronger relationship to the dependent variable from single models of the variable against change in relative abundance were preferred over variables with weaker relationships. Uncorrelated variables were then included in one full model. A linear relationship was assumed for all environmental variables apart from elevation, because there is evidence of preference for intermediate elevations for many species (Lomolino 2001). Interactions were not considered because the large number of variables in each model meant that further increases to model complexity caused problems with model convergence and overfitting. The environmental variables were centered and standardized using the Arm package (Gelman 2008, Gelman 2014) to allow direct comparison between them. Models residuals were examined visually to ensure a reasonable fit. A correlation test of predicted relative abundance change from the model against the raw relative abundance change was used to assess the predictive ability of the model.

To assess the impact that future changes in key drivers might have on Shorteared Owls, we used the models to make predictions under different scenarios of change. We identified variables which had a significant effect and reduced this list to variables that would be possible to alter through management. For example forest cover and the level of Willow Grouse management could be altered, whereas slope, elevation and climate would not be possible to alter. Then, individual plots were created for each target variable of the predicted relative abundance change for each increment of the target variable from the minimum value recorded in the dataset to the maximum. Whichever value of the target variable corresponded to the 75th percentile of the predicted relative abundance change was chosen as the new threshold. We used this threshold to alter the environmental dataset. For example if woodland was negatively correlated to abundance and the threshold value was 20% cover of woodland, hectads with woodland cover above 20% cover were reduced to this value. Similarly, Willow Grouse count would only be increased within the range of Willow Grouse (as determined from both BA1990 and BA2010). These scenarios

Table 1- Standardized parameter estimates of a GAM model of change in relative abundance of Short-eared Owl between the 2008-2011 Atlas and the 1988-1991 Atlas, using a Gaussian distribution, deviance explained = 21.6%, n = 328. Change is shown relative to abundance levels in 2008-2011.

Tabela 1 - Estimativas padronizadas dos parâmetros do modelo GAM da variação da abundância relativa de coruja-do-nabal entre o Atlas de 2008-2011 e o Atlas de 1988-1991, usando a distribuição Gaussiana, desvio explicado = 21,6%, n = 328. A alteração é calculada relativamente aos níveis de abundância de 2008-2011.

VARIABLE	MEAN ± SE	P
% Conifer	-0.031 ± 0.010	0.003*
% Young trees	0.001 ± 0.010	0.942
% Coastal	0.003 ± 0.010	0.748
Avian predator change	-0.002 ± 0.009	0.858
Mammal predators	-0.020 ± 0.033	0.543
Voles	0.097 ± 0.135	0.471
Willow Grouse change	0.040 ± 0.008	<0.001*
Mean elevation	-0.039 ± 0.034	0.252
Mean elevation squared	0.025 ± 0.029	0.393
Median slope	0.007 ± 0.012	0.543
Change in mean winter rain	-0.007 ± 0.011	0.497
Change in mean summer temperature	0.002 ± 0.010	0.874
Change in mean summer rain	0.004 ± 0.010	0.698

better replicate what would be possible to change with management action. The difference in Short-eared Owl relative abundance change prediction after altering the environmental data was calculated by subtracting the original predictions from the new predictions. The difference was then plotted as a map to illustrate the areas that would be most affected and the magnitude of this effect.

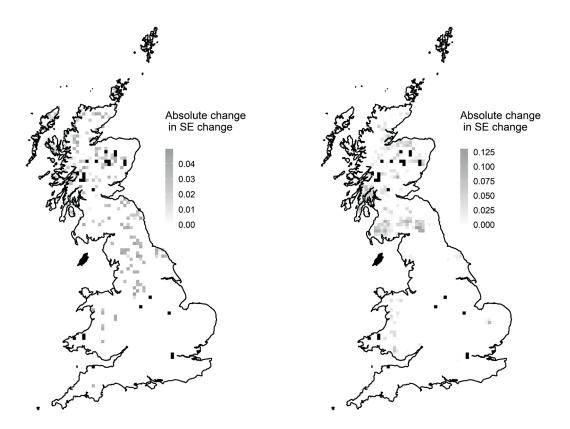
Results

Patterns of predicted change matched well with empirical observations of Short-eared Owl abundance (Pearson's Product Moment Correlation Coefficient (PPMCC) of observed versus predicted values: r = 0.46, P < 0.001). Abundance change was negatively associated with cover by coniferous forest (the majority of which are commercially managed plantations; Calladine et al. 2018) and was positively associated with increases in Willow Grouse numbers (Table 1).

