1Hen Harrier *Circus cyaneus* nest sites on the Isle of Mull are associated with habitat
2mosaics and constrained by topography

3

4Matthew Geary^{a*}, Paul F.Haworth^b, Alan H. Fielding^b,

5

6^a Conservation Biology Research Group, Department of Biological Sciences, University of

7Chester, Chester, United Kingdom

8^b Haworth Conservation Ltd, Buessan, Isle of Mull

9

10

11**Short Title:** Hen Harrier and habitat mosaics

12**Keywords**

13Forestry, Conservation planning, raptor, Point-process, species distribution model.

14*Corresponding author: M.Geary@Chester.ac.uk

15

16

17**Summary**

18**Capsule:** Hen Harrier on the Isle of Mull, UK, are associated with habitat mosaics consisting
19of moorland, scrub and forestry but avoid grazed land, suggesting that forested habitats
20could be managed sympathetically for Hen Harrier in the future should the current UK
21population increase.

22**Aims:** To use distribution modelling to investigate nesting habitat associations using a long
23term dataset for Hen Harrier on Mull.

24**Methods:** We develop area-interaction models using a LASSO penalty to explore the
25distribution of 102 Hen Harrier nest sites in relation to habitat and topography. Our model is
26then successfully validated in tests using data for 70 nest sites from subsequent years.

27**Results:** Our model is effective in predicting suitable areas for Hen Harrier nest sites and
28indicates that Hen Harriers on Mull are found in habitat mosaics below 200 m asl. Hen
29Harrier nest intensity is positively associated with increasing proportions of moorland and
30scrub, open canopy forestry and closed canopy forestry. Nest intensity is negatively
31associated with increasing proportions of grazed land.

32**Conclusion:** Hen Harrier avoid grazed areas but are relatively tolerant of other habitat
33combinations. These findings are supported by previous observations of Hen Harrier habitat
34use and have implications for the recovery of some Hen Harrier SPA populations and future
35forest management. Open canopy forest and forest mosaics could potentially be
36incorporated into landscape-scale conservation plans for Hen Harriers using the population
37in Mull as an example.

38

39

40

41 **1. Introduction**

42In anthropogenic landscapes such as upland Britain, management and protection of species
43of conservation concern present a complex challenge (Geary et al., 2015). Understanding
44species distributions both at the scale of species ranges and in terms of their distribution
45across available habitats is an integral part of species conservation and ecosystem
46management (Elith and Leathwick, 2009). Methods for the modelling and prediction of
47species' distributions cover a wide range of statistical and methodological techniques (Elith
48and Graham, 2009). Many share the common assumption that the species' distribution is in
49equilibrium within the landscape (Araújo and Pearson, 2005). This assumption has been
50relaxed in certain situations in particular when predicting the spread of invasive species
51(Gallien et al., 2012) or species responses to novel environmental conditions (Berry et al.,
522002). However, as models of invasive range expansion demonstrate, the results can differ
53depending on whether data are sourced from the native range (presumably close to
54equilibrium) or the invasive range (potentially not in equilibrium; Loo et al., 2007).

55

56Modelling species distributions, and investigating drivers delimiting those distributions, when
57the data available contain only presences provides some methodological difficulty (Hastie
58and Fithian, 2013). Breeding raptor surveys often result in presence only data as survey
59methods are targeted towards identifying occupied nest sites within the landscape and, as
60such, absences are implied by lack of presence rather than specifically recorded (Hardey,
612006). Until recently the machine learning method MaxEnt proved to be successful in
62modelling distributions using presence only data (Phillips and Dudík, 2008) but was the
63subject of some scrutiny due to its 'black box' nature (Royle et al., 2012) and because
64default parameters were often used unquestioningly resulting in loss of accuracy in models
65(Warren and Seifert, 2011). Recently a mathematical equivalence between MaxEnt and
66regression models using a LASSO penalty (Renner and Warton, 2013) has been
67demonstrated. Point process models which use a background sample of quadrature points

68to delimit the environmental space of the species distribution can be used with LASSO
69penalties to model species distributions using presence-only data (Renner et al., 2015). The
70LASSO penalty reduces overfitting by constraining parameter estimates – called
71‘regularisation’ in MaxEnt (Warton et al., 2013). Point process models predict the relative
72intensity, in terms of presence records per unit area, across the region of interest (Renner et
73al., 2015). A statistical explanation of how point process models are used to model species
74distributions can be found in Renner (2013).

75

76Hen Harrier *Circus cyaneus* is a medium sized, ground nesting raptor which, along with the
77closely related Northern Harrier *Circus hudsonius*, has a circumpolar boreal distribution
78(Sangster et al., 2016). Although Hen Harrier is considered to be of least concern globally
79(BirdLife International, 2015) it is of conservation importance in Great Britain and Ireland
80(Fielding et al., 2011). Hen Harrier are thought to have adapted to foraging in open
81landscapes over a long period of time (Simmons, 2000). They are known to forage
82extensively on field voles *Microtus agrestis*, young lagomorphs and small moorland
83passerines (Redpath et al., 2001; Smith et al., 2001). In mainland Britain the distribution of
84Hen Harrier is thought to be limited not solely by environmental conditions but by
85anthropogenic intervention (Anderson et al., 2009). The current status and distribution of
86Hen Harrier in Britain is thought to be strongly influenced by persecution, especially on
87moorland managed for sporting interests, in particular the driven shooting of red grouse
88*Lagopus lagopus* (Etheridge et al., 1997; Fielding et al., 2011). The recent population
89estimate of approx 660 breeding pairs is located mainly in Scotland with major strongholds
90on Orkney, the Hebrides, Arran, mainland Argyll, Ayrshire and Dumfries and Galloway
91(Hayhow et al., 2013). The UK Hen Harrier population was surveyed in 2016 and the results
92from this survey will indicate if those strongholds are still extant although anecdotal evidence
93suggests that the Ayrshire and Dumfries and Galloway population has collapsed (Haworth
94pers comm.). With a more enlightened attitude on grouse moors the UK population could

95expand to perhaps 2500 pairs (Fielding et al., 2011). The presence of large Hen Harrier
96populations on the Isle of Man (Hayhow et al., 2013; Sim et al., 2007) and outside the UK
97suggests that a wider range of nesting habitats than heather moor might prove suitable for
98Hen Harrier.

