



Mismatches between breeding success and habitat preferences in Hen Harriers *Circus cyaneus* breeding in forested landscapes

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During the past century, the upland breeding areas of Hen Harriers in Ireland have been extensively afforested. There is no evidence that this species avoids breeding in heavily forested landscapes and, indeed, young commercial forests in their second rotation are often selected as nest-sites. However, Hen Harriers have coexisted with these forested areas for only a few decades and it is possible that such landscapes are suboptimal. We examined the relationship between breeding success and habitat using a dataset spanning three years and four study areas in the south and west of Ireland. We assessed whether nest success and fledged brood size were related to habitat type, both at the nest-site and in the surrounding landscape. Neither measure of breeding productivity was related to total forest cover or to percentage cover of closed canopy forest in the landscape. However, in a subset of areas, high cover of second-rotation pre-thicket (young forests planted on land from which a first rotation has already been harvested) in the surrounding landscape was associated with low levels of breeding success. This may be due to factors related to predation, disturbance or prey availability. The fact that second-rotation pre-thicket is a preferred habitat for nesting in Ireland suggests that Hen Harriers may be making suboptimal decisions in the landscapes available to them.

Keywords: commercial forestry, conifer plantation, ground-nesting raptor, nest-site selection, Sitka Spruce.

Habitat change is the single most important driver of anthropogenic bird population declines (Bird-Life International 2000, 2004). For many species, the conversion of one habitat to another renders previously occupied areas unsuitable (Cerezo *et al.* 2010, Biamonte *et al.* 2011, Clavel *et al.* 2011), but other species may be able to cope with profound changes in habitat type, successfully utilizing very different habitats from those they evolved in (Sergio & Bogliani 1999, Møller 2009, Cardador

et al. 2011). However, birds occupying novel habitats may be less adapted than they initially appear, experiencing lower survival or reproductive success (Robertson & Hutto 2007, Gilroy *et al.* 2011). Anthropogenic environmental change has led to mismatches between habitat preferences exhibited by a species and the actual value of habitats to it – the 'ecological trap' described by Gates and Gysel (1978). Such mismatches challenge our understanding of species' habitat requirements and pose questions for conservation managers regarding the relative values of traditional and newly occupied habitats.

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One of the most profound and widespread habitat changes in recent times has been between forests and open habitats. Deforestation is of particular conservation concern, especially in tropical areas (Buchanan *et al.* 2009, Loiselle *et al.* 2010, Sodhi *et al.* 2008), but the conversion of open habitats of high conservation value to forest due to both land abandonment (Wretenberg *et al.* 2006, Brambilla *et al.* 2007, Sirami *et al.* 2008) and active afforestation (Riksen *et al.* 2006, Brockerhoff *et al.* 2008, Lantschner *et al.* 2008) has attracted much recent attention. Over the past 60 years, many previously open upland areas in Ireland have been extensively afforested (Avery & Leslie 1990, O'Leary *et al.* 2000), with total national forest cover rising from <2% to over 10% during this period. Many upland birds of conservation interest, including waders, raptors and passerines, respond negatively to afforestation (Hancock & Avery 1998, Buchanan *et al.* 2003, Whitfield *et al.* 2007), but others appear to be more compatible with newly established forested landscapes.

The Hen Harrier *Circus cyaneus*, which often nests in young upland conifer plantations, is an example of such a species. It is protected at both national and European levels, having suffered a large historical decline (BirdLife International 2004). It is one of Ireland's rarest breeding raptors, although the total number of breeding pairs in Ireland appears to have been relatively stable (between 100 and 200 pairs) during the last decade (Barton *et al.* 2006, Ruddock *et al.* 2011). Hen Harriers are regarded as birds of open and scrub-dominated habitats (Watson 1977, Cramp & Simmons 1980), although in most parts of their current Irish breeding range they now occupy heavily afforested landscapes (Norriss *et al.* 2002, Barton *et al.* 2006, Wilson *et al.* 2009a). In Britain and Ireland they use forests at the pre-thicket stage (prior to canopy closure) for both foraging and nesting (Barton *et al.* 2006, Haworth & Fielding 2009) but make limited use of forests with closed canopy (Madders 2003, Barton *et al.* 2006). At any one time, over two-thirds of the forest estate has a closed canopy and is therefore of little use to Hen Harriers (O'Flynn 1983, Sim *et al.* 2001). A recent study showed that Hen Harriers in Ireland select recently planted forests for nesting (Wilson *et al.* 2009a). In particular, that study demonstrated a strong preference for pre-thicket forest in its second rotation (i.e. planted after the harvest of a previous crop of timber). In 2005, despite occupying only 5% of the study areas,

pre-thicket second-rotation forests held almost a third of the Hen Harriers nesting in these areas (Wilson *et al.* 2009a). Another finding of the study was that, although Hen Harriers avoided landscapes with high proportions of intensively farmed pasture, they showed no avoidance of areas with a high proportion of closed-canopy forest. In fact, Hen Harrier nests in forested landscapes are often located in small openings within larger areas of closed-canopy forest.

