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Original Research Paper

Factors influencing Hen Harrier, *Circus cyaneus*, territory site selection and breeding success.

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Summary

Capsule

Our findings regarding Hen Harrier territory site selection and breeding success in Ireland offer an opportunity for the development of initiatives and conservation activities aimed at enhancing the suitability of upland areas for breeding Hen Harriers and ensuring the long-term future of the species.

Aims

To investigate landscape-scale associations between habitat composition and Hen Harrier territory site selection, and to explore the influence of habitat and climate on breeding success.

Methods

We used multi-model inference from Generalised Linear Models and Euclidean distance analyses to explore the influence of habitat, topographic, anthropogenic and climatic factors on Hen Harrier territory selection and breeding success in Ireland, based on data from national breeding surveys in 2010 and 2015.

Results

Hen Harrier territories were associated with heath/shrub and pre-thicket coniferous forests. Comparisons between territories and randomly-generated pseudo-absences (upland and lowland) showed that breeding pairs preferentially select for these habitats. Breeding success was negatively influenced by rainfall early in the breeding season and by climatic instability and was positively influenced by the presence of heather moorland and bog.

Conclusions

The results suggest that breeding success in a degraded landscape is compromised by the synergistic effects of climate, landscape composition and management. Effective conservation of Hen Harriers in Ireland will therefore rely on landscape-scale initiatives.

Introduction

Upland areas, typically found at higher elevation than enclosed farmland (O'Rourke & Kramm 2009), are of high conservation importance and support a diverse and characteristic assemblage of habitats and species (Thompson *et al.* 1995; Roche *et al.* 2014). However, uplands are also subject to a suite of pressures that result in the degradation and fragmentation of habitats (e.g. Douglas *et al.*, 2008; O'Riordan *et al.*, 2015; O'Rourke & Kramm 2009; Ratcliffe, 2010; Renou-Wilson *et al.* 2011). This has led to the decline of many upland bird populations (Marquiss *et al.* 1985; Brawn *et al.* 2001; Julliard *et al.* 2004)

Afforestation (the planting of forest in an area where there was little or no previous tree cover) has resulted in greater losses in upland bird populations than any other single factor (Thompson *et al.* 1988; Ratcliffe 2010). Following afforestation, the composition of avian assemblages associated with plantation forests is not temporally stable; while young plantation forests are associated with a diverse range of bird species (Wilson *et al.* 2006), bird communities change as the plantation ages, with forest species succeeding those of open habitats (Wilson *et al.* 2006). Furthermore, afforestation has negative implications for upland species beyond the immediate transformation of open habitats. For example, forest fragments act as reservoirs for generalist predators (Small & Hunter 1988; Andren 1992; Kurki *et al.* 1998), increasing the risk of depredation for ground-nesting birds near forest edges and/or driving avoidance of habitat patches associated with forest edges (Douglas *et al.* 2011; Wilson *et al.* 2014). Thus, the links between habitat abundance, quality and/or connectivity and the persistence of a species requires a nuanced understanding of the focal species' ecology. Thus far, afforestation has precipitated the decline of many upland, open-habitat species, including the Hen Harrier (*Circus cyaneus*; O'Flynn 1983).

Bird populations can also be negatively affected by temperature (Wingfield 1984) and rainfall (Elkins 1984) mediated by effects on reproductive success related to the thermoregulatory inefficiencies of young chicks (Nye 1964; Elkins 1984) and associated adult brooding behaviour. In cold environments, both chicks and adults may expend more energy counteracting heat loss, leading to greater food demands (Weathers 1979). This can result in adults spending more time foraging (Redpath *et al.* 2002), thus increasing chick vulnerability via exposure or, conversely, substantially increase brooding time which can result in chick mortality via starvation (Beintema & Visser 1989). The effects of cold temperatures may be exacerbated by rainfall as the downy feathers of young chicks are not fully water-repellent; wet chicks lose heat more rapidly than dry chicks (Nye 1964). However, while both temperature and rainfall have been shown to affect Hen Harrier breeding performance (García & Arroyo 2001; Redpath *et al.* 2002a; Schipper 1979), their impacts are not consistent across the species' range. For example, Hen Harrier brood size was positively related to temperature in Scotland (Redpath *et al.* 2002a) while the opposite was true in Spain (García & Arroyo 2001). Thus, understanding the relationship between climate and breeding performance in this species requires discrete, region-specific studies.

Hen Harriers are medium sized, ground-nesting birds of prey that are widely distributed throughout Eurasia, including the UK and Ireland (Millon *et al.* 2002; Redpath *et al.* 2002; Amar *et al.* 2008; Ruddock *et al.* 2016; Sachslehner *et al.* 2016). Populations have declined across the species' range and they are now a Species of European Conservation Concern (SPEC; Staneva & Burfield, 2017). They are listed under Annex I of the EU Birds Directive (European Council Directive 79/409/EEC) which requires EU Member States protect them where they occur within national boundaries. This includes the designation of Natura 2000 sites, or Special Protected Areas (SPAs), as per Article 4 (Directive 2009/ 147/EC), and the implementation of ongoing monitoring initiatives such as the regular national surveys of breeding Hen Harriers in Ireland (Norriss *et al.* 2002; Barton *et al.* 2006; Ruddock *et al.* 2012; Ruddock *et al.* 2016). Ireland's afforestation goals are ambitious, with forest estate coverage expected to expand from the current 11% of total land cover to 18% by 2046 (National Parks & Wildlife Service 2015). This represents a considerable change in land-use with implications for Hen Harrier conservation, particularly as forest plantations mature and become unusable for nesting and foraging (Picozzi 1978; Wilson *et al.* 2012).

Hen Harriers typically utilise upland habitats during the breeding season, often nesting in heather moorlands (Redpath *et al.* 1998; Amar *et al.* 2008; Watson 2017). In areas where their preferred habitat is not available, Hen Harriers are known to utilise other habitats, such as cereal fields and young forest plantations (Millon *et al.* 2002; Sachslehner *et al.* 2016); Ruddock *et al.*, 2016; Wilson *et al.*, 2009, 2012b) where the dense understory provides nesting habitat and foraging opportunities (Redpath *et al.* 1998; Madders 2000). The breeding success of Hen Harriers can be affected by many factors, including food availability (Amar & Redpath 2002; Amar *et al.* 2003), predation (Irwin *et al.*, 2012; Ruddock *et al.*, 2016), habitat (Amar *et al.* 2008; Wilson *et al.* 2012) and climate (García & Arroyo 2001; Redpath *et al.* 2002). Breeding success rates exhibit considerable spatial variation and the average number of chicks raised to fledging in Ireland is lower than observed in the UK (Fielding *et al.* 2011; Irwin *et al.* 2012). The subsequent survival of juveniles, and the proportion of which are recruited into the Irish breeding population, is largely unknown at present.