99

100Previous work on the distribution of Hen Harrier found a range of factors to be important in
101delimiting their distribution including topography, environmental drivers and species
102interactions. Tapia et al., (2004) used logistic regression to predict the presence/absence of
103Hen Harrier and Montagu's Harrier *Circus pygargus* in NW Spain where Hen Harrier
104presence was associated with fewer human settlements and the slope was less steep in
105occupied habitat. However, the final model was relatively uninformative in that it only
106retained minimum elevation as a predictor. Tapia et al., (2004) suggested that the main
107threats for Hen Harrier in their study region came from the proliferation of roads and massive
108afforestation of open scrub-pasture land. Cormier et al., (2008) also modelled the nesting
109habitat of Hen Harrier and Montagu's Harrier, but this time in central France (Poitou-
110Charentes region). They used two methods, discriminant function analysis and regression
111trees and concluded that the factors determining Hen Harrier nest selection were unclear but
112nests were usually found in plots where bosom heath *Erica scoparia* was > 1.87 m tall and
113that afforestation did not seem to benefit Hen Harrier. Massey et al., (2009) used a
114classification tree approach to model the distribution of the similar Northern Harrier on
115Nantucket Island (Cape Cod, Massachusetts). Their approach compared habitat, as
116measured by 70 landscape metrics, within 50 m, 200 m, 500 m and 1,000 m of nests sites
117and random locations. Classification trees were used to identify two important nesting
118habitats. The first was in, or adjacent to, wetlands and the second was in drier upland
119habitats. Both of these, as in the Tapia et al., (2004) study, shared an avoidance of
120developed land and forests, although this was less marked in wetlands.

121

122Anderson et al., (2009) used generalised linear models at two resolutions to model Hen
123Harrier distributions in the UK. They found no support for their hypothesis that climate
124directly determines the current UK distribution and although their habitat model was more
125successful it failed to predict some of the more important Scottish populations (e.g. Islay,
126Arran and the Uists). However, some of the problems with their model are probably related
127to the restricted Hen Harrier distribution data available to them. The status on Hen Harrier on
128the British mainland may also influence investigations on their distribution as they are absent
129from many areas in which suitable habitat is present and there is historical evidence of
130occupation (Hayhow et al., 2013).

131

132On the Isle of Mull, one of the Inner Hebrides, where a small population of breeding harriers
133was established in the north and east by the late 1960s and early 1970s (Sharrock, 1976),
134grouse moor and the anthropogenic pressures associated with this habitat are absent so the
135species may be occupying a more natural range of habitats. Results for the recent (2016)
136national survey suggest that this population now represents around 8% of the Scottish Hen
137Harrier population (Haworth pers. comm.). However, it should also be noted that Mull, much
138like the majority of the Scottish highlands, is far from a natural landscape with economically
139driven land use such as agriculture and commercial forestry predominating (Warren, 2002).
140The shorter vegetation of most land used for agriculture results in less prey and suitable Hen
141Harrier nesting habitats. However, there is strong evidence that afforestation is beneficial in
142the early pre-thicket stages, providing good cover for nests and an abundance of voles
143(Madders, 2000; Redpath et al., 1998). Subsequent canopy closure reverses this, although
144in some forests large patches of failed trees or unplanted ground develop into rank dwarf
145shrub and harriers continue to breed in such areas suggesting that there may be
146opportunities for forest planting schemes that are beneficial for Hen Harrier.

147

148Land use change will continue to affect grazing regimes and woodland management and
149economic pressures might result in wide scale changes in land use as they have in the past

150(Warren, 2002). Recently, the Irish National Parks and Wildlife Service completed a
151comprehensive review of the literature related to Hen Harrier ecology and forests (NPWS,
1522015) and the 2015 National Survey of Breeding Hen Harrier in Ireland (Ruddock et al.,
1532016) found that Hen Harrier in Ireland were most frequently recorded to forage in open
154non-afforested habitats (51.3%) compared to afforested habitats (40.6%) but recorded more
155frequently to nest in second rotation forest (58.3%) than heather moorland (25.9%). It is
156important therefore, to have a better understanding of Hen Harrier habitat requirements and
157an awareness of undesirable habitat. In particular, it is important in the case of the Hen
158Harrier to explore habitat preferences in areas where persecution and disturbance are rare
159so that absences are more likely to reflect habitat drivers rather than human interference.
160The distribution and habitat use of Hen Harrier on the Hebrides can help to shed light on this
161area of research. Here we use records of Hen Harrier nesting locations and habitat data on
162the Isle of Mull to investigate drivers of Hen Harrier distribution using a point-process
163regression model (Renner et al., 2015). This model will aid habitat and landscape managers
164to develop conservation strategies for Hen Harrier under scenarios where anthropogenic
165pressures are reduced and also provide a framework for modelling other Hen Harrier
166populations and other species.

167

168 **2. Methods**

1692.1 *Study area*

170Mull (56° 27'N 06° 00'W) covers 875 km² (924 km² including all subsidiary islands) and is the
171third largest of the Hebridean islands. Although Mull has a characteristic terraced landscape,
172derived from the predominant basaltic lava flows, there are also significant regions of schist,
173granite and sedimentary rock. The centre of the island is dominated by Ben More (966 m)
174and its surrounding mountains. Much of Mull is used for sheep and cattle grazing, although
175sheep densities are lower than many areas in the western Highlands and Islands of Scotland
176(Fuller and Gough, 1999). There are also large numbers of Red Deer *Cervus elaphus*

