



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

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ABSTRACT

Capsule: Our findings regarding Hen Harrier *Circus cyaneus* territory site selection and breeding success in Ireland offer an opportunity for the development of initiatives and conservation actions aimed at enhancing the suitability of upland areas for breeding Hen Harriers and ensuring the long-term persistence 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 generalized 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, bog 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 heath/shrub and bog.

Conclusions: The results suggest that Hen Harrier breeding success 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.

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Upland areas, typically found at higher elevation than nearby areas of 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 (Douglas *et al.* 2008, O'Rourke & Kramm 2009, Ratcliffe 2010, Renou-Wilson *et al.* 2011, O'Riordan *et al.* 2015). This has led to the decline of many upland bird populations (Marquiss *et al.* 1985, Brawn *et al.* 2001, Julliard *et al.* 2004).

Hen Harriers *Circus cyaneus* 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 European Union (EU) Birds Directive (European Council Directive 79/409/EEC) which requires that 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 directed in 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 (Norris *et al.* 2002, Barton *et al.* 2006, Ruddock *et al.* 2012, Ruddock *et al.* 2016).

Hen Harriers typically use upland habitats during the breeding season, often nesting in heather moorland (Redpath *et al.* 1998, Amar *et al.* 2008, Watson 2017). Elsewhere, Hen Harriers are known to use other habitats, such as cereal fields and young forest plantations (Millon *et al.* 2002, Wilson *et al.* 2009, 2012, Ruddock *et al.* 2016, Sachslehner *et al.* 2016) 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), proximity to wind farms (Fernandez-Bellon *et al.* 2015) and climate (García & Arroyo 2001, Redpath *et al.* 2002). Breeding success varies considerably between different areas 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 recruited into the Irish breeding population, are 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-twentieth century, peaking at a reported 200–300 pairs in the 1970s (Watson 2017) though the decline resumed thereafter (Norris *et al.* 2002, Barton *et al.* 2006, Ruddock *et al.* 2012, 2016). The current Hen Harrier population in Ireland is moderately small, with 108–157 breeding pairs 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).

Afforestation (the planting of forest in an area where there was little or no previous tree cover) has resulted in significant declines of some upland bird populations (Thompson *et al.* 1988, Ratcliffe 2010) including the Hen Harrier (O'Flynn 1983, Wilson *et al.* 2009). 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).

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 nest depredation, particularly near forest edges, and/or driving avoidance of habitat patches associated with forest edges (Douglas *et al.* 2011, Wilson *et al.* 2014). Thus, appreciating the links between habitat abundance, quality and/or connectivity and the persistence of a species requires a nuanced understanding of the focal species' ecology.

Bird populations can also be negatively affected by changes in 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 success (Schipper 1979, García & Arroyo 2001, Redpath *et al.* 2002), their impacts vary across the species' range, likely due to regional differences in climate. For example, Hen Harrier brood size was positively related to temperature in Scotland (Redpath *et al.* 2002) while the opposite was true in Spain (García & Arroyo 2001). Thus, understanding the relationship between climate and breeding success in this species requires discrete, region-specific studies.

Here we used data derived from national breeding Hen Harrier surveys in Ireland, 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. We hypothesize that: (i) Hen Harrier territories will be strongly associated with pre-thicket coniferous forests; (ii) breeding success will be negatively affected by the amount of coniferous forest in the landscape; and (iii) there will be no discernible effect of SPAs status on patterns of Hen Harrier settlement or breeding success. 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.

Methods

Data sources and preparation

A total of 668 records of potential Hen Harrier territories 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 comprised of all confirmed territories ($n = 236$; 2010 = 128, 2015 = 108; Figure 1(a)). The second was restricted to records with known breeding outcomes (i.e. success or failure; $n = 191$; 2010 = 94, 2015 = 97; Figure 1(b)).

Pseudoabsences (*pal*) were randomly generated within the altitudinal range of confirmed Hen Harrier territories ($n = 500$; 36 m–570 m). Each point (i.e. territory or pseudoabsence) was buffered to three distances (Graf *et al.* 2005): 1, 2 and 5 km, chosen to represent variable foraging distances from the nest and to enable comparisons with previous studies (Schipper 1977, Wilson *et al.* 2009, Arroyo *et al.* 2014). 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 and, in most centrally placed foragers, the intensity with which suitable foraging areas are used declines with distance from the nest or roost site to which individuals return (Arroyo *et al.* 2014). Hence, conservative distances were used.