Hen Harriers were once widespread in Ireland until historic habitat loss resulted in substantial reductions in both range and abundance (O'Flynn 1983; Whilde 1993). The population showed some signs of recovery during the mid-20th Century, peaking at a reported 200-300 pairs in the 1970s (Watson 2017) though the decline resumed thereafter due to habitat loss and persecution (see Barton *et al.* 2006; Norriss *et al.* 2002; Ruddock *et al.* 2012, 2016). The current Hen Harrier population in Ireland is moderately small, with fewer than 157 breeding pairs being recorded in 2015 (Ruddock *et al.* 2016). Thus, the species is of considerable conservation concern in Ireland (Colhoun & Cummins 2013). In 2007, six SPAs were established for Hen Harrier conservation in the Republic of Ireland. Afforestation, forest management, development (e.g. windfarms) and recreational activities are regulated in these areas and they include important breeding habitats such as heather moorland, bogs, rough grassland and young conifer plantations (Wilson *et al.* 2009). However, all SPAs contain considerable forest cover, primarily in the form of non-native conifer plantations (Moran & Wilson-Parr 2015). This is typical of upland areas in Ireland where large tracts of upland habitats have been afforested in recent decades (O'Leary *et al.* 2000).

Here we used data derived from national breeding Hen Harrier surveys, together with data on landscape, climate and man-made features to explore local factors affecting the location of breeding-pair territories and landscape-scale factors affecting breeding success and productivity. We hypothesise that: i) Hen Harrier territories will be strongly associated with pre-thicket coniferous forests; ii) breeding performance will be negatively affected by the amount of coniferous forest in the landscape; and iii) the effect of SPAs will be indistinguishable from that of non-designated areas. We discuss our findings in the context of previous work on the habitat associations of Hen Harriers in Ireland and Hen Harrier conservation. Consequently, we provide recommendations regarding habitat management and investigative avenues for future research which would provide a basis for the development of ecologically appropriate conservation and management measures.

Materials and methods

Data sources and preparation

A total of 668 records collected during national breeding Hen Harrier surveys in Ireland in 2010 and 2015 were provided by the National Parks and Wildlife Service (NPWS). These data were collected by an extensive network of staff, members and volunteers from the NPWS, Irish Raptor Study Group (IRSG), BirdWatch Ireland (BWI) and Golden Eagle Trust (GET), university researchers, as well as independent commercial and voluntary ornithological surveyors working across Ireland (Ruddock *et al.*, 2012, 2016). Two discrete datasets were derived from the raw data. The first was concerned with territory selection and included point data representing centroids of all confirmed territories (n = 236; 2010 = 128, 2015 = 108; Fig. 1a). The second was concerned with breeding success and productivity ('breeding success', hereafter). Thus, only territory centroids with known nest-success outcomes (i.e. success or failure) were included (n = 191; 2010 = 94, 2015 = 97; Fig. 1b). To account for spatial autocorrelation, i.e. clustering of presence records, Moran's I Index scores (Moran 1950) were calculated for each point using the Spatial Analyst function in the ArcGIS toolbox.

We investigated the effect of several variables on Hen Harrier territory location and breeding success, including: forest composition (broadleaved or coniferous); coniferous forest age; land class; temperature; rainfall; hilliness; elevation; SPA (inside/outside site boundary); proximity to windfarms; proximity to post-thicket coniferous forest; and proximal road density (Table 1). Data temporally relevant to the 2010 and 2015 Hen Harrier surveys (i.e. nest site/success, climate, weather, forest age) were grouped accordingly. Non-forest land class variables were assumed to be temporally consistent between surveys.

Forest data were extracted from the CORINE 2012 Land Cover dataset (European Environment Agency 2016) and were augmented with data from Coillte (public forests in Ireland), NPWS (private forests in Ireland) and the Forest Service Northern Ireland (public and private forests). Forest data were classified by type (broadleaved or coniferous); mixed forest where conifers accounted for ≤50% of the total area were classified as broadleaved and mixed forest with >50% conifers were classified as coniferous. Coniferous forests were further divided into three age categories, according to known Hen Harrier nest site selection preferences (Irwin *et al.* 2012; Wilson *et al.* 2012b): i) early (0 – 2 years, post-planting); ii) pre-thicket (3 – 12 years, post-planting); and iii) post-thicket (≥13 years, post-planting). Post-thicket forest data were merged with CORINE coniferous data, which represent mature forests. Early and pre-thicket forest data were then erased from the composite CORINE-post-thicket shapefile. The accuracy of derived forest shapefiles in describing total forest coverage was visually assessed via comparison with satellite optical imagery.

In order to investigate the effects of land-use, additional, non-forest land cover variables were extracted from the CORINE dataset: two composites (arable; heath/shrub) and four raw variables (bog; natural grassland; pasture; urban; Table 1). Temperature (ºC) and rainfall (mm) data were downloaded from Met Éireann (http://www.met.ie) and the Met Office (https://data.gov.uk). Data for 27 weather stations were included, based on the temporal resolution of their data (i.e. weekly measurements). Data for the breeding season, March – August inclusive, were included in the analyses. Rainfall data were further split into two sub-sets according to breeding season stage: early-to-mid breeding season ('early' hereafter; March – May, inclusive) and mid-to-late breeding season ('late' hereafter; June – August, inclusive). Mean weekly rainfall and associated variance were calculated for each period. Temperature measurements were found to be strongly correlated when separated into early and late breeding season sub-sets, therefore derived metrics - minimum weekly temperature and associated variance - spanned the entire breeding season. Variance was taken as a proxy for climatic stability. For example, low daily variance in rainfall would suggest that the amount of rain that fell on a daily basis was temporally consistent. In contrast, high variance could suggest irregular patterns of rainfall or a trend in rainfall over time. Interpolated regularised raster surfaces (Aggrey 2002) grid-based data structures) were constructed at 1km resolution for each climate metric using the Spline function in ArcGIS 10.4.1 (ESRI 2015), giving 100% coverage to the island of Ireland.

We used a 30 arc-second Digital Elevation Model (DEM) from NASA's Shuttle Radar Topography Mission (SRTM; https://eros.usgs.gov/) to derive elevation data for each point ('elevation'). Shapefiles describing SPA boundaries and the locations of windfarms – given as centroids - across Ireland, correct to 2016, were provided by the NPWS. Road data were downloaded from OpenStreetMap.org (https://www.openstreetmap.org). Only *roads*, *link roads* and *tracks* were included in our analyses (see https://wiki.openstreetmap.org/wiki/Key:highway for more on OSM highway categories), all of which included road types which were present in areas used by Hen Harriers. Road density was calculated as a function of the total length of roads divided by total polygon area (see sections 2.2 and 2.3). Shapefile and raster processing and manipulation were carried out using the statistical program R (R Core Team 2017), particularly the packages *raster* (Hijmans 2017), *rgeos* (Bivand & Rundel 2017), *rgdal* (Bivand *et al.* 2017) and *maptools* (Bivand & Lewin-Koh 2017) and ArcGIS 10.4.1 (ESRI 2015).