These findings are encouraging with regard to the future of Hen Harriers in forested landscapes in Ireland. However, the association of nesting Hen Harriers with forest habitats does not necessarily mean that these are optimal habitats for this species. In Scotland, Hen Harriers breeding in conifer forests were found to experience lower success than those breeding in unmanaged moorlands (Etheridge *et al.* 1997). The Hen Harrier has coexisted with extensive, commercially managed forests for less than 100 years, so its preferences may not be well matched to the value of forest plantation habitats for this species. Recent breeding output and subsequent recruitment of fledged young into breeding populations appear to be sufficiently low in Ireland to be a cause of concern (Irwin *et al.* 2011). Additionally, the most recent national survey in 2010 showed that breeding numbers have declined in some parts of their range, particularly in the southwest (Ruddock *et al.* 2011). Elucidating the relationship between habitat and Hen Harrier breeding success will enable more effective management of forested landscapes for this species, as well as adding to our understanding of the ecology of species responding to human-induced environmental change. We examined the relationship between breeding success and habitat using a dataset spanning 3 years (2007–2009) and four areas in the south and west of Ireland. Our aim was to assess whether breeding success varied according to (1) habitat type at the site of the nest, (2) total cover of forest in the landscape around nests and (3) cover of different forest types and non-forest habitats in the landscape.

METHODS

Study areas and fieldwork

Fieldwork was conducted in four study areas (Fig. 1), selected to maximize sample sizes according to the study's objectives. Together, these areas

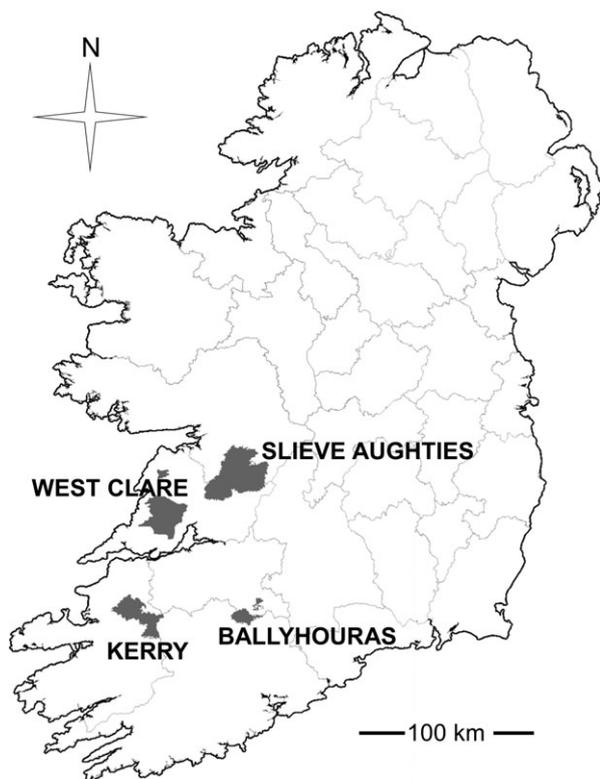


Figure 1. Locations of the four study sites in west and south Ireland.

held approximately one-third of the national breeding population (Barton *et al.* 2006). In each of the four study areas, active breeding territories were identified by the presence of displaying or paired birds in late March and April, with the locations of most nests identified during May and June. Initial visits were made to nests to assess nest contents, with a final visit to ring and wing-tag chicks and to assess pre-fledging brood size when they were approximately 3 weeks old. A maximum of three visits was made to each nest, conducted under licence and supervision of the National Parks and Wildlife Service (NPWS). In situations where nest visits were deemed to pose too great a risk to the success of the breeding attempt, the status of nests was monitored from a distance. All nests were monitored until they had failed or broods had fledged. Successful nests were identified by the presence of recently fledged juveniles in the nesting area. Young typically remain within a few hundred metres of the nest for a week or more after fledging, for most of which time they are vocally and/or visually conspicuous. At successful nests

that had been visited, the number of chicks fledged was estimated as the number of healthy chicks present during the final nest visit (typically around a week before fledging). All nests were visited for habitat assessment some weeks after fledging and, where nestlings were found to have died before fledging but subsequent to the final visit, the number of chicks fledged was amended appropriately. For nests that were not visited, the number of chicks fledged was estimated as the maximum number of fledged juveniles seen flying in the nesting area post-fledging. We tested for a difference in the size of successfully fledged broods between those estimated as the number of chicks present on the final visit and those estimated as the number of juveniles counted post-fledging, using a Mann–Whitney *U*-test.