177(average density about 10 deer per km²) and several hundred feral goats *Capra hircus*.
178Numbers of Red Grouse and Ptarmigan *Lagopus mutus*, common prey of Golden Eagles
179*Aquila chrysaetos* and some other raptors in many parts of Scotland, are low but there are
180significant numbers of the introduced Irish Mountain Hare *Lepus timidus hibernicus* and
181Rabbits *Oryctolagus cuniculus* are common in some coastal locations. Approximately 13,900
182ha (or 15% of the island) is covered with commercial conifer plantations (including recently
183felled plantation), partly on ground owned by Forestry Commission Scotland (FCS) but also
184by private and community ownership. The current trend is mainly towards schemes for
185planting or regeneration of native deciduous species under the UK government's Woodland
186Grant Schemes (WGS), which provides grant aid for establishing and early management of
187private woodland areas. However, the recent trend on the island has been an increase in
188felling with the National Forest Inventory indicating that the area of felled forest more than
189doubled between 2012 and 2014. Felling has been accompanied by an increase in ground
190preparation which suggests an increase in forest areas over the coming decade (Forest
191Research, 2013). Recently around 20% of the commercial forestry on Mull has been felled
192but is likely to be replanted in the future (Forest Research, 2016). In the same time period a
193similar amount of native woodland has been planted (Forestry Commission, 2014).

194

1952.2 Data

196Species data, Hen Harrier breeding locations, were collected in the field by PFH. As is often
197the case with ecological data from monitoring programmes, only species presence was
198recorded as nests were actively sought across the island. Surveys for breeding harriers were
199undertaken from April until August according the methods set out in (Hardey, 2006). Surveys
200for Hen Harrier nest locations (n = 102) were carried out each year between 2005 and 2014.
201Surveyed sites were spread across the island, often in conjunction with golden eagle
202surveys, and were not restricted to particular parts of the island and surveyed areas were not
203fixed across the years. The number of nests located per year varied between 12 (2006, 2009

204 and 2013) and 30 (2008). The median was 14 nests per year. In 2015 and 2016 the survey
 205 effort was increased to more than 60 days of dedicated Hen Harrier field surveys spread
 206 across the entire island. The aim was to provide a large data set that could be used for
 207 model validation. Data from 2015 (n=28) and 2016 (n=42) was retained for model testing.
 208 Topographic data were derived from the Ordnance Survey 50 m Digital Terrain Model (DTM),
 209 version 04/2010 supplied under the Ordnance Survey OpenData Licence. In addition to
 210 elevation, slope was calculated using the `slope()` function of the raster package (Hijmans
 211 and van Etten, 2012) in R (R Core Team, 2016). Habitat data were taken from Land Cover
 212 Map 2007 (LCM 2007) from the Centre for Ecology and Hydrology (Morton et al., 2011) and
 213 National Forest inventory 2013 (downloaded from the Forestry Commission Scotland; Forest
 214 Research 2013). LCM categories which represented grazed land (LCM2007 classes 3 – 8)
 215 and moorland or scrub (LCM2007 classes 9 – 12) as well as National Forest Inventory
 216 categories which represented open canopy forest (young forest and shrub) and closed
 217 canopy forest (coniferous, broadleaved and mixed) were selected for use in modelling. The
 218 proportion of each habitat type within a 1.1 km square surrounding each pixel was calculated
 219 using the `focal()` function of the 'raster' package in R (Hijmans and van Etten, 2012). Both
 220 the DTM and slope data were resampled in order to match the cell size and extent with the
 221 classified habitat raster files.

222

223 2.3 *Species distribution model*

224 Here we use a point process model with a LASSO penalty to model the intensity of Hen
 225 Harrier nest sites across Mull using elevation, slope, proportion of grassland/moorland,
 226 proportion of moorland and scrub, and proportion of both open canopy and closed canopy
 227 forest. All models were fitted using the `ppmlasso` package (Renner and Warton, 2013) in R.
 228 The design matrix for the model consisted of the variables themselves along with quadratic
 229 terms for the proportion of grazed land and elevation because Hen Harriers have been
 230 previously shown to prefer intermediate values for each of these variables (Fielding et al.,

2312011). Using quadratic terms for the two forest categories did not alter the predicted
 232relationship so simpler terms were preferred. The optimal LASSO penalty was selected from
 2331000 model fits by minimising the Bayesian information criterion (BIC; Renner et al., 2015).
 234The resolution for quadrature points used in the models was found using the findres()
 235function in ppmlasso which showed that a resolution of 100m (compared to 1000, 500, 400,
 236300, 200, 150, 120 and 110 m) gave the highest likelihood value without violating the
 237assumptions of the model. The initial fitted model showed significant clustering at distances
 238below 1000 m when compared to simulated Ripley's K envelopes (Baddeley and Turner,
 2392005) so an area-interaction model was preferred with a radius of point interaction of 200 m.
 240This interaction is likely to be caused by pairs using similar nesting sites across the years
 241surveyed but also because of locations where different nests are close to each other. The
 242area-interaction model reduces the impact of these similar nesting sites on the overall point
 243process. Although the profilepl() function in the 'spatstat' package (Baddeley and Turner,
 2442005) suggested a radius of 800m as optimal, a radius of 200m reduced spatial bias in the
 245residuals. Radii between 50 and 2500 m were considered as potential point interaction
 246settings based on Ripley's K plots for the point process models. The value for the radius of
 247point interactions was chosen by comparing the fit of models with different r values to
 248simulated realisations of a fitted Gibb's model (Renner et al., 2015). Model residuals were
 249evaluated both spatially and using lurking variable plots. Predicted intensities were
 250calculated by projecting the fitted model onto data for the whole island and converted to
 251intensities per 1 km².

252

2532.4 Model validation

254Models were validated using Hen Harrier nest locations collected in 2015 and 2016 ($n = 70$)
 255as test data with which to compare model predictions. To validate the models we used both
 256the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Fielding
 257and Bell, 1997) as well as the True Skill Statistic (TSS; Allouche et al., 2006). AUC ranges

between 0 and 1 with scores over 0.75 considered to represent good predictive power (Pearce and Ferrier, 2000). TSS ranges between -1 and 1 with values closer to 1 representing higher predictive accuracy (Allouche et al., 2006). The predicted intensity map from the area interaction model was rescaled (range 0 and 1) as a proportion of the maximum prediction. A threshold between presence and absence is required and we chose the maximum sum of sensitivity and specificity (Liu et al., 2005). Both were calculated using 100 background points in place of the unavailable absence values. This calculation was repeated over 1000 iterations using randomly selected background points.

