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Breeding habitat preferences and reproductive success of Northern Goshawk (*Accipiter gentilis*) in exotic Eucalyptus plantations in southwestern Europe

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Abstract

With ongoing degradation of natural forests and spread of forest plantations, plantations must play an increasingly important role in biodiversity conservation. Study of habitat selection and reproductive success of surrogate species in plantations can guide forest management decisions for increasing biodiversity. In this paper we studied the suitability of exotic Eucalyptus plantations managed at low intensity in northwestern Spain as breeding habitat for Northern Goshawk (*Accipiter gentilis*), a top predator frequently considered a surrogate species in conservation.

Goshawks showed high breeding density, high reproductive success and a regular spatial distribution of nesting territories. Territoriality was the most important determinant of habitat selection. Goshawks selected extra-mature Eucalyptus trees in areas of high structural complexity (high tree density, tree species richness, and number of tree strata) in the most heterogeneous forest stands (old-mixed Eucalyptus). Reproductive success decreased with increasing local density of breeding pairs, but reproductive success was not related to structural characteristics of nest stands.

The studied plantations provided a suitable breeding habitat for Goshawks. The birds preferred to nest in large Eucalyptus trees with appropriate structure in their immediate surroundings. The strong preference of Goshawks for structurally mature forest patches may make them useful as a surrogate species for assessing the ability of forest management practices to promote overall biodiversity in exotic Eucalyptus plantations exploited at low intensity.

Keywords: biodiversity surrogate; density trap; mature plantation; raptor; smallholding forestry; territoriality.

1. Introduction

Deforestation and forest degradation, major causes of global forest biodiversity loss (IUFRO 2014), can be counteracted to some extent by forest plantations, which should play an increasingly important role in the provision of ecosystem services and biodiversity conservation (Brockerhoff *et al.* 2008, Brockerhoff *et al*. 2013, Trumbore 2015). While global area of natural forest area has declined by 6% between 1990–2015, forest plantation area has increased by 66%, and it accounted for up to 7% of total forest area in 2015 (Keenan *et al*. 2015, FAO 2015). Most forest plantations (56%) are located in temperate latitudes, with more than half of these situated in Europe (Payn *et al*. 2015), where nearly half of plantations, mainly in central and southern regions of the continent, are made up of exotic species. In Spain and Portugal, the exotic species *Eucalyptus spp*. is particularly important; its planted area has reached approximately one million ha, and it continues to increase (Martín-Vallejo 2015).

The effects of forest plantations on biodiversity are still not fully understood (Bremer & Farley 2010). Many forest plantations appear to be less diverse than natural forests, with a simpler composition and structure, particularly in even-aged, single-species stands involving exotic species managed in short rotation periods (Martínez-Jáuregui *et al*. 2016). On the other hand, certain plantations can provide a valuable habitat for a wide variety of taxa, including native, threatened and top predator species such as forest raptors (Petty 1998, Sarasola & Negro 2006, Speziale & Lambertucci 2013, Olano *et al*. 2016). Analysis of plantations able to maintain species of conservation interest can help to identify forest management practices that favour biodiversity within plantations.

Top predators, such as forest raptors, are often associated with higher species richness because they usually select large-sized patches of habitat with relatively high primary productivity, structural complexity and spatial heterogeneity (Sergio *et al*. 2008). For this reason, dominant raptors can serve as surrogate species to represent the status of various species (Burgas *et al*. 2016) on a plantation and thereby inform comprehensive planning designed to support multiple species. Study of the relationship between breeding raptors and the composition and structure of forest plantations can help identify plantation characteristics that provide good-quality habitat for these species (Brockerhoff *et al*. 2008). Forest management can then focus on improving the habitat for surrogate raptors, bringing benefits to a wider range of species and thereby improving overall biodiversity.

Habitat selection is a behavioural process based on innate or learned preferences through which individuals choose a habitat to settle, forage and/or reproduce (Robertson & Hutto 2006). Habitat selection can be identified by the disproportionate use of some habitats compared to their availability in the environment, and it reveals essential requirements of the focal species (Johnson 1980, Orians & Wittenberger 1991). Breeding habitats should receive special attention because their availability is linked to long-term persistence of local populations (Boulinier *et al.* 2008). For birds, choosing nest location is critical because the nest must ensure concealment and protection during the long period from incubation to dispersal of fledglings (Orians & Wittenberger 1991). Prevailing theory suggests that habitat preferences of animals are adaptive, such that fitness is higher in preferred habitats (Robertson & Hutto 2006, Fuller 2012). Thus, we aimed to assess raptor habitat quality in forest plantations by focusing on breeding habitat selection and relating the observed habitat preferences to key demographic parameters such as reproductive success (Wilson *et al.* 2012).