Habitat classification

We compiled habitat maps of the study areas using the GIS software packages ARCVIEW 3.3 (ESRI 2002) and ARCGIS DESKTOP 9.2 (ESRI 2006). We derived forest habitat data from digitised forest inventory and felling information held by the Forest Service for privately owned forests, and by the semi-state forestry company Coillte for state-owned forests. Non-forest habitat data were derived from habitat maps of our study areas compiled by NPWS from 1:5000 digitised aerial photographs taken in 2005. We verified this information using aerial photographs and field-based ground-truthing. Each nest was classified into one of five site-scale habitat categories. Nests were classified as forest nests if they were located in any kind of forested area. Forest nests were further classified according to whether the surrounding forest was in its first or second commercial rotation (i.e. whether it was planted on previously non-forest habitat, or following the harvest of a previous timber crop). Non-forest nests were classified according to two broad habitat types: heather moorland and bog habitats; and non-heather scrub.

Previous studies have found that breeding Hen Harriers forage mostly within 2 km of their nests (Arroyo *et al.* 2006, M. W. Wilson unpubl. data). To conduct analysis of breeding success in relation to habitat at the landscape scale, the proportion of land within 2 km of each nest falling into each of seven categories was calculated. Again, forest habitat was distinguished from other habitats, and was further subdivided into three categories:

Table 1. Area and proportion of land in each of six habitat categories in the four study areas.

Habitat category	Slieve Aughties			West Clare
	Ballyhouras	Kerry		
Area (km ²)	674	106	292	412
1st rotation pre-thicket	0.09	0.06	0.17	0.13
2nd rotation pre-thicket	0.07	0.14	0.02	0.02
Post-closure forest	0.28	0.41	0.23	0.27
Improved grassland	0.08	0.07	0.12	0.07
Heath/bog	0.24	0.11	0.28	0.28
Rough grazing	0.20	0.10	0.17	0.18

first-rotation pre-thicket, second-rotation pre-thicket, and closed canopy. Pre-thicket forests are those which have yet to develop a closed canopy, and are generally < 5 m in height. For the purposes of classification at the landscape scale, first-rotation forests were defined as being pre-thicket when 12 years old or younger. Second-rotation forests are preceded by sparsely vegetated clearfell habitat and typically grow faster than first-rotation forests, so were defined as pre-thicket between 3 and 9 years after planting. The closed-canopy category comprised thicket and post-thicket forests of both rotations, typically between 4 and 20 m in height. Although commercial forests were widespread in all four study areas, forest cover and age structure varied between study areas (Table 1), reflecting the time since the start of intensive and widespread forestry activity in these areas. Further details of these habitat categories are given in Wilson *et al.* (2009a).

Data analysis

All spatial analyses were carried out using ARCVIEW 3.3 (ESRI 2002). The Tabulate Areas function of the Spatial Analyst extension in ARCVIEW 3.3 was used to calculate the area occupied by each habitat type within a 2-km radius around each nest. We investigated two separate measures of breeding success: nest success (a binary variable describing whether any chicks fledge from a nest) and fledged brood size (the numbers of chicks fledged from a successful nest). We use the term productivity to refer to the number of fledged chicks per breeding pair (including pairs that did not breed successfully). To assess the relative contributions of fledged brood size and nest success to overall productivity, we simulated brood-size-independent

productivity values for each nest over 1000 randomised runs. In each run, nests were randomly assigned brood sizes from among the brood sizes recorded at successful nests, while the success of each nest was kept constant at its original value. Simulated productivity values were calculated for each nest by averaging over all 1000 runs. The contribution of nest success to variation in productivity was estimated by linear regression as the proportion of variation in observed productivity among study areas and years that was explained by simulated productivity values.

Two of our study sites, Kerry and West Clare, were similar in terms of the levels of productivity in all three study years and also in terms of habitat composition (Tables 1 and 2). We combined these into a single 'Western' category, enabling a more effective investigation of interactions between study area and other explanatory variables. However, the number of study areas coded for by this factor did not greatly affect the final output of any model.

The effects of study area, year and habitat on components of breeding success were analysed using GLM (generalized linear modelling). Nest success was modelled in MARK 6.1 (White & Burnham 1999) using the nest survival analysis procedure (Rotella *et al.* 2004). This takes account of the influence of nest stage at time of finding on apparent survival, calculating a daily survival rate for each nest. Fledged brood size was modelled in R.2.13.1 (R Development Core Team 2011) using Poisson GLM in the package 'glm'. The explanatory variables considered for inclusion in both the survival and the fledged brood size models were study area, year and the 12 habitat variables (five at the nest scale and seven at the landscape scale) described above. Each nest-site category was coded as a dummy variable, with the relevant habitat

Table 2. Mean productivity per breeding pair in the four study areas from 2007 to 2009. Number of pairs in each sample follows in parentheses. Mean values \pm standard error are given for all years and all sites.