Territory selection models

Putative Hen Harrier territories were assessed based on interpretation of (i) nest locations, (ii) Hen Harrier observations, (iii) Hen Harrier activity, and (iv) the behavioural category by which each record was defined during each breeding Hen Harrier survey (see Ruddock *et al.*, 2016). Hen Harrier territory sites were compared to hypothetical territory sites (i.e. pseudoabsences) in the wider landscape to establish the ecological distinctiveness of territories relative to other habitat mosaics. Pseudoabsences (*pa1*) were randomly generated within the altitudinal range of confirmed Hen Harrier territories (n = 500; 36m – 570m). Each point (i.e. territory or pseudoabsence) was buffered to three distances (Graf *et al.* 2005) – 1 km, 2 km and 5 km - that were chosen to represent variable foraging distances from the nest and to ease comparisons with previous studies (Arroyo *et al.* 2014; Schipper 1977; Wilson *et al.* 2009). Breeding Hen Harriers in Ireland have been reported to travel over 11 km from an active nest, via GPS tracking (Irwin *et al.* 2012) and males in Scotland have been observed travelling up to 9 km from nests (Arroyo *et al.* 2014). However, typical foraging ranges are reported to be much smaller (Arroyo *et al.* 2014). Moreover, the maximum distance travelled from a nest site does not necessarily equate to consistent trends in foraging strategy and may not be representative of typical Hen Harriers in Ireland. Hence, conservative distances were used. The total area of each land cover variable and forest category and road density were calculated within each buffer. The effect of spatial scale was explored by constructing GLMMs for individual variables across all buffers. The most suitable buffer distance for each variable was chosen, *a priori,* based on the size of the regression coefficients from these exploratory models; selected scales had the largest coefficients. Euclidean distances were calculated from each point to the nearest windfarm and stand (edge) of post-thicket forest. Elevation (m above sea level) was extracted for each point.

Territory selection was examined using binomial, log-linked Generalised Linear Mixed Models (GLMMs) and model weighting using the R packages lme4 (Bates *et al.* 2015) and *MuMIn* (Bates *et al.* 2015). The presence or pseudoabsence of a territory was fitted as the dependent variable; Moran's *I* scores were fitted as a random factor. Predictor variables were tested for multicollinearity, ensuring that Tolerance values were >0.2, Variance Inflation Factor (VIF) values were <10.0 and bivariate correlations had an r <0.5 (Quinn & Keogh 2002). Variables were standardized to have a $\bar{x}=0$ and $\sigma = 1$ prior to analysis, thus permitting the direct comparison of regression coefficients. We used the Akaike Information Criterion (AIC) to rank all possible model permutations. The top subset of models was defined by the threshold ΔAIC

≤2 units (Burnham & Anderson 2002). The model with the lowest Akaike weight (ω_i) was identified as being the best approximating model within the top subset of N models. To determine the relative importance of each variable, the $\Sigma\omega_i$ of all models containing the focal variable within the top subset was calculated (McAlpine *et al.* 2006), where the $\Sigma\omega_i$ of omnipresent variables = 1. The effect size (β coefficient) of each variable was determined via multi-model inference and model averaging (Burnham & Anderson 2002). Variables were ranked, first by $\Sigma\omega_i$, and, secondarily where variables had equal $\Sigma\omega_i$ values, by the magnitude of their regression coefficients. The performance of the best approximating model was assessed using a 60% training set and a 40% test set with 10-fold cross-validation (R package *caret*; Kuhn 2017).

Territory records and *pa1* were augmented by an additional set of pseudoabsences (*pa2*) to facilitate inferential exploration of habitat choice via ecological distance analysis. To create *pa2*, we generated 500 randomly-placed points across the remaining Irish landscape, beyond elevational constraints described above. These additional locations provided a broader context for interpretation of ecological distances between territory locations and *pa1*. Principal Component Analysis was used to reduce climate and habitat variables associated with all locations to five hypothetical axes with eigenvalues >1. We calculated a single measure of ecological, Euclidean distance between groups (territories, *pa1*, *pa2)* in *n*th-dimensional space across all Principal Components simultaneously. Euclidean distances were calculated using the R package *pdist* (Wong 2013) and the base function *dist*.

Breeding performance models

Breeding performance models were constructed to explore factors affecting Hen Harriers at mixed landscape scales using the methods described for territory models (see *Territory selection models*, above) but on the subset of territories with known nest success outcomes (i.e.

success/failure). Territory centroids were assumed to be nest locations (and are referred to as such, hereafter) based on the best available data. Additional point data for each nest location was extracted for SPA (inside or outside the boundary); minimum temperature; the variance of minimum temperature across the breeding season; mean weekly rainfall in the early breeding season; and mean weekly rainfall in the late breeding season. 86 nests were located inside SPAs with 112 occurring outside SPA boundaries (2010 = 36:65; 2015 = 50:47).

Breeding performance was examined using a poisson GLMM; the number of chicks successfully fledged (Fig. 1b) was fitted as the dependent variable and Moran's I was fitted as a random factor. Model construction, selection and evaluation followed the same methods described for territory selection models (see *Territory selection models*, above). In addition, the relative abundance of each habitat was explored across all buffered distances for nest locations and across the total area of each SPA.

3. Results

Hen Harrier territory locations exhibited significant spatial autocorrelation (I = -0.003 ± 0.005, $p < 0.0001$; Fig. 2). There was no evidence of site fidelity between years, even assuming that the nearest territories were established by the same pair; 2010 territories were located at least 141m ($\bar{x}$ = 3.80km ± 7.61km) from the nearest territory in 2015, The top subset (ΔAIC ≤2) consisted of 18 models (see Appendix I, Table 1A). The best approximating model for territory site selection was positively influenced by heath/shrub, pre-thicket forest and bog at 1km, indicating that Hen Harrier territories were strongly associated with habitats that ostensibly offer an appropriate nesting environment. There was a negative association with pasture at 2km and with broadleaved woodland at 5km, two habitats that are not typically associated with breeding Hen Harriers. Territories were also positively associated with increased elevation, being found at higher altitudes than *pa1* (Fig. 3). The predictive accuracy of the best-approximating model, assessed via 10-fold cross-validation, was 0.82 (± 0.02).

According to single-metric *n*th-dimensional Euclidean distance analyses, territory locations were on average 17% further away from *pa2* than *pa1* and 27% further away than *pa1* and *pa2* were from each other (Fig. 4). This indicates that Hen Harriers are not only utilising upland habitats as territory locations but that they are specifically utilising the landscape according to a narrow range of habitat features.

Hen Harrier territory locations with known breeding success outcomes exhibited significant spatial autocorrelation ($I = -0.118 \pm 0.001$, $p = 0.002$). The top subset ($\Delta AIC \leq 2$) consisted of 23 models (Appendix I, Table 1B). The best approximating model for breeding success was negatively influenced by mean weekly rainfall early in the breeding season, mean weekly minimum temperatures and the variance in mean weekly minimum temperature. The direction? of the climatic effects suggests that chicks are most vulnerable to stochastic changes in minimum temperature, possibly exacerbated by rainfall that could cause prolonged chilling, during the early stages of the breeding season. There were positive associations with mean weekly rainfall late in the breeding season, heath/shrub habitat at the 1km scale and bog at 2km. Both habitats are typically associated with breeding Hen Harriers elsewhere in the species' range. In contrast to territory analyses, coniferous forest age classes did not feature in the best approximating model for breeding success (Fig. 4). The predictive accuracy of the best-approximating model, assessed via 10-fold cross-validation, was 0.76 (± 0.01).