Two alternative scenarios were modelled whereby changes in the two significant factors were manipulated to mimic more favourable conditions for breeding Short-eared Owls: (a) increasing the minimum relative density of Willow Grouse to the 75th percentile of that recorded empirically in all hectads within the distribution of breeding Willow Grouse; and (b) decreasing the maximum extent of coniferous forest to 15% (the 25th percentile recorded empirically) in all hectads. Where

Figure 1 - Alternative scenarios to have a positive effect on Short-eared Owl population trends. The maps show the absolute change in the predicted Short-eared Owl trend between *BA1990* and *BA2010* under each scenario for each hectad of Britain, a) promote Willow Grouse, b) decrease coniferous woodland. Note that the black squares show areas with insufficient data (bird and/or environmental) for modelling.

Figura 1 - Cenários alternativos com efeito positivo nas tendências populacionais de coruja-do-nabal. Os mapas representam a variação absoluta na tendência prevista de coruja-do-nabal entre o *BA1990* e o *BA2010* em cada cenário para cada quadrícula de 10x10km da Grã-Bretanha; a) promoção do lagópode-escocês, b) declínio da floresta de coníferas. Note-se que as quadrículas a preto representam áreas com informação insuficiente (sobre aves e/ou o ambiente) para a modelação.



Willow Grouse densities were greater than the 75th percentile or where coniferous forest was less than the 25th percentile, then the original values were retained in the respective predictive model. Management that permitted more extensive high densities of Willow Grouse was predicted to have increased densities of Short-eared Owls through most of their breeding range (Figure 1a) with the exception of the few remaining lowland sites (outside the range of Willow Grouse, where no effect of the modelled changes would be expected) and also some areas which retained

high owl densities (e.g. the south-eastern fringe of the Scottish Highlands) (Figure 1a). Interestingly some expansion of range in the south-west of Britain was predicted.

The modelled effect of decreasing the extent conifer forests (predominantly plantations) predicted marked increases in the most forested areas of Britian, the north-east and south-west of Scotland and across the England-Scotland borders. Interestingly, a range expansion was predicted for the now forested areas of the brecklands in south-east England (Figure 1b).

Discussion

Identified threats to and opportunities for breeding Short-eared Owls in Britain were associated with forest cover and with grouse moor management. Both are major land uses in the remaining range of Short-eared Owls in upland Britain and therefore important to consider in Short-eared Owl conservation management actions.

Expansion of coniferous plantations was found to negatively affect Short-eared Owls, presenting a potential threat. New plantations are typically planted on semi-natural open moorland and grassland habitats (Calladine et al. 2018) thereby replacing the habitats preferred by breeding Short-eared Owls. Consequently, reducing forest cover, particularly conifer forest, represents a potential opportunity for population growth and expansion. Young growth stage plantations can offer some nesting opportunities for Short-eared Owls but generally this is restricted to newly planted sites, with plantations generally avoided after canopy closure (Shaw 1995) and second and subsequent rotation plantings are not nearly as attractive to breeding Short-eared Owls as first rotation new plantings (Calladine et al. 2018). Improved modelling of difference in suitability of later rotation plantings from first rotation young growth stages may be achieved where historical data on forest stand age classes and planting histories (through archived forest management plans) are available.

Increases in Willow Grouse were positively associated with Short-eared Owls. Therefore, expansion of the area managed as grouse moor is one potential opportunity to enable increases in range and abundance in Short-eared Owls. Conversely, reductions in the areas and/or intensity of management associated with grouse moors represented a threat to Short-eared Owls. This relationship is unlikely to be driven by Willow Grouse as prey for owls; although young can be taken, they are not known to be important in the diet in Britain (Glue 1977). Manage-

ment for grouse frequently aims to increase proportional cover with heather and manage it through rotational burning to ensure the availability of young growth as food for grouse (Chapman et al. 2009, Oldfield et al. 2003). Although Short-eared Owls can nest among heather, ongoing studies using GPS-satellite telemetry show distinct preferences for hunting over grassland areas within the mosaic of moorland habitat (pers. obs., see also McGarry 1998, Calladine & Morrison 2013). Such areas will support the most voles but can be targeted by moorland managers for heather expansion to increase resources for grouse. Therefore the most intensively managed grouse moors where management aims to maximise heather cover and thereby decrease suitability for voles could actually be a limitation or threat for Short-eared Owls.