	2007	2008	2009	All years
Slieve Aughties	0.4 (9)	1.4 (11)	0.9 (12)	0.9 \pm 0.2
Ballyhouras	0.9 (11)	1.4 (13)	1.2 (9)	1.2 \pm 0.2
Kerry	2.5 (13)	2.1 (17)	0.9 (14)	1.8 \pm 0.2
West Clare	2.3 (10)	2.0 (11)	1.3 (10)	1.9 \pm 0.2
All sites	1.6 \pm 0.2	1.7 \pm 0.2	1.0 \pm 0.2	1.5 \pm 0.1

category being represented by 1 and all other habitats represented by 0. Initial candidate models included all possible combinations of habitat variable, study area and year, with and without first- and second-order interactions. These models were ranked according to AICc (Akaike information criterion corrected for small sample sizes, calculated using the R package 'AICcmodavg'), the top model being the one with the lowest AICc score. The strength of inference for each model depended on its Δ AICc score, whether and to what extent the confidence intervals (CI) of the model parameters overlapped with zero, and the magnitude of the biological effects estimated by the model over the relevant conditions of interest in the study. A deviance-based r^2 value (r_d^2) was calculated for each of the top models, following White and Burnham (1999). This is a measure of the variation accounted for by each model of interest, relative to the variation accounted for by a general model containing all terms of interest. First, the residual deviance (D) was calculated for three models: the null (intercept only) model (MN), the model being tested (MT) and a general model (MG) containing all main and first-order interaction terms in the model set. ANODEV was then calculated as:

$$r_d^2 = (D_{MT} - D_{MG}) / (D_{MN} - D_{MG})$$

We addressed the potential for over-dispersion due to unmeasured influences on response variables associated with territory using an estimated measure of over-dispersion, \hat{c} . Values of $\hat{c} > 1$ indicate over-dispersion and can be used to inflate AIC values and the variance of model parameters (Bishop *et al.* 2008). Values of $\hat{c} < 1$ indicate that the inclusion of data from the same territories in multiple years did not result in over-dispersion (Bishop *et al.* 2008). We generated 10 000 bootstrapped sets of data by sampling of territories with replacement from the original dataset and specified a moderately well-parameterised nest survival model with relatively low deviance (survival \sim study area \times 2nd rotation in 2 km) using the nest survival procedure in MARK 6.1. We estimated daily survival rates according to this model for each bootstrapped dataset. The mean and standard deviation of all bootstrapped estimates of survival were calculated as mean_1 and sd_1 . We then calculated the mean and standard errors of the estimates of daily survival rates from a run with the original data as mean_2 and se_2 , and estimated \hat{c} as $\text{sd}_1^2 / \text{se}_2^2$.

A similar procedure was used to calculate \hat{c} for fledged brood size, using a Poisson GLM (fledged brood size \sim study area + 1st rotation nest habitat) in R.2.13.1.

RESULTS

The outcomes of 140 nests from the four study areas were recorded between 2007 and 2009. Among the study sites, average productivity was lowest in the Slieve Aughty Mountains (henceforth Slieve Aughties) and highest in the Kerry and West Clare (Western) sites (Table 2). Linear regression of the productivity randomisations against observed productivity values indicated that 70% of the variation in overall breeding productivity was explained by nest survival. There was no significant difference in the estimated size of successfully fledged broods between those estimated as the number of chicks present on the final visit (2.6 ± 0.1 young, $n = 50$) and those estimated as the number of juveniles counted post-fledging (2.3 ± 0.1 young, $n = 33$; Mann–Whitney $U = 901.5$, $P = 0.24$).

Estimates of \hat{c} for both nest survival and fledged brood size models were < 1 (0.90 and 0.89, respectively), indicating no overdispersion in either dataset. AICc scores, weights and deviance are given for the top 20 nest survival and fledged brood size models in Table 3. Parameter estimates, 95% CI around these parameters, and ANODEV (r_d^2) values are presented for the parameters of all models that are within 2 of the AICc score of the top model, and with lower AICc scores than the null model, in Table 4.