To account for spatial autocorrelation, i.e. clustering of presence records, Moran's *I* Index scores were calculated for each point using the cluster and outlier analysis (Anselin Local Moran's *I*) function in the ArcGIS toolbox, that calculates a Local Moran's *I* value for each point data in the dataset, allowing the identification of spatially autocorrelated data (e.g. hot-spots, outliers).

We investigated the effect of several, ecologically relevant 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 (see Table 1 for variable-specific references). 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; see Table 1 for CORINE class details) 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 in Northern Ireland). Forest data were classified by type (broadleaved or coniferous); mixed forest where conifers accounted for $\leq 50\%$ 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.* 2012): (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; see Table 1 for CORINE class details).

The total area of each land cover variable and forest category and road density were calculated within each point 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 stand (edge) of post-thicket forest.

Weekly temperature ($^{\circ}\text{C}$) and rainfall (mm) data were obtained from 27 weather stations dispersed across the

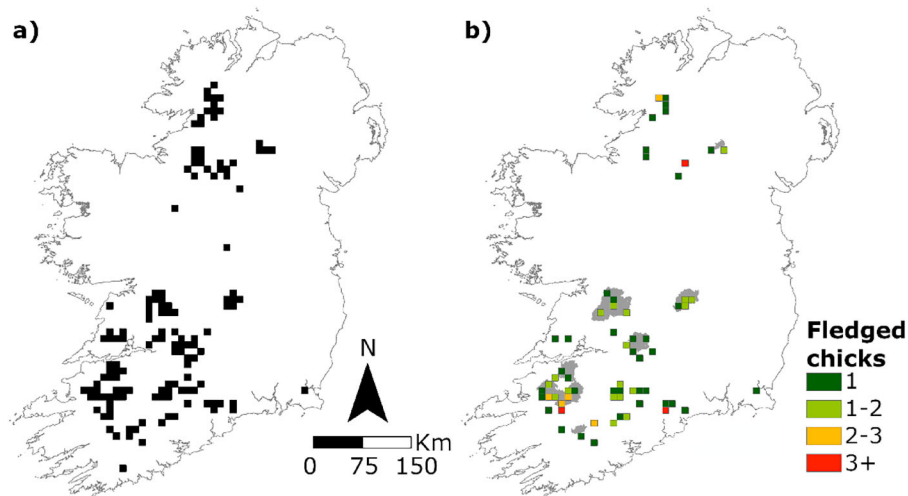


Figure 1. (a) Confirmed territory locations and (b) mean productivity (number of chicks fledged) of Hen Harriers in Ireland in 2010 and 2015, combined. Special Protection Areas (SPAs) are represented by grey polygons in (b).

island of Ireland, from Met Éireann (<http://www.met.ie>) and the Met Office (<https://data.gov.uk>). Rainfall data were further split into 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 – mean of weekly minima and associated variance – were calculated across 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