266

267 3. Results

The optimum fitted area-interaction model used a LASSO penalty of 0.00005 selected by minimising BIC and predicted highest Hen Harrier nest presence intensity across small areas of Mull (Fig. 1). Although, the predicted nest presence intensity was low in all areas, with a maximum of 0.043 per 1 km², low densities are consistent with recorded nesting densities (Fielding et al, 2011). The model (Table 1) showed a positive relationship with the proportion of scrub moorland, proportion of open canopy forestry and proportion of closed canopy forestry. (Fig. 2a) and a positive relationship with forest cover (Fig. 2.b). Hen Harrier nest presence intensity had a negative relationship with increasing proportions of grazed land (Fig. 2d) and increasing elevation (Fig.2e) with evidence of non-linearity shown by the quadratic terms for both variables and a negative relationship with slope (Fig 2f). The area interaction term for the model was positive meaning that there is a tendency within the data for nests to be clustered to some degree. All other terms in the models were reduced to $\beta = 0$ due to the LASSO penalty.

281

Table 1. Parameter estimates and standard error for the optimum area interaction model using a LASSO penalty of 0.00005, selected by minimising BIC, to predict the intensity of

284 *Hen Harrier nest presence using the proportion of important habitat types on the Isle of Mull,*
285 *Scotland.*

Model term	β	S.E.
Intercept	-19.35	0.05
Proportion of grazed land	-0.37	0.008
Proportion of grazed land ²	-0.23	0.005
Proportion of scrub/moorland	0.28	0.004
Proportion of Open Forest	0.14	0.001
Proportion of closed forest	0.23	0.003
Elevation	-4.3	0.09
Elevation ²	-3.67	0.08
Slope	-0.23	0.005
Area-Interaction term	0.44	0.001

286

287

288 **Figure 1.** Predicted intensity of Hen Harrier nest presence per 1 km² for the optimum area
289 interaction model using a LASSO penalty of 0.00005, selected by minimising BIC, to predict
290 the intensity of Hen Harrier nest presence using the proportion of important habitat types on
291 the Isle of Mull, Scotland.

293

294**Figure 2.** Plots of predicted Hen Harrier nest presence intensity against (a) proportion of
 295scrub/moorland, (b) proportion of open canopy forestry, (c) proportion of closed canopy
 296forestry, (d) proportion of grazed land, (e) elevation and (f) slope for the optimum area
 297interaction model using a LASSO penalty of 0.00005, selected by minimising BIC, to predict
 298the intensity of Hen Harrier nest presence using the proportion of important habitat types on
 299the Isle of Mull, Scotland.

300

301

3023.1 Model validation

303The area-interaction model performed well in terms of predicting suitable areas for nest sites
 304when tested against independent survey data from 2015 and 2016. The median AUC value

305 was 0.82 (range 0.73 – 0.89) and the median TSS was 0.55 (range 0.43 – 0.71). The
306 intensity of Hen Harrier nest locations on Mull was spatially similar to those predicted by the
307 model. In particular, high intensity areas are present in the East and South West of the island
308 which are also present in our predictions. Density in the North of the Island was generally
309 lower and more localised.

310

311 4. Discussion

312 Our area-interaction model indicates that Hen Harrier distribution on Mull is characterised by
313 habitat mosaics of moorland and forest and low proportions of grazed land. The model had
314 good predictive accuracy when tested with data from 2015 and 2016 which demonstrates an
315 ability to predict suitable breeding habitat for Hen Harriers on Mull. The spatial distribution of
316 predicted Hen Harrier intensity reflect the distribution of nests found on the island, however,
317 our predicted intensity was lower than actual intensities which suggests that our models are
318 conservative in their estimates. It is worth noting that extensive island wide surveys for
319 breeding Golden Eagle, White-tailed Eagle *Haliaeetus albicilla* and Hen Harrier since 1982
320 have yet to locate a single Hen Harrier breeding attempt outwith the predicted areas
321 (Haworth, pers. comm.). Both open and closed canopy forestry were positively associated
322 with Hen Harrier nest intensity, however, response plots showed that, as suggested by
323 previous research, the relationship with open canopy forestry was more clearly positive
324 (Redpath et al., 1998). Elevation and slope were important in determining Hen Harrier
325 distribution on the island, our model indicating that Hen Harriers prefer narrow ranges of
326 both variables with an elevation limit at around 200 m and avoidance of steep slopes. The
327 elevation limit for Hen Harrier recorded on the mainland is around 550 m (Gilbert et al.,
328 2011) which is noticeably higher than on Mull despite the presence of extensive higher
329 ground. Previous models of Hen Harrier distribution have also noted the importance
330 variables related to topography (Tapia et al., 2004). The difference in elevation limit between
331 Mull and mainland Scotland may be due to its topography but could also be due to higher

densities of Golden Eagle territories which are thought be avoided by Hen Harriers (Fielding et al., 2011). Our model included an area-interaction term which suggests that Hen Harrier nests are found close to each other within the landscape or similar locations are used in different years. We believe that this clustering reflects clustering among Hen Harrier nest sites due to levels of philopatry, and use of nest sites in subsequent years, within the population (Watson and Thirgood, 2001) or possible evidence of conspecific attraction as seen in Montagu's harriers (Cornulier and Bretagnolle, 2006). Different methods identified different optimal values for the radius of this area-interaction within our models which suggests that the processes driving this clustering may operate at more than one spatial scale.