4. Discussion

Across the 2010 and 2015 Hen Harrier national survey data, the influence of land class and associated parameters on the utilisation of habitats for territories contrasted with their influence on subsequent breeding success and productivity.

Hen Harrier territories in Ireland were found to be positively associated with heath/shrub, bog, high elevation and pre-thicket coniferous forest (i.e. 0-2 years old and 3-12 years old). The positive association with typically preferred habitat (i.e. bog and heath/shrub), reinforced by breeding success models, emphasises the importance of these habitats for breeding and foraging Hen Harriers (e.g. Redpath *et al.* 1998; Madders 2000; Amar *et al.* 2008; Arroyo *et al.* 2009). There was a particular association with pre-thicket forests (i.e. 0-12 years post-planting). While previous studies at a number of locations across Ireland and the UK have described similar associations with pre-thicket forest (Madders 2000; Barton *et al.* 2006; Wilson *et al.* 2009; O'Donoghue 2010; Irwin *et al.* 2012), this is the first to do so on such a large scale. Pre-thicket forest undergrowth may consist of heather (Ericaceae sp.), gorse (*Ulex* sp.) and bramble (*Rubus fruticosus agg.*), providing nest security against potential predators (O'Flynn 1983) and making these areas attractive to breeding Hen Harriers. Utilisation of these habitats by Hen Harriers as described by territory selection models and *n*th dimensional ecological distance analyses may, therefore, be indicative of a lack of more suitable nesting and/or foraging habitat in the wider landscape. Furthermore, areas of ostensibly suitable upland habitat may also be degraded and/or exposed to disturbance via peat extraction (O'Riordan *et al.* 2015), over-grazing (Douglas *et al.* 2008), burning or changes to land management (Renou-Wilson *et al.* 2011). These factors may have implications for adult behaviour and subsequent chick survival, creating a potential ecological trap where Hen Harriers select breeding habitats that ultimately result in reduced fitness (Schlaepfer *et al.* 2002). This was previously reported at one study site in Ireland (Slieve Aughty SPA; Wilson *et al.* 2012b). The current study shows that this phenomenon may be occurring across the island of Ireland, on a much wider scale, and with greater implications for Hen Harrier populations, than previously thought. Further afforestation of open upland areas and maturation of the existing forest estate will result in further fragmentation of foraging habitat, decreasing the overall landscape suitability for breeding Hen Harriers and ultimately impacting on breeding success.

The location of nests relative to SPA boundaries (i.e. inside or outside) was consistently retained across the top subset of breeding success models, including the best approximating model. This is the first scientific evidence that the best areas for Hen Harriers were selected during the SPA designation process. Proposed interventions within SPAs (e.g. road construction, clear-felling, afforestation) are subject to a suite of regulations in Ireland, many of which are aimed at mitigating disturbance of breeding Hen Harriers in high sensitivity areas (i.e. ‘Red Areas’, NPWS 2015). The apparent success of SPAs in facilitating greater breeding success appears to be skewed by increased success in locations where heather and moorland nesting and foraging habitats may be of higher quality and/or less fragmented. It is important to note, however, that over 50% of the breeding Hen Harrier population was located outside of the six breeding Hen Harrier SPAs during both survey years and that the Hen Harrier population in the SPA network has declined over this time (Ruddock *et al.* 2012, 2016). The value of the wider countryside to Hen Harrier conservation is twofold. First, a species with a wider breeding range will be more robust to pressures acting at a site level. Second, it is possible that, due to the maturation of the forest estate in Ireland combined with other pressures in SPAs, the breeding population could drop below a critical level. A sufficiently large and persistent population outside of the SPA network could improve the recolonization potential for those SPAs that are at risk of local extinctions. It is essential, therefore, that conservation initiatives aimed at bolstering Hen Harrier populations in Ireland embrace a landscape-scale approach and do not focus on SPAs alone.

Hen Harrier breeding success and productivity were affected by temperature and climatic instability (i.e. the variation in minimum temperature) throughout the breeding season and by rainfall in the early breeding season. The mechanisms by which temperature and rainfall influence Hen Harrier breeding success are unclear at present, as studies elsewhere in the species' range reveal regionally variable effects (e.g. García & Arroyo 2001; Redpath *et al.* 2002a; Schipper 1979). This suggests that climate may be masking discrete ecological and behavioural phenomena. For example, poor foraging opportunities in the surrounding landscape may be placing a larger provisioning burden on both parents who consequently have to travel greater distances to find food (e.g. see flight distances in Irwin *et al.* 2012). Decreased parental attendance may also result in greater vulnerability of eggs and chicks to predation. Potential predators of Hen Harrier nests in Ireland include red foxes (*Vulpes vulpes*), badgers (*Meles meles*), pine martens (*Martes martes*), American minks (*Neovison vison*), stoats (*Mustela erminea*), buzzards (*Buteo buteo*), ravens (*Corvus corax*) and hooded crows (*Corvus corone corvix*). Such predators are often more abundant in fragmented habitats (Andren 1992; Kurki *et al.* 1998) and can have substantial negative impacts on ground-nesting birds (Paton 1994; Fletcher *et al.* 2010). Foxes and pine martens have been observed depredating Hen Harrier chicks in studies using remote-sensing camera traps (Irwin *et al.* 2012; Monaghan 2015; Ruddock *et al.* 2016; Fernández-Bellon *et al.* 2017). Furthermore, increased rainfall may place an additional thermoregulatory burden on young chicks via increased metabolic costs and greater food demands (Weathers 1979; Olsen & Olsen 1992; Redpath *et al.* 2002). These impacts could be exacerbated by the stochastic effects of an increasingly unpredictable climate such that young chicks are rendered particularly vulnerable to chilling during the coldest periods. Thus, the synergistic effects of reduced parental attendance, increased predation risk and increased energetic demands of exposed chicks via unsupported thermoregulation could go some way to explaining the observed impacts of climate on Hen Harrier breeding success in the current study.

Our findings have implications for the long-term viability and security of Hen Harrier populations in Ireland under continued land use change and future climate change. The early months of the Hen Harrier breeding season are predicted to get increasingly warmer and wetter under future climate change scenarios, while summer months (i.e. late breeding season) will be drier (Gleeson *et al.* 2013). Many studies have demonstrated the impacts of climate change on breeding birds via several mechanisms, including egg-laying phenology (Crick *et al.* 1997; Geyer *et al.* 2011), disease (Benning *et al.* 2002) and changes in prey availability (e.g. Pearce-Higgins 2010). For example, a decline in the availability of upland invertebrates can lead to reduced productivity of insectivorous passerine species which comprise a large proportion of the Hen Harrier's diet. Such phenological mismatches, along with other changes in species interactions, may be among the most important negative impacts of climate change (Cahill *et al.* 2012). Furthermore, climate change impacts may be exacerbated by changes in land management that could simultaneously reduce the proportion of suitable foraging habitat in the landscape (e.g. Kleijn *et al.* 2010). It is therefore imperative that the potential impacts of climate change on Irish Hen Harrier breeding performance and distribution are mitigated using long-term conservation strategies.