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. CORINE class details are given in parentheses where appropriate. 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; CORINE (3.1.1. Broad-leaved forest)	Moran & Wilson-Parr (2015)
Coniferous forest	Polygon data	Raw	Coillte; NPWS; Forest Service Northern Ireland; CORINE (3.1.2. Coniferous forest)	Madders (2000), Wilson <i>et al.</i> (2009), Wilson <i>et al.</i> (2012), Sachslehner <i>et al.</i> (2016)
Arable	Polygon data	Composite data	CORINE (2.1.1. Non-irrigated arable land; 2.4.2. Complex cultivation patterns; 2.4.3. Land principally occupied by agriculture)	Wilson <i>et al.</i> (2012), Feys <i>et al.</i> (2013), Sachslehner <i>et al.</i> (2016), Geary, Haworth & Fielding (2018)
Heath/shrub	Polygon data	Composite data	CORINE (3.2.2 Moors and heathland; 3.2.4. Transitional woodland shrub; 3.3.3. Sparsely vegetated areas)	Madders (2000), Amar & Redpath (2005), Cormier <i>et al.</i> (2008), Arroyo <i>et al.</i> (2009), Wilson <i>et al.</i> (2012)
Bog	Polygon data	Raw	CORINE (4.1.2. Peat bogs)	Madders (2000), Arroyo <i>et al.</i> (2009), Irwin <i>et al.</i> (2011), Wilson <i>et al.</i> (2012)
Natural grassland	Polygon data	Raw	CORINE (3.2.1. Natural grassland)	Madders (2000), Amar & Redpath (2005), Arroyo <i>et al.</i> (2009), Wilson <i>et al.</i> (2012)
Pasture	Polygon data	Raw	CORINE (2.3.1. Pastures)	Madders (2000), Amar & Redpath (2005), Arroyo <i>et al.</i> (2009), Wilson <i>et al.</i> (2012)
Urban	Polygon data	Composite data	CORINE (1.1.1 Continuous urban fabric; 1.1.2. Discontinuous urban fabric)	Tapia, Dominguez & Rodriguez (2004)
Temperature	Point data	Interpolated raster	Met Éireann; Met Office	García & Arroyo (2001), Redpath <i>et al.</i> (2002)
Rainfall	Point data	Interpolated raster	Met Éireann; Met Office	García & Arroyo (2001), Redpath <i>et al.</i> (2002)
Elevation DEM	Surface raster	Raw	NASA	Geary <i>et al.</i> (2018)
SPA boundaries	Polygon data	Raw	NPWS	Ruddock <i>et al.</i> (2012), Moran & Wilson-Parr (2015), Ruddock <i>et al.</i> (2016)
Roads	Polyline data	Raw	OpenStreetMap	Tapia <i>et al.</i> (2004)
Windfarms	Point data	Raw	NPWS	Fernández-Bellon <i>et al.</i> (2015), Wilson <i>et al.</i> (2017)
Hen Harrier territories	Point data	Raw	NPWS	Ruddock <i>et al.</i> (2012), Ruddock <i>et al.</i> (2016)

consistent. In contrast, high variance could suggest irregular patterns of rainfall or a trend in rainfall over time. Interpolated regularized raster surfaces (grid-based data structures; Aggrey 2002) were constructed at 1 km resolution for each climate metric using the Spline function in ArcGIS 10.4.1 (ESRI 2015), giving 100% coverage to the island of Ireland. Climate measurements for each nest were taken as the interpolated value for the 1 km square within which the point was located.

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. Euclidean distances were calculated from each point to the nearest windfarm. 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 OpenStreetMap 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. 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

The centres of putative Hen Harrier territories were estimated as nest locations, where these were known, or as the approximate midpoint of observations involving behaviours and activities consistent with breeding, for other breeding territories identified during the survey (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.

Territory selection was examined using binomial, log-linked generalized 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 $r < 0.5$ (Quinn & Keogh 2002). Variables were standardized to have a mean of zero and a standard deviation of 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 $\Delta AIC \leq 2$ 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 success models

Breeding success 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 based on the best available data. Additional point data for each centroid were 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. Eighty six centroids were located inside SPAs with 112 occurring outside SPA boundaries (2010 = 36:65; 2015 = 50:47).

Breeding success was examined using a Poisson GLMM; the number of chicks successfully fledged (Figure 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). Data used in this project were subject to confidentiality and data sharing agreements. However, code used to manipulate data and shapefiles and construct models and plots can be found at <http://doi.org/10.5281/zenodo.3549584>.

Results

Hen Harrier territory locations exhibited significant spatial autocorrelation ($I = -0.003 \pm 0.005$, $P < 0.0001$; Figure 2). Hen Harrier nest sites are typically used in successive years, though not necessarily by the same breeding pair (Korpimäki 1984, Picozzi 1978, 1984, Watson 2017). Here, 2010 territories were located at least 141 m (mean \pm sd = 3.80 ± 7.61 km) from the nearest territory in 2015. The top subset ($\Delta AIC \leq 2$) consisted of 18 models (supplementary online Table S1). The best approximating model for territory site

selection was positively influenced by heath/shrub, pre-thicket forest and bog at 1 km, 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 2 km and with broadleaved woodland at 5 km, 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* (Figure 3). The predictive accuracy of the best-approximating model, assessed via 10-fold cross-validation, was $0.82 (\pm 0.02)$.