Our results suggest that Hen Harriers on Mull prefer open mosaics which can include both forestry categories but avoid open, grazed land. All nests located in 2015 and 2016 were situated in areas with no sheep and cattle grazing although varying numbers of red deer were often present. The use of a range of habitat types but avoidance of grazed land shown in the results is in agreement with findings on Hen Harrier habitat preference in both Scotland (Arroyo et al., 2009) and Ireland (Wilson et al., 2009). Our model shows a response to increasing scrub/moorland cover suggesting that areas with proportions over 80% are optimal. On the Scottish mainland it is often assumed that Hen Harriers show a preference for open moorland (Redpath et al., 1998) and in particular are associated with moorland managed for upland grouse shooting (Thompson et al., 2009). However, our results on the Isle of Mull suggest that Hen Harriers are more diverse in their habitat preference, at least in this population. Higher predicted nest intensities are also associated with areas containing open canopy and closed canopy forest. Hen Harriers only appear to actively avoid areas in which the vegetation height is low. The highest predicted intensities were in areas with less than 20% grazed land. Indeed Hen Harriers are known for using edge habitats for hunting which habitat mosaics are likely to provide (Redpath, 1992; Schipper, 1977) and nesting in tall crops in parts of France (Cormier et al., 2008). Our models suggest that the exact

359makeup of habitat mosaics can be variable but that either moorland, scrub or open canopy
360forestry should be the dominant habitat types.

361

362Hen Harriers are known to use first rotation forestry plantations as foraging habitat before
363canopy closure (Redpath et al., 1998) and have been noted to use second rotation
364restocked plantations in the same way in Ireland (Wilson et al., 2009). Further clarification is
365required on the likely use of restocked forests for breeding Hen Harriers and the timeframe
366for its suitability as nesting habitat. Additionally, further research on the makeup and
367management of forested areas within Hen Harrier territories will be beneficial. However, our
368model clearly indicates the importance of forested areas as constituents of suitable areas for
369breeding Hen Harrier on Mull. In areas where grazing is heavy, pre-thicket plantations can
370provide more foraging potential than open areas (Madders, 2003). As such, we suggest that
371more complex habitat mosaics surrounding nest sites have the potential to be used as
372foraging habitat by Hen Harriers. It is likely that that dense, closed canopy plantation forests
373may be unsuitable for hen harrier. Indeed our models suggest that territory densities are
374highest in areas where the proportion of closed canopy forest is low. However, the
375combinations of habitat variables indicated as suitable by our model indicates that more
376open forested landscapes with a mixture of vegetation cover can form part of hen harrier
377territories. The potential nature of these forested areas warrants further investigation with
378particular emphasis on the appropriate scale of habitat mosaics.

379

380Anderson et al. (2009) suggest that the discrepancy between the predictions of their
381climatically based and habitat based models may be due to the impact of current and
382historical persecution. This may be the case for areas such as the North of England where
383Hen Harriers are currently extremely scarce (Potts, 1998) but the available habitats are
384similar to those found in 'suitable' landscapes for Hen Harriers further to the north. According
385to our models, Hen Harriers might potentially find 'suitable' landscapes across large areas of
386Britain and Ireland where grazing pressure is not too high (Madders, 2003) if current

387populations were able to increase to close to carrying capacity. Grouse moors themselves,
388may be attractive to harriers because of high prey densities due to human management
389(Smith et al., 2001) rather than features of the habitat itself and can impact on Hen Harrier
390populations due to reduced breeding success and survival (Green and Etheridge, 1999).
391More complex habitat mosaics in these areas would potentially provide higher densities of
392alternative prey items such as meadow pipit *Anthus pratensis* (Vanhinsberg and
393Chamberlain, 2001). This investigation concentrated on habitat variables and Hen Harrier
394presence, as such, did not consider the success of Hen Harriers in different habitat types. In
395order to provide more comprehensive recommendations for upland mosaics, demographic
396information should be incorporated into habitat models.

397Due to the economically driven land use change experienced in working landscapes such as
398the Scottish uplands (Pack, 2010; Warren, 2002), habitat heterogeneity has decreased
399during the last century (Benton et al., 2003; Maclean, 2010). Our model suggests that
400increased habitat heterogeneity could be beneficial for Hen Harrier. This would be potentially
401also benefit other species, such as Short-eared Owl (Wheeler, 2008) and Black Grouse
402*Tetrao tetrix* (Geary et al., 2013). Increasing grazing pressure was implicated in the decline
403of Hen Harrier populations on Orkney (Amar et al., 2011) and our results would suggest that
404wider grazing reductions could contribute to beneficial mosaics for Hen Harrier. There is
405already evidence for a reduction of grazing pressure across Scotland (Fuller and Gough,
4061999; Scottish Government, 2003). Due to the economic incentives and current Scottish
407government targets related to upland afforestation (Scottish Executive, 2006; Warren, 2002),
408we can expect further increases in tree cover in Britain and Ireland. However, with careful
409consideration of the structure of the resulting landscapes it is possible to find compromises
410between land management and conservation outcomes (Polasky et al., 2008).

411 Our model along with populations on Mull, and other islands, may provide some evidence
412that landscapes currently considered 'unsuitable' due to a lack of Hen Harrier warrant
413management to make them as Hen Harrier friendly as possible. The exact details of 'Hen

414Harrier friendly' management would benefit from further research as Hen Harrier in other
415locations are likely to be influenced by other factors to those which are important on Mull.
416Government policy aims to expand the area under some form of woodland in Scotland from
41717% in 2007 to 25% by the second half of this century (Forestry Commission 2009; Forestry
418Commission 2016). This includes creating 10,000ha per year between 2014 and 2020. This
419presents an opportunity, via sympathetic management, to enhance the availability of habitat
420for breeding Hen Harrier although it is important to link breeding habitat with suitable
421foraging habitat.

422In this case we suggest that forestry is integrated more fully into landscape mosaics, that
423areas with high proportions of open canopy forestry are not overlooked as possible Hen
424Harrier habitat and that grazing pressure is reduced where possible. The current extent and
425persistence of harriers breeding in restocked forests is largely unknown but could be an
426important, even if it is a somewhat locally and regionally transient feature of the harrier
427population in the future. The evidence from Ireland (Ruddock et al., 2016; Wilson et al.,
4282009) is that second rotation forest can represent a significant nesting resource for Hen
429Harriers. At a much more local scale open areas within forests such as those where there is
430deep peat, and areas left unplanted due to a lack of soil, are also important for nesting
431harriers (Fielding et al., 2011). The proximity, extent and management of open land
432surrounding forests is also likely to have a bearing on the success of breeding harriers in
433terms of potential prey availability and potential predation pressures (Arroyo et al., 2009;
434Wilson et al., 2012).