As ground-nesting birds, Short-eared Owls are vulnerable to ground-based predators and it is most likely that they benefit from the active control of such predators that is also part of grouse moor management (Fletcher et al. 2010). Therefore reduced levels of predator control through reduction or abandonment of grouse moor management could be a threat to the status of breeding Short-eared Owls in Britain. A negative association for breeding Short-eared Owls with the abundance of predators is also supported by their presence on islands that have both voles but also an absence of most mammalian ground predators. Further refinement of the modelling approach with more appropriate data on mammal distribution, were it available, would probably tease out these associations. However the introduction of predators on islands should also be recognised as a significant threat to Short-eared Owls (Fraser et al. 2015) as has also been demonstrated for assemblages of other ground-nesting birds (Calladine et al. 2017).

Our analyses failed to identify statistically significant fixed limitations for Short-eared Owls in Britain, but that is arguably a result of lack of statistical power and/or the quality

of environment data sets that were available. For example, the abundance and distribution of voles, their preferred prey is known to influence the spatial and temporal occurrence of Short-eared Owls (Village 1987, Korpimäki & Norrdahl 1991) and despite evidence that suggests an association across the British Isles, their influence was not recognised through the models. For example, among the archipelagos around the north and west of Scotland, some islands support voles while they are absent from others. In the Western Isles, Short-eared Owls breed on the Uists where voles occur but generally not on Barra or Lewis and Harris where voles are absent. Similarly in the northern isles, they breed in Orkney (with voles) but not Shetland (voles absent). Voles are also naturally absent from Ireland (not included in our analyses because of a different availability of environmental data sets), where the owls are also generally absent as breeding species in contrast to the main island of Britain (Balmer et al. 2013). The potential for modelling associations with the presence of voles could be further complicated by the fact that their abundance can vary markedly between years (Petty et al. 2000, Korpimäki et al. 2002) and empirical data on vole abundance and how it varies is not available over the extent of Britain. Exploration of the use of data describing vegetation types and structure (e.g. derived using Lidar) as proxies for vole abundance might prove useful in the further development of a conservation framework for the owls.

Further work to develop an effective conservation framework for Short-eared Owls, as identified by our models, will require: (i) improve monitoring to better understand the nature and distribution of change, though this would be challenging for this species (Calladine et al. 2010); (ii) more refined predictive models to include variables that could act as proxies for vole availability; (iii) a better understanding of the role of habitat interactions at their interface (e.g. forest and moorland); and (iv) better understanding of

the role of intra-guild relationships among predators that may affect Short-eared Owls. As a species, Short-eared Owls lie towards the irruptive end of the continuum of migration strategies (Newton 2006, Calladine et al. 2012) and can be remarkably fecund when conditions are suitable. They are able to shift and establish breeding territories to follow temporally variable abundances of appropriate prey within areas of suitable habitat and appropriate conditions (Village 1987, Korpimäki & Norrdahl 1991) with distances between territories held by individuals in sequential years (and potentially even within the same season) of 1000 km being recorded (pers. obs. from ongoing telemetry studies). Improved knowledge of their migrations, year-round habitat requirements and of connectivity between owls breeding in different areas will also be important elements in any conservation strategy for the species.

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References

Akçakaya, H.R. & Sjögren-Gulve, P. 2000. Population viability analyses in conservation planning: an overview. Ecological Bulletins 9-21.

Arnold, H.R. 1993 Atlas of mammals in Britain. HMSO, London.