Hen Harriers in Ireland currently face an uncertain future. Rainfall and climatic instability early in the breeding season were found in this study to have strong negative effects on subsequent breeding success, suggesting that the population is at further risk under future climate change. Hen Harriers in this study preferentially selected pre-thicket coniferous forests, that provide nesting and foraging opportunities, for territory locations. However, this habitat was also negatively associated with breeding success. Given our understanding of Hen Harrier ecology, including factors known to affect productivity, it seems likely that there are synergistic effects across and between climate, landscape composition and management, parent and chick behaviour, and predation that are resulting in egg and/or chick mortality and, hence, negatively impacting breeding success and, consequently, population levels. The cumulative effects of climate, habitat, parental attendance, prey abundance and predation result in reduced availability of optimum nesting and foraging habitat at the landscape scale. Afforestation of upland areas, along with maturation of the existing 'usable' forest estate, therefore pose the greatest threats to the ecological security of Hen Harriers in Ireland while pre-thicket conifer plantations represent an ecological trap, attracting breeding pairs to a sub-optimal landscape. An optimal habitat mosaic would offer nest concealment and protection from predators and sufficient prey to support near-nest foraging throughout the critical stages of the breeding season. Furthermore, it is clear that while some SPAs benefit breeding Hen Harriers, the majority of the breeding population are found outside of the SPA network and the population within the SPA network has declined, making the conservation of the species in a broader context more important than ever before. Effective conservation of Hen Harriers in Ireland therefore relies on landscape-scale initiatives, including the creation /restoration of suitable nesting and breeding habitat and protection for this species within and beyond the boundaries of the SPA network.

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Appendices

Appendix I

Table A1. Generalised Linear Mixed Model (GLMM) results for variables affecting Hen Harrier territory site selection. Models within the top subset of *n* models (ΔAIC < 2) are given. *t* = confirmed terriory/pseudoabsence; *a* = arable (5km); *b* = bog (1km); *bf* = broadleaved forest (5km); *df* = distance to mature coniferous forest; *dw* - distance to windfarm; *e* = elevation; *ef* = coniferous forest (0-2 years post-planting; 1km); *h* = heath/shrub (1km); *lf* = coniferous forest (13+ years; 1km); *m* = Moran's I (random factor to account for spatial autocorrelation); *n* = natural grassland (5km); *p* = pasture (5km); *pf* = coniferous forest (3-12 years; 1km); *r* = road density. Models were ranked according to their Akaike's Information Criterion (AIC) value; the best approximating (i.e. top-ranked) model is given in bold.

Formula	AIC	ΔAIC
$t \sim bf + b + ef + e + h + p + pf + (m)$	**416.09**	**0.00**
$t \sim b + ef + e + h + p + pf + (m)$	416.19	0.10
$t \sim bf + b + ef + e + h + p + pf + (m)$	416.22	0.13
$t \sim bf + b + ef + e + df + h + p + pf + (m)$	416.23	0.14
$t \sim bf + b + ef + e + n + h + p + pf + (m)$	416.24	0.15
$t \sim b + ef + h + p + pf + (m)$	416.50	0.41
$t \sim b + ef + e + lf + h + p + pf + (m)$	416.78	0.69
$t \sim b + ef + lf + n + h + p + pf + (m)$	416.83	0.74
$t \sim bf + b + ef + e + lf + h + p + pf + (m)$	417.03	0.94
$t \sim b + ef + e + h + p + pf + (m)$	417.41	1.32
$t \sim a + bf + b + ef + df + lf + h + p + pf + (m)$	417.42	1.33
$t \sim a + bf + b + ef + h + p + pf + (m)$	417.44	1.35
$t \sim b + ef + e + df + h + p + pf + (m)$	417.53	1.44
$t \sim b + ef + lf + n + h + p + pf + (m)$	417.55	1.46
$t \sim bf + b + ef + e + df + lf + h + p + pf + (m)$	417.89	1.80
$t \sim bf + b + ef + n + h + p + pf + dw + (m)$	417.92	1.83
$t \sim b + ef + n + h + p + pf + r + (m)$	418.02	1.93
$t \sim bf + b + ef + e + df + lf + n + h + p + pf + (m)$	418.05	1.96

Table 2A. Generalised Linear Mixed Model (GLMM) results for variables affecting Hen Harrier breeding success. Models within the top subset of n models (ΔAIC < 2) are given. c = breeding success (i.e. number of chicks successfully raised to fledging); a = arable (5km); b = bog (2km); bf = broadleaved forest (2km); df = distance to mature coniferous forest; dw - distance to windfarm; e = elevation; ef = coniferous forest (0-2 years post-planting; 5km); h = heath/shrub (1km); lf = coniferous forest (13+ years; 5km); m = Moran's I (random factor to account for spatial autocorrelation); n = natural grassland (2km); p = pasture (5km); pf = coniferous forest (3-12 years; 2km); r = road density; re = rain early in the breeding season; rl = rain late in the breeding season; s = inside/outside Special Protection Areas (SPA); t = minimum weekly temperature; tv = variance in minimum weekly temperature. Models were ranked according to their Akaike's Information Criterion (AIC) value; the best approximating (i.e. top-ranked) model is given in bold.

Formula	AIC	ΔAIC
$\boldsymbol{c \sim b + e + h + \ + t + \ + tv + re + rl + (m)}$	**580.26**	**0.00**
$c \sim b + ef + e + h + t + tv + pf + re + rl + s + (m)$	580.45	0.19
$c \sim bf + ef + e + h + t + tv + re + rl + (m)$	580.69	0.43
$c \sim b + dl + ef + e + h + p + re + rl + (m)$	580.73	0.47
$c \sim b + bf + ef + t + tv + re + rl + (m)$	581.10	0.84
$c \sim dw + h + t + p + re + rl + (m)$	581.14	0.88
$c \sim b + dw + e + lf + t + tv + p + pf + re + rl + (m)$	581.15	0.89
$c \sim bf + dw + h + t + tv + p + pf + re + rl + s + (m)$	581.25	0.99
$c \sim dw + e + h + t + tv + re + rl + s + (m)$	581.32	1.06
$c \sim b + bf + ef + lf + h + t + n + re + rl + r + s + (m)$	581.39	1.13
$c \sim a + b + ef + t + n + re + rl + (m)$	581.42	1.16
$c \sim a + bf + e + h + t + re + rl + r + (m)$	581.42	1.16
$c \sim b + bf + dw + e + tv + re + rl + r + s + (m)$	581.49	1.23
$c \sim a + b + e + h + t + tv + re + r + (m)$	581.51	1.25
$c \sim a + b + ef + lf + h + t + tv + p + re + rl + (m)$	581.51	1.25
$c \sim b + dl + dw + ef + h + t + p + pf + re + rl + (m)$	581.57	1.31
$c \sim a + dl + dw + e + h + t + tv + pf + re + rl + s + (m)$	581.77	1.51
$c \sim b + dw + e + lf + t + tv + p + re + rl + (m)$	582.01	1.75
$c \sim a + b + dl + lf + t + tv + re + r + s + (m)$	582.05	1.79
$c \sim a + b + dw + ef + e + h + n + re + rl + r + (m)$	582.07	1.81
$c \sim bf + dl + ef + e + lf + h + tv + pf + re + rl + r + s + (m)$	582.12	1.86
$c \sim a + b + bf + dl + dw + ef + h + t + tv + p + re + rl + r + s + (m)$	582.12	1.86
$c \sim a + b + bf + dw + e + lf + h + t + n + p + re + rl + r + (m)$	582.20	1.94