4354.1 Conclusion

436The area interaction model with LASSO penalty was successful in modelling Hen Harrier
437nest intensity in relation to habitat on Mull. In this case the spatial interaction would have
438meant that the assumptions of similar models, such as MaxEnt, would have been violated
439whereas the point-process framework gave us the flexibility to deal with this issue. Our
440results indicate that Hen Harrier have the potential to occupy a diverse range of habitat types

441where taller vegetation is available including those with forest cover. As such, wider areas of
442Britain and Ireland may be suitable for Hen Harrier in the future, given a reduction in
443persecution and expansion of the current population, if sympathetically managed to include
444variety of habitat types. Sympathetic management, according to our results, would have
445implications for forest management across large scales and require further research and
446long-term planning. Our results provide information on Hen Harrier habitat preference,
447although not necessarily breeding success or productivity, which can inform future survey
448work aimed at locating breeding Hen Harrier as our models have proved successful in
449predicting Hen Harrier nest locations in 2015 and 2016. Using this information surveys can
450be more targeted, which would be more efficient in terms of effort and less costly. Similarly,
451maintaining, managing and enhancing areas to encourage breeding Hen Harrier can be
452more clearly focussed if habitats suitable for breeding are geographically restricted in some
453regions and, using information on habitat preference, their effectiveness can be maximised
454as part of economically driven changes. Our work explores these preferences on the Isle of
455Mull but the same principles could be applied to a wider area across Great Britain and
456Ireland as part of conservation plans.

457

458

459

460**Acknowledgements**

461The authors would like to thank Forestry Commission Scotland for providing the forest
462inventory used in our analysis as well as the Centre for Ecology and Hydrology for provision
463of LCM2007 and Ordnance survey for the Digital Terrain Model. This work was supported by
464the Forestry and Raptors Joint Working Group ([http://www.snh.gov.uk/land-and-](http://www.snh.gov.uk/land-and-sea/managing-the-land/forestry-and-woodlands/raptors-forestry/)
465[sea/managing-the-land/forestry-and-woodlands/raptors-forestry/](http://www.snh.gov.uk/land-and-sea/managing-the-land/forestry-and-woodlands/raptors-forestry/)). We would also like to
466thank Professor Stuart Marsden, Dr Achaz von Hardenberg, Dr Mark Wilson, Dr Daniel

467 Hayhow, the University of Chester Conservation Biology Research Group and several
468 anonymous reviewers for comments which improved the manuscript.

469

470

471

472

473

474References

- Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* 43, 1223–1232. doi:10.1111/j.1365-2664.2006.01214.x
- Amar, A., Davies, J., Meek, E., Williams, J., Knight, A., Redpath, S., 2011. Long-term impact of changes in sheep *Ovis aries* densities on the breeding output of the Hen Harrier *Circus cyaneus*. *J. Appl. Ecol.* 48, 220–227.
- Anderson, B.J., Armsworth, P.R., Eigenbrod, F., Thomas, C.D., Gillings, S., Heinemeyer, A., Roy, D.B., Gaston, K.J., 2009. Spatial covariance between biodiversity and other ecosystem service priorities. *J. Appl. Ecol.* 46, 888–896. doi:10.1111/j.1365-2664.2009.01666.x
- Araújo, M.B., Pearson, R.G., 2005. Equilibrium of species' distributions with climate. *Ecography* 28, 693–695.
- Arroyo, B., Amar, A., Leckie, F., Buchanan, G.M., Wilson, J.D., Redpath, S., 2009. Hunting habitat selection by Hen Harriers on moorland: implications for conservation management. *Biol. Conserv.* 142, 586–596.
- Baddeley, A., Turner, R., 2005. Spatstat: an R package for analyzing spatial point patterns. *J. Stat. Softw.* 12, 1–42.
- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18, 182–188.
- Berry, P.M., Dawson, T.P., Harrison, P.A., Pearson, R.G., 2002. Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Glob. Ecol. Biogeogr.* 11, 453–462.
- BirdLife International, 2015. *Circus cyaneus*. The IUCN Red List of Threatened Species 2015: e.T22727733A80213525.

Cormier, J.-P., Fustec, J., Pithon, J., Choisy, P., 2008. Selection of nesting habitat by Montagu's Harriers *Circus pygargus* and Hen Harriers *Circus cyaneus* in managed heaths: Capsule Montagu's Harriers avoided tree plantations and selected plots with dense heath of intermediate height, while sympatric Hen Harriers preferred afforested or taller plots of heath. *Bird Study* 55, 86–93.

Cornulier, T., Bretagnolle, V., 2006. Assessing the influence of environmental heterogeneity on bird spacing patterns: a case study with two raptors. *Ecography* 29, 240–250.

Elith, J., Graham, C.H., 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography* 32, 66–77.
doi:10.1111/j.1600-0587.2008.05505.x

Elith, J., Leathwick, J.R., 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annu. Rev. Ecol. Evol. Syst.* 40, 677–697.
doi:10.1146/annurev.ecolsys.110308.120159

Etheridge, B., Summers, R.W., Green, R.E., 1997. The effects of illegal killing and destruction of nests by humans on the population dynamics of the Hen Harrier *Circus cyaneus* in Scotland. *J. Appl. Ecol.* 1081–1105.

Fielding, A., Haworth, P., Whitfield, P., McLeod, D., Riley, H., 2011. A Conservation Framework for Hen Harriers in the United Kingdom. JNCC Rep. No 441.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49.
doi:10.1017/S0376892997000088

Forest Research, 2013. National Forest Inventory. <https://www.forestry.gov.uk/inventory>

Forest Research 2016. National Forest Inventory. <https://www.forestry.gov.uk/inventory>

Forestry Commission. 2009. The Scottish Government's Rational for Woodland Expansion. Forestry Commission Scotland, Edinburgh.