- Balmer, D.E., Gillings, S., Caffrey, B.J., Swann, R.L., Downie, I.S. & Fuller, R.J. 2013. Bird Atlas 2007–11: the Breeding and Wintering Birds of Britain and Ireland. BTO, Thetford.
- Booms, T.L., Holroyd, G.L., Gahbauer, M.A., Trefry, H.E., Wiggins, D.A., Holt, D.W., Johnson, J.A., Lewis, S.B., Larson, M.D., Keyes, K.L. & Swengel, S. 2014. Assessing the status and conservation priorities of the short-eared owl in North America. The Journal of Wildlife Management 78: 772–778.
- Border, J.A., Newson, S.E., White, D.C.J. & Gillings, S. 2017. Predicting the likely impact of urbanisation on bat populations using citizen science data, a case study for Norfolk, UK. Landscape & Urban Planning 162: 44–55.
- Brambilla, M., Casale, F., Bergero, V., Crovetto, G.M., Falco, R., Negri, I. & Bogliani, G. 2009. GIS-models work well, but are not enough: Habitat preferences of *Lanius collurio* at multiple levels and conservation implications. Biological Conservation 142: 2033-2042.
- Bright, J., Langston, R., Bullman, R., Evans, R., Gardner, S. & Pearce-Higgins, J. 2008.
 Map of bird sensitivities to wind farms in Scotland: A tool to aid planning and conservation. Biological Conservation, 141: 2342-2356.
- Burfield, I.J. 2008. The conservation status and trends of raptors and owls in Europe. Ambio 37: 401–407
- Calladine, J., Garner, G., Wernham, C. & Buxton, N. 2010. Variation in the diurnal activity of breeding Short-eared Owls *Asio flammeus*: implications for their survey and monitoring. Bird Study 27: 89-99.
- Calladine, J., du Feu, C. & du Feu, R. 2012.

- Changing migration patterns of the Short-eared Owl *Asio flammeus* in Europe: an analysis of ringing recoveries. Journal of Ornithology, 153: 691-698.
- Calladine, J. & Morrison, N. 2013. Diurnal and nocturnal ranging behaviour by moorland breeding Short-eared Owl Asio flammeus in Scotland. Bird Study 60: 44-51.
- Calladine, J., Humphreys, E.M., Gilbert, L., Furness, R.W., Robinson, R.A., Fuller, R.J., Littlewood, N.A., Pakeman, R.J., Ferguson, J. & Thompson, C. 2017. Continuing influences of introduced hedgehogs *Erinaceus europaeus* as a predator of wader (*Charadrii*) eggs four decades after their release on the Outer Hebrides, Scotland. Biological Invasions 19: 1981-1987
- Calladine, J., Díaz, M., Reino, L., Jardine, D. & Wilson, M. 2018. Plantations of non-native tree species: In: Mikusinski, G., Roberge, J.M. & Fuller, R.J. (eds). Ecology and Conservation of Forest Birds. Cambridge University Press, Cambridge, Pp 350 386.
- Chapman, D.S., Termansen, M., Quinn, C.H., Jin, N.L., Bonn, A., Cornell, S.J., Fraser, E.D.G., Hunacek, K., Kunin, W.E. & Reed, M.S. 2009. Modelling the coupled dynamics of moorland management and upland vegetation. Journal of Applied Ecology 46: 278-288.
- Eaton, M.A., Balmer, D.E., Bright, J., Cuthbert, R., Grice, P.V., Hall, C., Hayhow, D.B., Hearn, R.D., Holt, C.A., Knipe, A., Mavor, R., Noble, D.G., Oppel, S., Risely, K., Stroud, D.A. & Wotton, S. 2013. The state of the UK's birds 2013. RSPB, BTO, WWT, NRW, JNCC, NE, NIEA and SNH, Sandy, Bedfordshire.
- ESRI.2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

- Fletcher, K., Aebischer, N.J., Baines, D., Foster, R. & Hoodless, A.N., 2010. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. Journal of Applied Ecology 47: 263–272.
- Fraser, E.J., Lambin, X., McDonald, R.A. & Redpath, S.M. 2015. Stoat (*Mustela erminea*) on the Orkney Islands assessing risks to native species. Scottish Natural Heritage Commissioned Report No. 871
- Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27: 2865-2873.
- Gelman, A. 2014. Package 'arm'. Version 1.7-07.
- Gibbons, D.W., Reid, J.B. & Chapman, R.A. 1993. The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991. T. & A.D. Poyser, London.
- Goddard, T.R. 1935. A census of Short-eared Owls (*Asio f. flammeus*) at Newcastleton, Roxburghshire, 1934. Journal of. Animal Ecology 4: 113–118.
- Glue, D.E. 1977. Feeding ecology of the Short-eared Owl in Britain and Ireland. Bird Study, 24, 70-78.
- Grainger, J. 2003. Short-eared Owl. In: Elkins, N., Reid, J.B., Brown, A.W., Robertson, D.G. & Smout, A.M. (eds). The Fife Bird Atlas. Woodland Studios, Dunfermline.
- Kassara, C., Fric, J. & Sfenthourakis, S. 2014. Distribution modelling of Eleonora's Falcon Falco eleonorae Géné, 1839 occurrence in its wintering grounds: a nichebased approach with satellite telemetry data. Bird Conservation International 24: 100-113.