Of the top 23 survival models, all but one included study area, strongly indicating that this variable was related to nest success (Table 3). The top model, for which r_d^2 was 0.17, also included area covered by second-rotation pre-thicket within 2 km of the nest and the interaction between this variable and study area. Parameter estimates for this interaction term indicate that the area of second-rotation pre-thicket at a landscape scale was negatively related to nest success in the Slieve Aughties but that there is no evidence of a similar relationship in the other two study areas (Table 4). The relationship between second-rotation pre-thicket within 2 km and the daily survival rates estimated by this model varied between the three study areas (Fig. 2). No survival models containing total forest cover, closed-canopy forest cover,

Table 3. Summary properties of (a) MARK nest survival models and (b) fledged brood size models, with AIC weights of 0.02 or more within their model sets. The explanatory variables included in each model are listed in the Formula column as follows: Area (three-level factor coding for study area); Year (three-level factor coding for study year); habitat variables ending in ‘_2 km’ coding for the proportion of land within 2 km of the nest occupied by all forests (Forest), 1st rotation pre-thicket (1str), 2nd rotation pre-thicket (2ndr), closed-canopy forest (Closed), intensively managed grassland (IG), heath/bog habitats (HB) and rough grazing (RG); and two-level habitat variables describing whether the nests were located in forest of any type (Forest), 1st rotation forests of all ages (FirstRo), 2nd rotation forests of all ages (SecondRo), heath and bog habitats (HB) and non-peatland areas of open scrub (Scrub). Where two variables are separated by an asterisk, the interaction between these variables was included in the model. Variables separated from one another by a plus sign indicate that only the main effects were included in the model. The other columns represent K (the number of parameters in the model), AICc, AIC weight (Wt), the cumulative AIC weight (Cum. Wt), residual deviance, and the pseudo- r_d^2 .

Model	K	AIC _c	Wt	Cum. Wt	Deviance	r_d^2
(a)						
~Area * 2ndr_2 km	6	363.2	0.11	0.11	351.2	0.17
~Area + HB_2 km	4	363.9	0.08	0.20	355.9	0.12
~Area	3	365.2	0.04	0.24	359.2	0.08
~Area + SecondRo	4	365.3	0.04	0.28	357.3	0.10
~Area * 2ndr_2 km + Year	8	365.5	0.04	0.31	349.5	0.18
~Area + 2ndr_2 km	4	365.6	0.04	0.35	357.6	0.10
~Area + Year * HB_2 km	8	365.7	0.03	0.38	349.7	0.18
~Area + Forest	4	365.7	0.03	0.42	357.7	0.10
~Area + Year * RG_2 km	8	365.8	0.03	0.45	349.7	0.18
~Area * Year + SecondRo	10	366.1	0.03	0.47	346.0	0.22
~Area + HB	4	366.2	0.03	0.50	358.2	0.09
~Area + RG_2 km	4	366.5	0.02	0.52	358.5	0.09
~Area + Forest_2 km	4	366.6	0.02	0.54	358.6	0.09
~Area * HB_2 km	6	366.7	0.02	0.56	354.6	0.13
~Area + Scrub	4	366.8	0.02	0.58	358.8	0.09
~Area * Year + HB_2 km	10	366.8	0.02	0.60	346.8	0.21
~Area + IG_2 km	4	367.1	0.02	0.62	359.1	0.08
~SecondRo	2	367.2	0.02	0.63	363.2	0.04
~Area + Closed_2 km	4	367.2	0.02	0.65	359.2	0.08
~Area + 1str_2 km	4	367.2	0.02	0.66	359.2	0.08
~Area + FirstRo	4	367.2	0.02	0.68	359.2	0.08
~Area + Year + HB_2 km	6	367.3	0.02	0.70	355.3	0.12
(b)						
~FirstRo	2	252.3	0.08	0.08	31.7	0.12
~Area + FirstRo	4	252.9	0.06	0.13	27.9	0.26
~RG_2 km	2	253.1	0.05	0.18	32.5	0.09
~HB	2	253.4	0.05	0.23	32.7	0.08
~1	1	253.4	0.04	0.27	34.9	0.00
~2ndr_2 km	2	253.5	0.04	0.31	32.9	0.07
~Forest_2 km	2	253.6	0.04	0.36	32.9	0.07
~Area	3	253.6	0.04	0.40	30.8	0.15
~Forest	2	253.8	0.04	0.43	33.1	0.06
~HB_2 km	2	253.8	0.04	0.47	33.1	0.06
~Area + 1str_2 km	4	254.3	0.03	0.50	29.3	0.20
~Area + HB	4	254.9	0.02	0.52	29.9	0.18
~Year + FirstRo	4	255.1	0.02	0.54	30.1	0.17
~Area + RG_2 km	4	255.2	0.02	0.56	30.2	0.17
~IG_2 km	2	255.3	0.02	0.57	34.7	0.01
~SecondRo	2	255.3	0.02	0.59	34.7	0.01
~Area + Scrub	4	255.4	0.02	0.61	30.4	0.16
~Area*Scrub	4	255.4	0.02	0.62	30.4	0.16
~Closed_2 km	2	255.4	0.02	0.64	34.8	0.00
~Area + Forest	4	255.5	0.02	0.65	30.5	0.16
~Scrub	2	255.5	0.02	0.67	34.9	0.00
~Year + RG_2 km	4	255.5	0.02	0.68	30.5	0.16
~1str_2 km	2	255.5	0.02	0.70	34.9	0.00

Table 4. Parameter estimates, standard errors (SE) and lower and upper confidence intervals (LCI and UCI, respectively) for the top models among (a) nest survival models and (b) fledged brood size models. See Table 3 for an explanation of codes. Wherever models include one or more factors, level 1 of each factor (as well as that of any interactions) are incorporated within the intercept, as is standard practice in GLMs. Area level1 (incorporated in the intercept) is the Slieve Aughties, Area level2 is the Ballyhouras, and Area level3 is the Western study area.