Table 1. Variables used in Hen Harrier territory site selection and breeding performance models. 'Raw' variables were not manipulated prior to analyses. Variables are listed according to the order in which they occur in the main text. References are given to support the inclusion of each variable.

Variable	Data product	Manipulation	Source	References
Broadleaved forest	Polygon data	Raw	Coillte; NPWS; Forest Service Northern Ireland	Moran & Wilson-Parr 2015
Coniferous forest	Polygon data	Raw	Coillte; NPWS; Forest Service Northern Ireland	Madders 2000; Wilson *et al.* 2009; Wilson *et al.* 2012; Sachslehner *et al.* 2016
Arable	Polygon data	Composite data: Complex cultivation patterns; land principally occupied by agriculture; non-irrigated arable land	CORINE	Wilson *et al.* 2012; Feys *et al.* 2013; Sachslehner *et al.* 2016; Geary, Haworth & Fielding 2018
Heath/shrub	Polygon data	Composite data: Moors and heathland; sparsely vegetated areas; transitional woodland shrub	CORINE	Madders 2000; Amar & Redpath 2004; Cormier *et al.* 2008; Arroyo *et al.* 2009; Wilson *et al.* 2012
Bog	Polygon data	Raw	CORINE	Madders 2000; Arroyo *et al.* 2009; Irwin *et al.* 2011; Wilson *et al.* 2012
Natural grassland	Polygon data	Raw	CORINE	Madders 2000; Amar & Redpath 2004; Arroyo *et al.* 2009; Wilson *et al.* 2012
Pasture	Polygon data	Raw	CORINE	Madders 2000; Amar & Redpath 2004; Arroyo *et al.* 2009; Wilson *et al.* 2012
Urban	Polygon data	Raw	CORINE	Tapia, Dominguez & Rodriguez 2004
Temperature	Point data	Interpolated raster	Met Éireann; Met Office	García & Arroyo 2001; Redpath *et al.* 2002

Rainfall	Point data	Interpolated raster	Met Éireann; Met Office	García & Arroyo 2001; Redpath *et al.* 2002
Elevation DEM	Surface raster	Raw	NASA	Geary *et al.* 2018
SPA boundaries	Polygon data	Raw	NPWS	Ruddock *et al.* 2012; Moran & Wilson-Parr 2015; Ruddock *et al.* 2016
Roads	Polyline data	Raw	OpenStreetMap	Tapia *et al.* 2004
Windfarms	Point data	Raw	NPWS	Fernández-Bellon *et al.* 2015; Wilson *et al.* 2017
Hen Harrier territories	Point data	Raw	NPWS	Ruddock *et al.* 2012; Ruddock *et al.* 2016

Legends to figures

Figure 1. (a) Confirmed territory locations and (b) mean productivity (number of chicks fledged) of Hen Harriers in Ireland in 2010 and 2015, combined.

Figure 2. Relative importance of variables in explaining the locations of confirmed Hen Harrier territories relative to pseudoabsences at multiple spatial scales (1 km, 2 km and 5 km, selected *a-priori*)., except for elevation which was extracted at each point location. D_ = distance to. Variables were ranked according to the sum of their Akaike weights within the top set of models (ΔAIC<2). Black bars indicate variables that were present in the best approximating model; white bars indicate variables otherwise included in the top subset. Standardised coefficients ± SEs and p values are given to the right, where * = p<0.05, ** = p<0.001 and *** = p<0.0001. The inset plot describes model accuracy as evaluated using randomly split 60:40 training:test datasets with 10-fold cross-validation.

Figure 3. Euclidean distances (± 1SD) across five Principal Component scores for pairwise combinations Hen Harrier territory locations (t), upland pseudoabsences (pa1) and pseudoabsences distributed across the rest of Ireland (pa2).

Figure 4. Relative importance of variables in explaining the breeding success of nesting Hen Harriers at multiple spatial scales (1 km, 2 km and 5 km, selected *a-priori*). Variables were ranked according to the sum of their Akaike weights within the top set of models (ΔAIC<2). Black bars indicate variables that were present in the best approximating model; white bars indicate variables otherwise included in the top subset. Standardised coefficients ± SEs and p values are given to the right, where * = p<0.05, ** = p<0.001 and *** = p<0.0001. The inset plot describes model accuracy as evaluated using randomly split 60:40 training:test datasets with 10-fold cross-validation.

Figure 5. (a) Habitat composition of Special Protection Areas (SPAs) in Ireland which contained (b) successful Hen Harrier nests (i.e. produced ≥ 1 fledged chick) in 2010 and 2015. Natural grassland was omitted as it comprised a small fraction of available habitats across all SPAs. MMM = Mullaghanish to Musheramore Mountains; SAM = Slieve Aughty Mountains SPA; SBe = Slieve Beagh; SBM = Slieve Bloom Mountains; SMW = Stacks to Mullaghareirk Mountains, West Limerick Hills and Mount Eagle; SSM = Slievefelim to Silvermines Mountains. SPA areas were derived from the NPWS SPA shapefile 2017_06.