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 from *pa1* than *pa2* were from each other (Figure 4). This indicates that Hen Harriers are not only using upland habitats as territory locations but that they are specifically using the landscape non-randomly with regard to habitat availability.

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 (online Table S2). 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. This suggests that

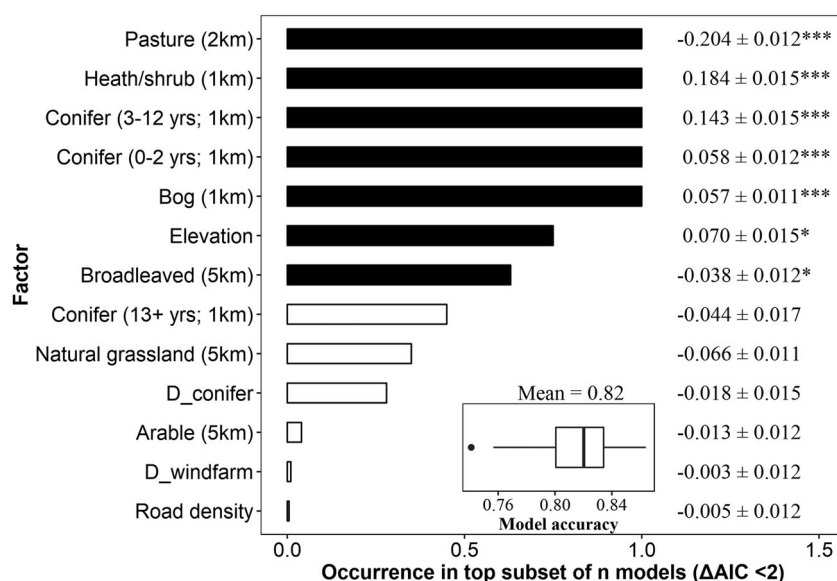


Figure 2. Relative importance of variables in explaining the locations of confirmed Hen Harrier territories relative to pseudoabsences at multiple spatial scales (1, 2 and 5 km, selected a priori), except for elevation which was extracted at each point location. D_ = distance to. Variables were ranked according to the sum of their Akaike weights within the top set of models ($\Delta AIC < 2$). Black bars indicate variables that were present in the best approximating model; white bars indicate variables otherwise included in the top subset. Standardized coefficients \pm se 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.

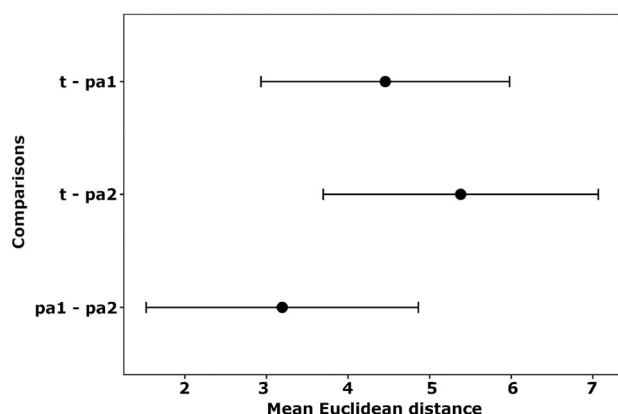


Figure 3. Euclidean distances (± 1 sd) across five Principal Component scores for pairwise combinations Hen Harrier territory locations (t), upland pseudoabsences (pa1) and pseudoabsences distributed across the rest of Ireland (pa2).

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 1 km scale and bog at 2 km. 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 (Figure 4). The predictive accuracy of the best-approximating model, assessed via 10-fold cross-validation, was $0.76 (\pm 0.01)$.