- Forestry Commission. 2014. Scotland's Native Woodlands Results from the Native Woodland Survey of Scotland. Forestry Commission Scotland, Edinburgh.
- Forestry Commission. 2016. Woodland Area, Planting and Restocking. Forestry Commission Scotland, Edinburgh.
- Fuller, R.J., Gough, S.J., 1999. Changes in sheep numbers in Britain: implications for bird populations. *Biol. Conserv.* 91, 73–89.
- Gallien, L., Douzet, R., Pratte, S., Zimmermann, N.E., Thuiller, W., 2012. Invasive species distribution models—how violating the equilibrium assumption can create new insights. *Glob. Ecol. Biogeogr.* 21, 1126–1136.
- Geary, M., Fielding, A.H., Marsden, S.J., 2013. Designing mosaic landscapes for Black Grouse *Tetrao tetrix* using multi-scaled models. *Ibis* 155, 792–803. doi:10.1111/ibi.12090
- Geary, M., Fielding, A.H., McGowan, P.J.K., Marsden, S.J., 2015. Scenario-Led Habitat Modelling of Land Use Change Impacts on Key Species. *PLoS ONE* 10, e0142477. doi:10.1371/journal.pone.0142477
- Gilbert, G., Gibbons, D.W., Evans, J., 2011. Bird Monitoring Methods: A Manual of Techniques for Key UK Species. Pelagic Publishing Limited, Exeter.
- Green, R.E., Etheridge, B., 1999. Breeding success of the Hen Harrier *Circus cyaneus* in relation to the distribution of grouse moors and the red fox *Vulpes vulpes*. *J. Appl. Ecol.* 36, 472–483.
- Hardey, J., 2006. Raptors: a field guide to survey and monitoring. The Stationery Office, London.
- Hastie, T., Fithian, W., 2013. Inference from presence-only data; the ongoing controversy. *Ecography* 36, 864–867. doi:10.1111/j.1600-0587.2013.00321.x

Hayhow, D.B., Eaton, M.A., Bladwell, S., Etheridge, B., Ewing, S.R., Ruddock, M., Saunders, R., Sharpe, C., Sim, I.M., Stevenson, A., 2013. The status of the Hen Harrier, *Circus cyaneus*, in the UK and Isle of Man in 2010. *Bird Study* 60, 446–458.

Hijmans, R.J., van Etten, J., 2012. raster: Geographic analysis and modeling with raster data. R package version 1.9-63. <http://CRAN.R-project.org/package=raster>

Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28, 385–393.

Loo, S.E., Nally, R.M., Lake, P.S., 2007. Forecasting New Zealand mudsnail invasion range: model comparisons using native and invaded ranges. *Ecol. Appl.* 17, 181–189.

Maclean, N., 2010. *Silent Summer: the state of wildlife in Britain and Ireland*. Cambridge University Press, Cambridge.

Madders, M., 2003. Hen Harrier *Circus cyaneus* foraging activity in relation to habitat and prey. *Bird Study* 50, 55–60.

Madders, M., 2000. Habitat selection and foraging success of Hen Harriers *Circus cyaneus* in west Scotland. *Bird Study* 47, 32–40. doi:10.1080/00063650009461158

Massey, B.H., Griffin, C.R., McGarigal, K., 2009. Habitat Use by Foraging Northern Harriers on Nantucket Island, Massachusetts. *Wilson J. Ornithol.* 121, 765–769.

Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R., Simpson, I., 2011. Final Report for LCM2007-the new UK land cover map. Countryside Survey Technical Report No 11/07.

NPWS, 2015. Hen Harrier Conservation and the Forestry Sector in Ireland. Report prepared by NPWS to inform the Hen Harrier Threat Response Plan (HHTRP) (No. 3.2. 1-50.).

Pack, B., 2010. The road ahead for Scotland: Final report of the inquiry into future support for agriculture in Scotland. Scottish Government, Edinburgh.

Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model.* 133, 225–245.

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.

doi:10.1111/j.2007.0906-7590.05203.x

Polasky, S., Nelson, E., Camm, J., Csuti, B., Fackler, P., Lonsdorf, E., Montgomery, C., White, D., Arthur, J., Garber-Yonts, B., Haight, R., Kagan, J., Starfield, A., Tobalske, C., 2008. Where to put things? Spatial land management to sustain biodiversity and economic returns. *Biol. Conserv.* 141, 1505–1524. doi:10.1016/j.biocon.2008.03.022

Potts, G.R., 1998. Global dispersion of nesting Hen Harriers *Circus cyaneus*; implications for grouse moors in the U.K. *Ibis* 140, 76–88. doi:10.1111/j.1474-919X.1998.tb04544.x

R Core Team, 2016. R: A language and environment for statistical computing [Internet]. Vienna, Austria: R Foundation for Statistical Computing; 2013. Doc. Free. Available Internet [Httpwww R-Proj. Org](http://www.R-Project.org).

Redpath, S., Madders, M., Donnelly, E., Anderson, B., Thirgood, S., Martin, A., Mcleod, D., 1998. Nest site selection by Hen Harriers in Scotland. *Bird Study* 45, 51–61. doi:10.1080/00063659809461077

Redpath, S.M., 1992. Behavioural interactions between Hen Harriers and their moorland prey. *Ornis Scand.* 73–80.

Redpath, S.M., Thirgood, S.J., Leckie, F.M., 2001. Does supplementary feeding reduce predation of red grouse by Hen Harriers? *J. Appl. Ecol.* 38, 1157–1168. doi:10.1046/j.0021-8901.2001.00683.x

Renner, IW. 2013. Advances in presence-only methods in ecology. PhD Thesis, University of New South Wales.