- Korpimäki, E. & Norrdahl, K. 1991. Numerical and functional responses of Kestrels, Short-eared Owls, and Long-eared owls to vole densities. Ecology 72: 814-826.
- Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N.C. 2002. Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. Proceedings of the Royal Society of London B 269: 991-997.
- Lomolino, M.A.R.K. 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography 10: 3-13.
- Maleki, S., Soffianian, A.R., Koupaei, S.S., Saatchi, S., Pourmanafi, S. & Sheikholeslam, F. 2016. Habitat mapping as a tool for water birds conservation planning in an arid zone wetland: The case study Hamun wetland. Ecological Engineering 95: 594-603.
- McGarry, O.C. 1998. Short-eared Owl. In Murray, R., Holling, M., Dott, H.&Vandome, P.(eds). Atlas of Breeding Birds of South-east Scotland. Scottish Ornithologists' Club, Edinburgh, Pp 180–181.
- Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R. & Simpson, I.C. 2011. Final Report for LCM2007 the new UK Land Cover Map. Countryside Survey Technical Report No. 11/07 NERC/Centre for Ecology & Hydrology 112pp. (CEH Project Number: C03259).
- Newton, I. 2006. Advances in the study of irruptive migration. Ardea 94: 433-460.
- Oldfield, T.E., Smith, R.J., Harrop, S.R. & Leader-Williams, N. 2003. Field sports and conservation in the United Kingdom. Nature 423: 531-533.



- Perry, M. & Hollis, D. 2005. The generation of monthly gridded datasets for a range of climatic variables over the UK. International Journal of Climatology 25: 1041–1054.
- Petty, S.J., Lambin, X., Sherratt, T.N., Thomas, C.J., Mackinnon, J.L., Coles, C.F., Davison, M. & Little, B. 2000. Spatial synchrony in field vole Microtus agrestis abundance in a coniferous forest in northern England: the role of vole-eating raptors. Journal of Applied Ecology 37: 136-147.
- Roberts , J.L. & Bowman, N. 1986. Diet and ecology of Short-eared Owls *Asio flammeus* breeding on heather moor. Bird Study 33: 12-17
- Sharrock, J.T.R. 1976. The Atlas of Breeding Birds in Britain and Ireland. T. & A.D. Poyser, London.
- Shaw, G. 1995. Habitat selection by Short-eared Owls *Asio flammeus* in young coniferous forests. Bird Study 42: 158-164.
- Taylor, D.W., Davenport, D.L. & Flegg, J.J.M. 1981. Birds in Kent. Meresborough Books, Gillingham.
- Tharme, A.P., Green, R.E., Baines, D., Bainbridge, I.P. & O'Brien, M. 2001. The effect of management for Willow Grouse shooting on the population density of breeding birds on heather-dominated moorland. Journal of Applied Ecology 38: 439–457.
- Tinoco, B.A., Astudillo, P.X., Latta, S.C. & Graham, C.H. 2009. Distribution, ecology and conservation of an endangered Andean hummingbird: the Violet-throated Metaltail (*Metallura baroni*). Bird Conservation International 19: 63-76.

- Village, A. 1987. Numbers, territory-size and turnover of Short-eared Owls *Asio flammeus* in relation to vole abundance. Ornis Scandinavica 18: 198-204.
- Yost, A.C., Petersen, S.L., Gregg, M. & Miller, R. 2008. Predictive modeling and mapping sage grouse (*Centrocercus urophasianus*) nesting habitat using Maximum Entropy and a long-term dataset from Southern Oregon. Ecological Information 3: 375-386.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.