Parameters	Estimate	SE	LCI	UCI
(a)				
~Area * 2ndr_2 km				
(Intercept)	5.27	0.61	4.07	6.46
Area level2	-0.51	0.82	-2.12	1.10
Area level3	-0.25	0.68	-1.58	1.08
2ndr_2 km	-10.82	4.11	-18.87	-2.77
Area level2:2ndr_2 km	10.72	4.45	1.99	19.45
Area level3:2ndr_2 km	4.18	9.82	-15.07	23.44
~Area + HB_2 km				
(Intercept)	3.43	0.37	2.71	4.14
Area level2	1.18	0.42	0.35	2.01
Area level3	0.89	0.31	0.28	1.50
HB_2 km	2.13	1.22	-0.26	4.53
~Area				
(Intercept)	3.97	0.23	3.52	4.43
Area level2	0.76	0.36	0.05	1.47
Area level3	0.89	0.31	0.29	1.50
(b)				
~FirstRo				
Intercept	0.96	0.07	0.81	1.10
~FirstRo level2	-0.45	0.27	-1.02	0.04
~Area + FirstRo				
Intercept	0.90	0.18	0.52	1.23
Area2	-0.17	0.24	-0.64	0.30
Area3	0.17	0.20	-0.21	0.58
FirstRo level2	-0.43	0.27	-1.00	0.06
~RG_2 km				
Intercept	0.76	0.13	0.50	1.00
~RG_2 km	1.35	0.86	-0.37	3.01
~HB				
Intercept	0.84	0.09	0.66	1.01
~HB level2	0.22	0.15	-0.07	0.50

non-forest habitat cover or any nest-site-scale habitat variables had a lower AICc score than the model containing only study area. Moreover, in all models apart from the top model, only the parameter estimates for study area did not overlap with zero (Table 4).

Only four of the fledged brood size models had a lower AICc score than the null model, and r_d^2 for the top model was 0.12 (Table 3). The 95% CI for all parameter estimates contained in these models overlapped with zero (Table 4). We therefore have little confidence that any of these models

describe the variation in fledged brood size between nests any better than the null model.

DISCUSSION

We found no effect of either total forest cover or closed-canopy forest cover on the measures of breeding success we examined. However, nest success in one study area was negatively related to the proportion of pre-thicket second-rotation cover in the surrounding landscape. Model estimates of daily survival rates (DSRs) in this area varied from 0.99 (95% CI 0.98–1.00) when this habitat was absent to 0.94 (95% CI 0.86–0.97) when it was at its most abundant (Fig. 2). Over an 80-day nesting period, these DSRs translate into overall nest survival probabilities of 0.66 (95% CI 0.26–0.88) and 0.01 (95% CI 0.00–0.12), respectively. There was no evidence for a similar effect of second-rotation forest (or any other habitat) at the nest-site scale on nest success. Recent studies have shown that second-rotation pre-thicket forest can be strongly preferred as a breeding habitat, both in Ireland (Barton *et al.* 2006, Wilson *et al.* 2009a) and in parts of western Scotland (Haworth & Fielding 2009), even when it is less abundant than other nesting habitats. Moreover, controlling for habitat at the nest-site scale, nesting Hen Harriers select landscapes with a relatively high proportion of second-rotation pre-thicket forest cover (Wilson *et al.* 2009a). In the current study, there seemed to be plenty of alternative nest-sites available to many of the Hen Harriers that chose to nest in landscapes with relatively high levels of second-rotation pre-thicket forest, particularly in the Slieve Aughties where the negative relationship between this habitat and breeding success was apparent.