- Renner, I.W., Elith, J., Baddeley, A., Fithian, W., Hastie, T., Phillips, S.J., Popovic, G., Warton, D.I., 2015. Point process models for presence-only analysis. *Methods Ecol. Evol.* 6, 366–379. doi:10.1111/2041-210X.12352
- Renner, I.W., Warton, D.I., 2013. Equivalence of MAXENT and Poisson point process models for species distribution modeling in ecology. *Biometrics* 69, 274–281.
- Royle, J.A., Chandler, R.B., Yackulic, C., Nichols, J.D., 2012. Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods Ecol. Evol.* 3, 545–554. doi:10.1111/j.2041-210X.2011.00182.x
- Ruddock, M., Mee, A., Lusby, J., Nagle, T., O'Neill, S., O'Toole, L., 2016. The 2015 National Survey of Breeding Hen Harrier in Ireland (report). National Parks and Wildlife Service.
- Sangster, G., Collinson, J.M., Crochet, P.-A., Kirwan, G.M., Knox, A.G., Parkin, D.T., Votier, S.C., 2016. Taxonomic recommendations for Western Palearctic birds: 11th report. *Ibis* 158, 206–212. doi:10.1111/ibi.12322
- Schipper, W.J.A., 1977. Hunting in three European harriers (*Circus*) during the breeding season. *Ardea* 65, 63–71.
- Scottish Executive, 2006. The Scottish forestry strategy. Forestry Commission Scotland, Edinburgh.
- Scottish Government, S.A.H., 2003. Agriculture Statistics Tables by Topic: Sheep [WWW Document]. URL <http://www.gov.scot/Topics/Statistics/Browse/Agriculture-Fisheries/agritopics/Sheep> (accessed 2.7.17).
- Sharrock, J.T.R., 1976. The Atlas of Breeding Birds in Britain and Ireland. A&C Black, London.
- Sim, I.M., Dillon, I.A., Eaton, M.A., Etheridge, B., Lindley, P., Riley, H., Saunders, R., Sharpe, C., Tickner, M., 2007. Status of the Hen Harrier *Circus cyaneus* in the UK and Isle of Man in 2004, and a comparison with the 1988/89 and 1998 surveys: Capsule The population of

breeding Hen Harriers in the UK and Isle of Man increased between 1998 and 2004, although country and regional trends differed. *Bird Study* 54, 256–267.

Simmons, R.E., 2000. *Harriers of the world: their behaviour and ecology*. Oxford University Press, Oxford.

Smith, A.A., Redpath, S.M., Campbell, S.T., Thirgood, S.J., 2001. Meadow pipits, red grouse and the habitat characteristics of managed grouse moors. *J. Appl. Ecol.* 38, 390–400.

Tapia, L., Dominguez, J., Rodriguez, L., 2004. Modeling habitat use and distribution of Hen Harriers (*Circus cyaneus*) and Montagu's Harrier (*Circus pygargus*) in a mountainous area in Galicia, northwestern Spain. *J. Raptor Res.* 38, 133–140.

Thompson, P.S., Amar, A., Hoccom, D.G., Knott, J., Wilson, J.D., 2009. Resolving the conflict between driven-grouse shooting and conservation of Hen Harriers. *J. Appl. Ecol.* 46, 950–954. doi:10.1111/j.1365-2664.2009.01687.x

Vanhinsberg, D.P., Chamberlain, D.E., 2001. Habitat associations of breeding Meadow Pipits *Anthus pratensis* in the British uplands. *Bird Study* 48, 159–172.
doi:10.1080/00063650109461214

Warren, C.R., 2002. *Managing Scotland's Environment*. Edinburgh University Press, Edinburgh.

Warren, D.L., Seifert, S.N., 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* 21, 335–342.

Warton, D.I., Renner, I.W., Ramp, D., 2013. Model-Based Control of Observer Bias for the Analysis of Presence-Only Data in Ecology. *PLoS ONE* 8, e79168.
doi:10.1371/journal.pone.0079168

Watson, M., Thirgood, S., 2001. Could translocation aid Hen Harrier conservation in the UK? *Anim. Conserv.* 4, 37–43.

Wheeler, P., 2008. Effects of sheep grazing on abundance and predators of field vole (*Microtus agrestis*) in upland Britain. *Agric. Ecosyst. Environ.* 123, 49–55.

Wilson, M.W., Irwin, S., Norriss, D.W., Newton, S.F., Collins, K., Kelly, T.C., O'Halloran, J., 2009. The importance of pre-thicket conifer plantations for nesting Hen Harriers *Circus cyaneus* in Ireland. *Ibis* 151, 332–343. doi:10.1111/j.1474-919X.2009.00918.x

Wilson, M.W., O'donoghue, B., O'mahony, B., Cullen, C., O'donoghue, T., Oliver, G., Ryan, B., Troake, P., Irwin, S., Kelly, T.C., Rotella, J.J., O'halloran, J., 2012. Mismatches between breeding success and habitat preferences in Hen Harriers *Circus cyaneus* breeding in forested landscapes. *Ibis* 154, 578–589. doi:10.1111/j.1474-919X.2012.01236.x

475Tables

476**Table 1.** Parameter estimates for the optimum area interaction model using a LASSO
 477penalty of 0.00005, selected by minimising BIC, to predict the intensity of Hen Harrier nest
 478presence using the proportion of important habitat types on the Isle of Mull, Scotland.
 479Confidence intervals (95%) are presented across the 1001 model runs.

Model term	β	95% C.I.
Intercept	-19.35	0.1
Proportion of grazed land	-0.37	0.02
Proportion of grazed land ²	-0.23	0.01
Proportion of scrub/moorland	0.28	0.01
Proportion of Open Forest	0.14	0.002
Proportion of closed forest	0.23	0.01
Elevation	-4.3	0.18
Elevation ²	-3.67	0.16
Slope	-0.23	0.01
Interaction	0.44	0.002

480

481 **Figure Legends**

482 **Figure 1.** Predicted intensity of Hen Harrier nest presence per 1 km² for the optimum area
483 interaction model using a LASSO penalty of 1.69, selected by minimising BIC, to predict the
484 intensity of Hen Harrier nest presence using the proportion of important habitat types on the
485 Isle of Mull, Scotland.

486 **Figure 2.** Plots of predicted Hen Harrier nest presence intensity against (a) proportion of
487 scrub/moorland, (b) proportion of open canopy forestry, (c) proportion of closed canopy
488 forestry, (d) proportion of grazed land, (e) elevation and (f) slope for the optimum area
489 interaction model using a LASSO penalty of 0.00005, selected by minimising BIC, to predict
490 the intensity of Hen Harrier nest presence using the proportion of important habitat types on
491 the Isle of Mull, Scotland.