Discussion

Across the 2010 and 2015 Hen Harrier national survey data, the influence of land class and associated parameters on the utilization of habitats for territories contrasted with their influence on subsequent breeding success. Hen Harrier territories in Ireland were positively associated with heath/shrub, bog, areas at high elevation, and pre-thicket coniferous forest (i.e. 0–12 years old), confirming our first hypothesis. Breeding success was similarly positively associated with heath/shrub and bog. However, there was a negative association with rain in the early months of the breeding season and minimum temperature metrics. In contrast to territory models, pre-thicket forests were not observed to have an effect on breeding success, rejecting our second hypothesis. SPAs were not included in the best approximating breeding success model but were observed to have a moderate positive effect on breeding success, leading us to reject our third hypothesis.

The strong positive associations between habitats typical of open, upland landscapes in Ireland (i.e. heath/shrub and bog) and both territory location and breeding success models emphasize the importance of these habitats for breeding and foraging Hen Harriers (Redpath *et al.* 1998, Madders 2000, Amar *et al.* 2008, Arroyo *et al.* 2009). Optimal nesting habitat should offer a complex vegetation structure for nest concealment and protection, while good foraging habitats will have high prey availability. These factors asynchronously contribute towards determining how prospecting Hen Harriers choose their territories and subsequent foraging behaviour and breeding success. Research has shown that while male Hen Harriers forage independently of nest location, females frequently hunt within 300–500 m of the nest (Arroyo *et al.* 2009). Hen Harrier breeding success in one UK SPA was positively related to a greater abundance of preferred foraging habitat within 2 km of nest sites (Amar *et al.* 2008) and breeding success can be affected by food availability before and during nesting (Amar & Redpath 2002, Amar *et al.* 2003, 2005). Thus, territory location and the proximity of good quality foraging habitats are strongly linked. It is possible that differences in prey species assemblages, abundance and availability (Wilson *et al.* 2012) between habitats could help explain the observed differences between territory selection and breeding success models in the current study. Given the importance of health/shrub and bog

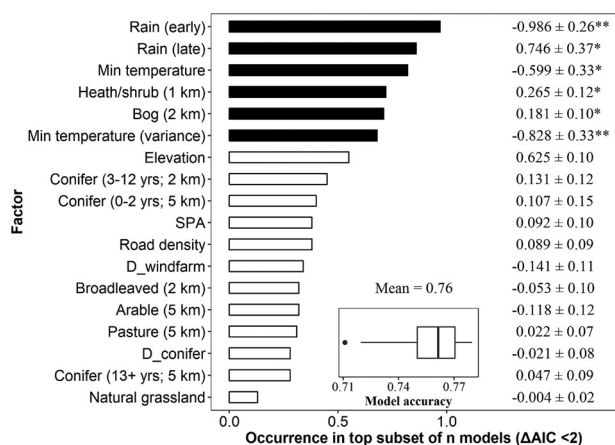


Figure 4. Relative importance of variables in explaining the breeding success of nesting Hen Harriers at multiple spatial scales (1, 2 and 5 km, selected a priori). Variables were ranked according to the sum of their Akaike weights within the top set of models ($\Delta AIC < 2$). Black bars indicate variables that were present in the best approximating model; white bars indicate variables otherwise included in the top subset. Standardized coefficients \pm se 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.

habitats across both models, conservation measures targeted at stabilizing and subsequently increasing the Hen Harrier population in Ireland should aim to improve the quality and abundance of these important habitats.

There was a particular association between Hen Harrier territories and pre-thicket forests 3–12 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 consider this on such a large scale (the whole of Ireland). Pre-thicket forest undergrowth may consist of heather (*Ericaceae*), 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. The use of these habitats by Hen Harriers may be indicative of a lack of more suitable nesting and/or foraging habitat in the wider landscape. While there was no apparent impact of pre-thicket forests on breeding success, they were sub-optimal when compared to heath/shrub and bog. Indeed, Hen Harriers breeding in coniferous forest in Scotland exhibit lower breeding success than those that nest in moorlands (Etheridge *et al.* 1997). Furthermore, while Hen Harriers can and do make use of pre-thicket forests for nesting and foraging, maturation of forests beyond the pre-thicket stage to closed canopies results in unsuitable nesting habitat and limits foraging opportunities (Madders 2003, though see Wilson *et al.* 2012). Afforestation of heath/shrub and bog habitats would, therefore, result in a net decline in Hen Harrier breeding success in afforested upland areas.