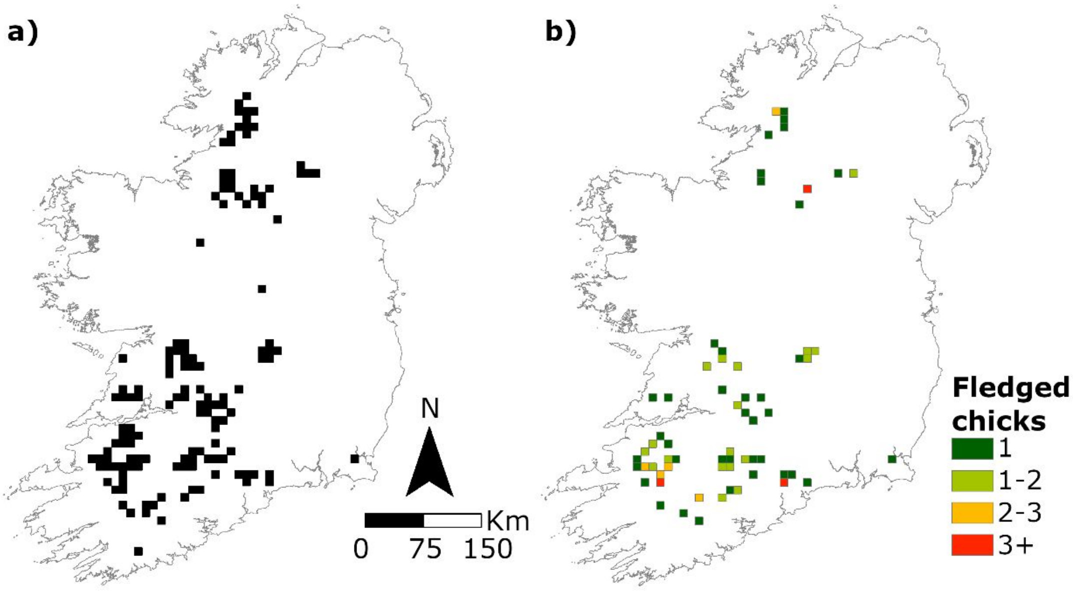
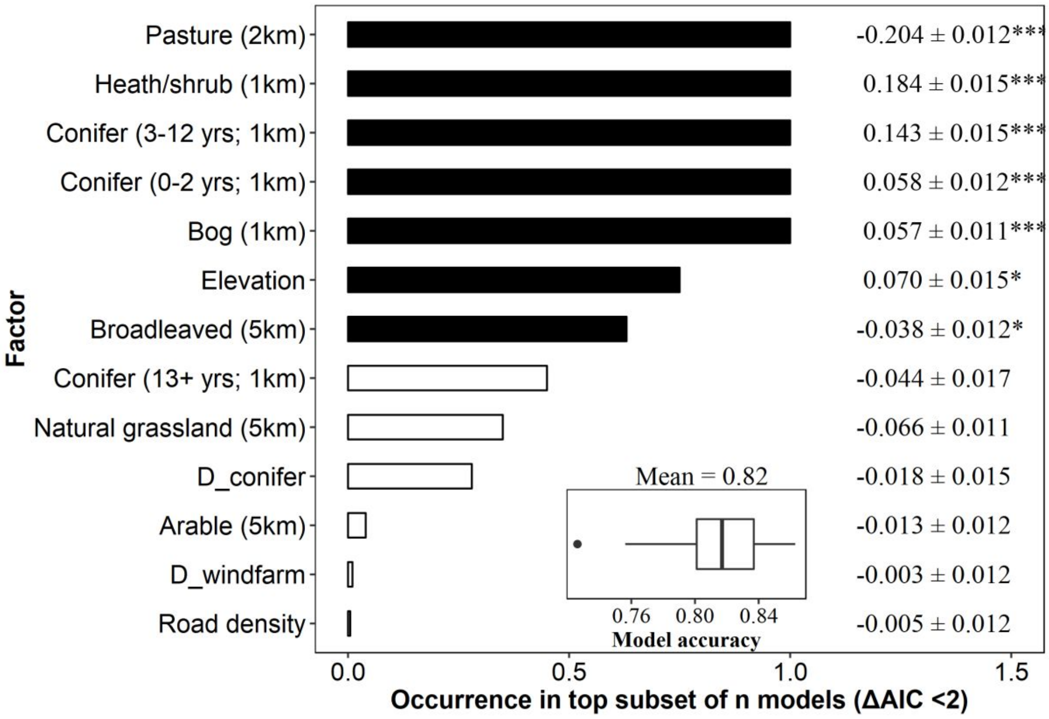


Figure 1.



Pasture (2km)
Heath/shrub (1km)
Conifer (3-12 yrs; 1km)
Conifer (0-2 yrs; 1km)
Bog (1km)
Elevation
Broadleaved (5km)
Conifer (13+ yrs; 1km)
Natural grassland (5km)
D_conifer
Arable (5km)
D_windfarm
Road density
Factor
-0.204 ± 0.012***
0.184 ± 0.015***
0.143 ± 0.015***
0.058 ± 0.012***
0.057 ± 0.011***
0.070 ± 0.015*
-0.038 ± 0.012*
-0.044 ± 0.017
-0.066 ± 0.011
-0.018 ± 0.015
-0.013 ± 0.012
-0.003 ± 0.012
-0.005 ± 0.012
Mean = 0.82
0.76
0.80
0.84
Model accuracy
0.0
0.5
1.0
1.5
Occurrence in top subset of n models (ΔAIC <2)

Figure 2.

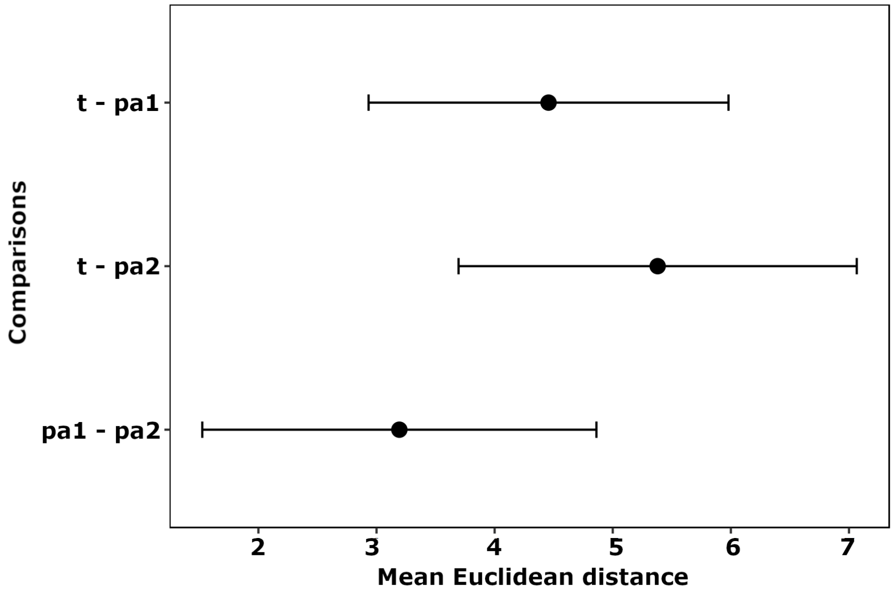
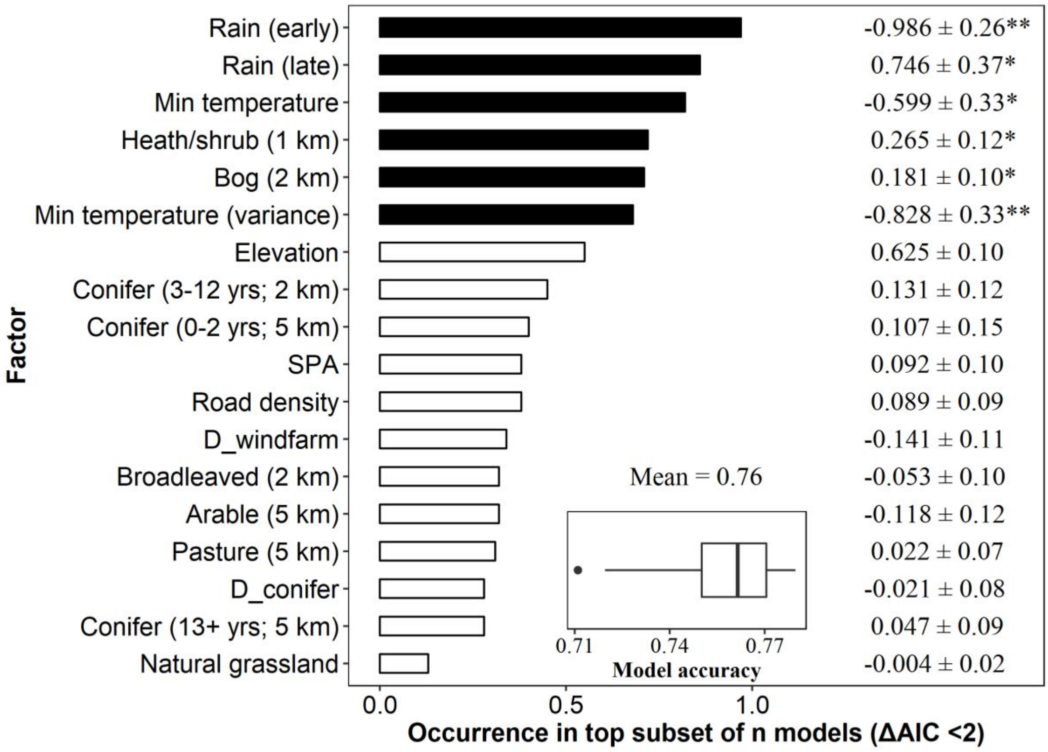