Hen Harriers can breed in pre-thicket forests in both their first and second rotations (Wilson *et al.* 2009a). However, as the Irish forest estate matures, an increasing proportion of new forests will be converted to second-rotation habitat by clearfell harvesting and replanting. As can be seen from Table 1, the average level of forest cover within 2 km of Hen Harrier nests in the different study sites ranged from 42 to 61% and, eventually, all of this forest will enter into the second and subsequent rotations. The value of second-rotation forests for Hen Harriers is therefore likely to become increasingly important for this species, although only about a quarter of each rotation is spent in the pre-thicket stage, during which forests are

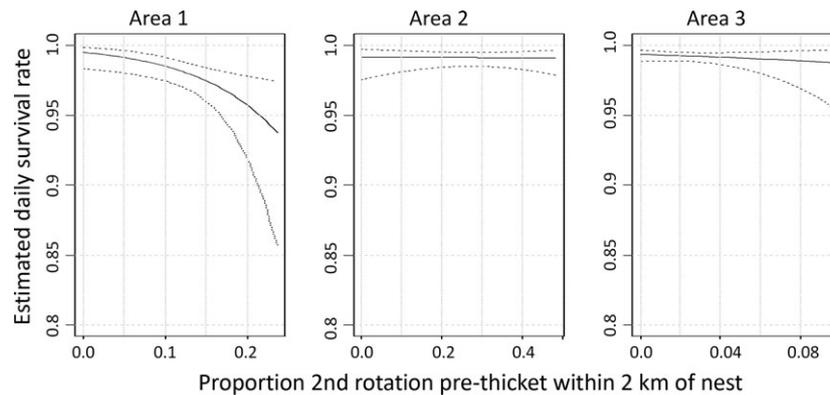


Figure 2. Daily survival rates estimated by the top model for nest survival (see Tables 3 and 4) plotted against the proportion of land within 2 km occupied by second-rotation pre-thicket forests, for each of the three study areas. Estimated values are represented by the solid black lines, with upper and lower 95% CI represented by the broken lines on either side. Area 1 is the Slieve Aughties, Area 2 is the Ballyhouras, and Area 3 is the Western study area.

most intensively used by Hen Harriers for nesting and foraging (Madders 2003, Wilson *et al.* 2009a, Haworth & Fielding 2009).

Buffer effects can result in differences in breeding density and performance between habitats, due to non-preferred sites being occupied last and by the lowest quality individuals. However, given that second-rotation pre-thicket has been shown by previous studies to be strongly preferred by Hen Harriers, one would not expect lower breeding success to result from buffer effects. In this context, the lower breeding success experienced by Hen Harriers breeding in landscapes with high levels of second-rotation pre-thicket described here are counter-intuitive – one might expect that Hen Harriers breeding in such landscapes would be more successful than in other habitats. It should be emphasized that these relationships were not consistent across all study areas and that, over the whole dataset, the model including both second-rotation pre-thicket and study area explained just 9% more variation than the model with study area alone (Table 3). Moreover, we cannot be certain that these relationships were causal, but even if they were, it is likely that second-rotation forests are often valuable for Hen Harriers in Ireland, enabling them to breed in areas where they would otherwise be scarcer or absent.

Nevertheless, it is worth considering the possibility that a preference for second-rotation pre-thicket could, at least in some situations, be disadvantageous to Hen Harriers. Preferences for sub-optimal nest locations have previously been implicated in decreased breeding performance of

harriers. Hen Harriers and Montagu's Harriers *Circus pygargus* breeding in Spain and France frequently nest in arable fields where many pairs would, in the absence of conservation intervention, suffer high rates of nest failure due to crops being harvested before young have fledged (Arroyo *et al.* 2002, Millon *et al.* 2002). This kind of mismatch between preferences for and value of habitats has been described as an ecological trap (Gates & Gysel 1978, Kokko & Sutherland 2001) and has been observed in several species. In North America, Olive-sided Flycatcher *Contopus cooperi* is adapted to nesting in post-fire forests but has taken readily to nesting in clearfelled areas, where it experiences lower breeding success due to elevated rates of nest predation (Robertson & Hutto 2007). A similar situation is also plausible for Hen Harriers, which have existed for centuries in Irish landscapes with little or no forest cover. Young second-rotation forests provide dense vegetative cover that is attractive to nesting Hen Harriers (Wilson *et al.* 2009a). However, there may be factors associated with this habitat that negate any advantage conferred by nesting cover but that Hen Harriers do not take into account during nest-site selection. There are several ways in which the habitat around nests could impact on breeding success. Studies in Orkney have shown that Hen Harrier breeding success can be affected by availability of food both before and during the nest period (Amar & Redpath 2002, Amar *et al.* 2003, 2005). If the abundance or availability of prey is lower in pre-thicket second rotation than in alternative hunting habitats, Hen Harriers breeding

in landscapes with a high proportion of this habitat could be disadvantaged. The presence of woody debris left after forest operations might result in access to by harriers to prey being more restricted in young second-rotation forests than in other habitats.