The location of centroids relative to SPA boundaries (i.e. inside or outside) was retained in the top subset of breeding success models (46% of all models), though it was not retained in the best approximating model and SPAs were positively associated with breeding success. Proposed land use changes and industrial activities 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 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 (Figure 5). It is important to note, however, that over 50% of the breeding Hen Harrier population was located outside of the six breeding Hen

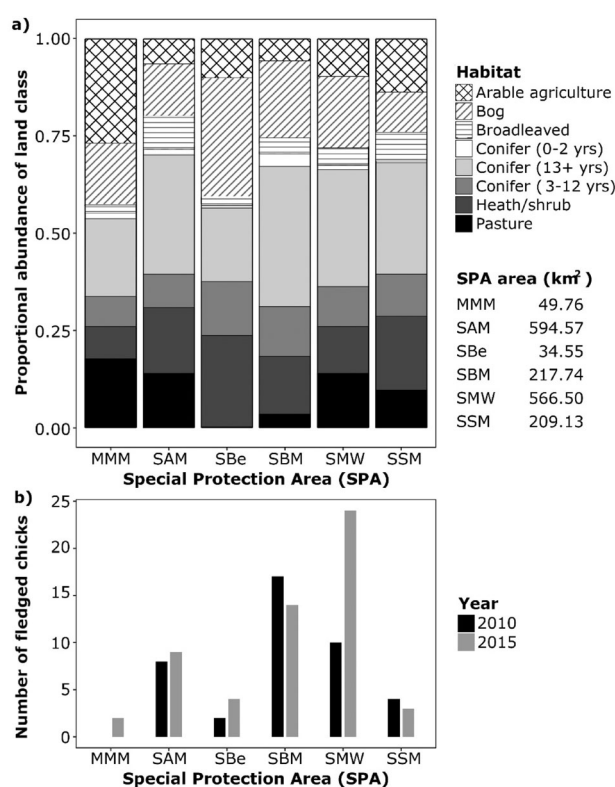


Figure 5. (a) Habitat composition of Special Protection Areas (SPAs) in Ireland that contained (b) successful Hen Harrier nests (produced at least 1 fledged chick) in 2010 and 2015. Natural grassland was omitted as it comprised a small fraction of available habitats across all SPAs. MMM = Mullaghanish 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.

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 the breeding population within SPAs 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. We recommend, 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 was 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 (Schipper 1979, García & Arroyo 2001, Redpath *et al.* 2002). 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 must 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*, European Badgers *Meles meles*, Pine Martens *Martes martes*, American minks *Neovison vison*, Stoats *Mustela erminea*, Common Buzzards *Buteo buteo*, Ravens *Corvus corax* and Hooded Crows *Corvus cornix*. Such predators are typically 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 (Monaghan 2015, Ruddock *et al.* 2016, Fernández-Bellon *et al.* 2018). 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 become 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 that climate change can impact 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). Climate change impacts may be exacerbated by changes

in land management that could simultaneously reduce the proportion of suitable foraging habitat in the landscape (Kleijn *et al.* 2010). It is therefore important that the potential impacts of climate change on Irish Hen Harrier breeding success and distribution are monitored and that appropriate mitigation measures are explored and established.

Hen Harriers in Ireland currently face an uncertain future. Hen Harriers in this study preferentially selected heath/shrub and pre-thicket coniferous forests, habitats that provide nesting and foraging opportunities, for territory locations. Rainfall and climatic instability early in the breeding season were found to have strong negative effects on subsequent breeding success, suggesting that the population is at further risk under future climate change. Upland habitats typically used by Hen Harriers elsewhere, i.e. heath/shrub and bog, were positively associated with breeding success of Hen Harriers in this study, emphasizing the importance of such habitats for this threatened species. Continued afforestation of upland areas, moorlands and bog in particular, along with maturation of the existing 'usable' forest estate beyond the pre-thicket stage, and the impacts of climate change, will likely negatively impact Hen Harrier populations in Ireland. Effective conservation of Hen Harriers in Ireland is therefore likely to rely 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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