Comparisons
t - pa1
t - pa2
pa1 - pa2
2
3
4
5
6
7
Mean Euclidean distance

Figure 3.



Factor
Rain (early)
Rain (late)
Min temperature
Heath/shrub (1 km)
Bog (2 km)
Min temperature (variance)
Elevation
Conifer (3-12 yrs; 2 km)
Conifer (0-2 yrs; 5 km)
SPA
Road density
D_windfarm
Broadleaved (2 km)
Arable (5 km)
Pasture (5 km)
D_conifer
Conifer (13+ yrs; 5 km)
Natural grassland
-0.986 ± 0.26**
0.746 ± 0.37*
-0.599 ± 0.33*
0.265 ± 0.12*
0.181 ± 0.10*
-0.828 ± 0.33**
0.625 ± 0.10
0.131 ± 0.12
0.107 ± 0.15
0.092 ± 0.10
0.089 ± 0.09
-0.141 ± 0.11
-0.053 ± 0.10
-0.118 ± 0.12
0.022 ± 0.07
-0.021 ± 0.08
0.047 ± 0.09
-0.004 ± 0.02
Mean = 0.76
0.71
0.74
0.77
Model accuracy
0.0
0.5
1.0
Occurrence in top subset of n models (ΔAIC <2)

Figure 4.

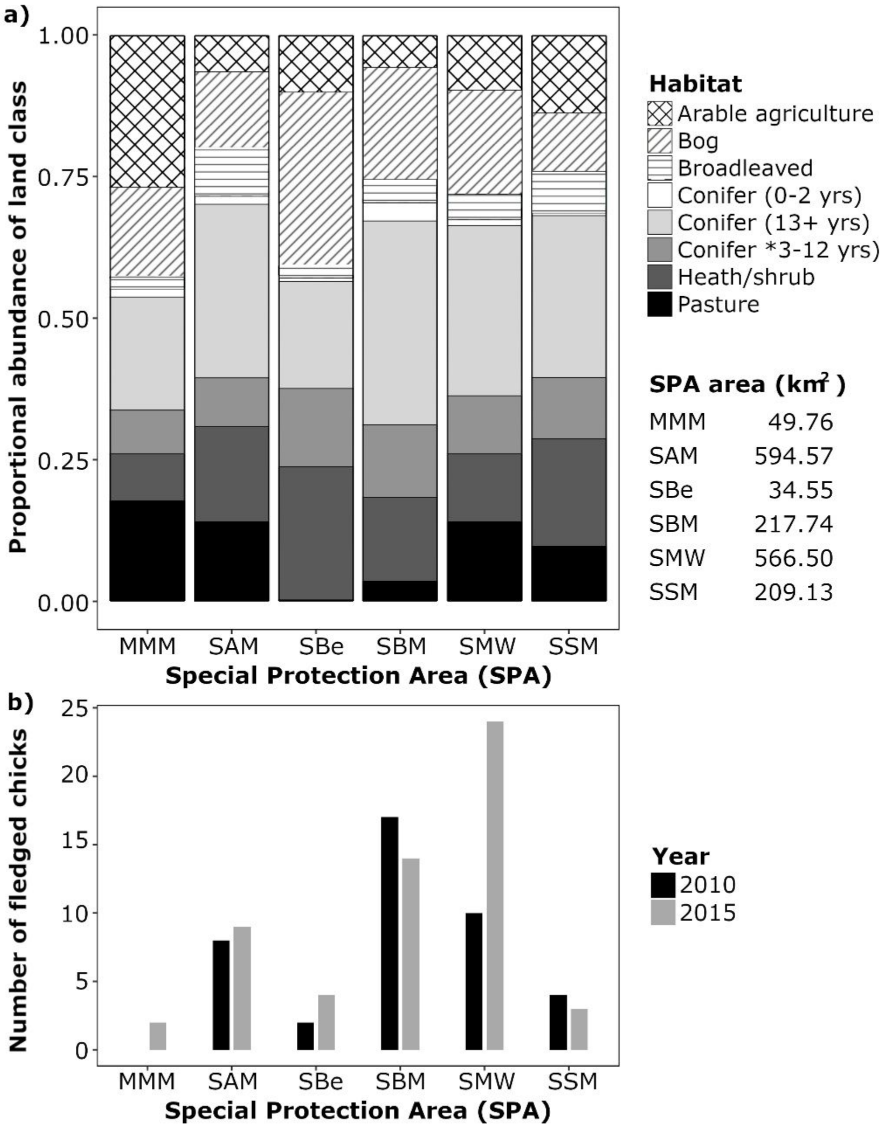

a)
1.00
0.75
0.50
0.25
0.00
Proportional abundance of land class
MMM SAM SBe SBM SMW SSM
Special Protection Area (SPA)
Habitat
Arable agriculture
Bog
Broadleaved
Conifer (0-2 yrs)
Conifer (13+ yrs)
Conifer *3-12 yrs)
Heath/shrub
Pasture
SPA area (km²)
MMM 49.76
SAM 594.57
SBe 34.55
SBM 217.74
SMW 566.50
SSM 209.13
b)
25
20
15
10
5
0
Number of fledged chicks
MMM SAM SBe SBM SMW SSM
Special Protection Area (SPA)
Year
2010
2015

Figure 5.