Microtine rodents make an important contribution to the diet of breeding Hen Harriers in many parts of Europe (Millon *et al.* 2002, Redpath *et al.* 2002, Amar & Redpath 2005) including our study areas (O'Donoghue 2010). Bank Vole *Myodes glareolus* is not native to Ireland but is found at high densities in young forest plantations (Smiddy & Sleeman 1994, Madders 2003) and is present in all of our study areas (Meehan & Hayden 2006). However, its abundance is probably lowest in the Slieve Aughties, which is furthest from the site of its introduction in the 1960s (Smal & Fairley 1984). It is possible that differences in prey assemblages reduced the quality of second-rotation pre-thicket habitat in the Slieve Aughties relative to other study areas. This could help to explain the inter-area difference in the relationship between this habitat and breeding success.

Our data support previous studies showing nest success to be more important than brood size in determining overall variation in Hen Harrier breeding success between different years and populations (e.g. Etheridge *et al.* 1997, Whitfield & Fielding 2009). Food supply can influence breeding success but several effects of food supply on reproduction (e.g. clutch size and reductions in the numbers of eggs and chicks prior to fledging; reviewed in Chamberlain *et al.* 2009, and Martin 1987) are related to number of young fledging from successful nests. This did not differ either between study areas or in relation to cover of second-rotation pre-thicket forest. It is therefore more likely that the elevated rates of nest loss associated with habitat and study area are due to differences in nest predation or abandonment, which typically result in complete loss of broods (Skutch 1985, Yanes & Suarez 1996).

One factor that might lead to nest predation being more prevalent in landscapes with a high proportion of second-rotation forest is the positive relationship between this variable and the density of internal forest edges. Many studies have associated high levels of nest loss and predation with edge habitats (e.g. Weldon & Haddad 2005, Hoover *et al.* 2006, Pedersen *et al.* 2009). Also, the proportion of second-rotation forest is highest in

areas where plantation forests have been established for the greatest length of time. Such areas may support greater concentrations of Hen Harrier nest predators such as foxes, corvids and mustelids, densities of which can increase after the creation of forest and forest-edge habitats (Chadwick *et al.* 1997, Smedshaug *et al.* 2002, Carey *et al.* 2007). Pine Marten *Martes martes*, a forest mustelid which opportunistically preys on bird eggs, is of particular interest in this regard. Pine Marten abundance has increased in Ireland during the past three decades, and is greatest in areas where suitable habitat such as conifer forest has existed longest (National Parks and Wildlife Service 2008). If nest success is affected by predators such as Pine Marten, this could also help to explain the difference in the apparent effect of second-rotation pre-thicket between study areas, as the abundance of this species is probably higher in the Slieve Aughties than in our other study areas (O'Mahony *et al.* 2006, D. O'Mahony pers. comm.).

As well as the possibility that forests support higher densities of nest predators than other habitats, it is also possible that Hen Harriers breeding in forested areas may be less able to assess the threat to nest success posed by predator populations. In open habitats, predators may be more visible, allowing resident birds to gain an impression of predator activity in different areas. Conversely, ground-based predators in forested areas will spend much of their time under canopy cover and out of sight of aerial birds, making it harder for Hen Harriers to assess the threat of nest predation. In addition to increased predation risk, longer-established forests also tend to have more developed networks of roads, and to be more heavily utilized for recreation, which could increase rates of nest failure due to human-related disturbance (Ruddock & Whitfield 2007). A recent analysis carried out on a subset of the data in this study found that failure rate was negatively related to distance from the nearest track (O'Donoghue 2010).

CONCLUSIONS

Afforestation, the harvesting and replanting of existing forests, and non-forest factors such as wind farm development and agricultural land abandonment will continue to alter the landscapes occupied by Hen Harriers in Ireland. In the face of such change it is increasingly important to understand the habitat requirements of Hen Harriers, to

ensure that the areas they occupy remain suitable for them. Investigations into prey populations (O'Donoghue 2010) and foraging behaviour of breeding Hen Harriers (Wilson *et al.* 2009b) are ongoing. Another potentially important topic for investigation is the effect of habitat on the numbers and activity of predators. Such research should help to clarify the interactions between food availability, foraging preferences, predation and landscape composition, and their consequences for breeding populations of Hen Harriers.

The area-specific relationship between breeding success of Hen Harriers and second-rotation pre-thicket forests serves to illustrate that, especially in anthropogenically altered landscapes, habitat preferences do not necessarily reflect habitat quality. Such a mismatch might be expected where individuals are colonizing areas occupied by habitat types that have not regularly been encountered by their species in the past, or where the area already occupied by a population undergoes novel habitat changes. Both of these situations are plausible consequences of human-induced environmental change, and could lead to declines in species of high conservation concern. The causes of such declines are likely to be harder to identify than more obvious threats, such as the destruction or deterioration of a species' optimal habitat. Successfully diagnosing such mismatches will require detailed understanding of the determinants of habitat quality, and its consequences for individual fitness.

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