In this study we analysed the suitability of exotic Eucalyptus plantations as a breeding habitat for top predators in northwestern Spain, using the Goshawk (*Accipiter gentilis*) as a model. We explored breeding habitat preferences of Goshawks at several spatial scales, asking whether they would select mature-like sites in Eucalyptus plantations, similar to their habitat preferences in other forest types. Then we assessed whether the observed breeding habitat preferences had adaptive value by testing whether they correlated with reproductive success. We expected that reproductive success would be greater, reflected in earlier laying dates and greater fledgling production, in preferred habitats. Identifying Goshawk breeding habitat preferences and understanding their relationship to reproductive success may guide forest management decisions to favour this top predator, thereby generating broader benefits for overall biodiversity in exotic Eucalyptus plantations.

2. Material and methods

2.1. Study area

The study area (183 km^2) is located in northwestern Spain (Morrazo peninsula, Galicia, 42º 20' N, 8º 47' E). The climate is wet temperate oceanic (*Cfb* Köppen type) with annual average precipitation of 1402 mm and temperature of 14.2 ºC (Cortizas & Alberti 1999), and frequent wind and rain storms in winter and spring (Cabalar 2005). The landscape is rugged, in that there are hills and valleys, with a mountainous axis with dominant direction SW-NE that divides the peninsula in a North and a South face. Average altitude is 169 m (range 0–628 m). The upper parts are occupied by gorse (*Ulex europaeus*) and rocky outcrops. Forests form a more or less continuous mass dominating the steeply sloping hillsides. Some small isolated forest patches within the agricultural matrix are also present. Lower parts of the hillsides and valley bottoms have been intensively cultivated and urbanised (Figure A1 and Table A1 in the Appendix A). Human population density is high (480 inhabitants km^{-2}).

Forest formations cover up to 51% of the study area, mainly exotic Eucalyptus plantations (*Eucalyptus globulus*), which began to be planted at the end of the 19th century and nowadays represent 85% of the total forest area (IFN3 1997–2007, Manuel- Valdés & Gil-Sánchez 2006). The region comprises primarily private smallholding, giving rise to overall rudimentary, low-intensity forest management (Ambrosío *et al*. 2003). Each forest owner generally has fewer than 1.5 ha of land, often distributed across several plots, 80% of which are smaller than 0.5 ha. Intensity of exploitation and mechanisation are low and silvicultural and phytosanitary treatments are rarely applied. Logging usually takes the form of clear-cuttings affecting small areas. The resulting forest landscape is a heterogeneous mosaic of small Eucalyptus plantations with different origins (plantation, resprouting), age and tree density, and rotation periods. Many abandoned parcels with extra-mature trees are present, often of unknown ownership (Ambrosío *et al*. 2003, Álvarez-Taboada 2005, IFN3 1997–2007). Within these plantations, native tree species such as Pedunculate Oak (*Quercus robur*) and Laurel (*Laurus nobilis*), and other formerly introduced tree species such as Chestnut (*Castanea sativa*) and Pine (*Pinus pinaster*) are common, appearing clumped in certain plots, or ranged as tree lines along the boundaries between plots, or scattered as isolated individuals immersed within the Eucalyptus stands.

2.2. Study species

Goshawk (*Accipiter gentilis*) is a medium-sized diurnal forest raptor distributed across Europe and more widely globally in a Holarctic pattern. It is a generalist top predator that shows strong territorial behaviour with respect to both breeding territory and nest sites (Kenward 2006). Goshawks use a wide range of habitats for nesting, including conifer and hardwood forests, and forest plantations (Kenward 2006). They show preference for nesting in mature areas of extensive forests, although they also use small patches of woodland in fragmented agroforestry landscapes (Rutz *et al.* 2006). This species is sensitive to human activities, and it has been used as an ecological indicator of changes in ecosystems and effects of forest management (Crocker-Bedford 1990, Reynolds *et al.* 1992, Widen 1997, Penteriani & Faivre 2001, Mc Grath *et al.* 2003, Selås *et al.* 2008). Nest sites of Goshawks have also been associated with higher levels of biodiversity of several taxa, making them useful as a surrogate species in conservation (Sergio *et al.* 2006, Burgas *et al.* 2014, 2016).

2.3. Nest searches, laying dates and reproductive success

For the period 2004–2011, the entire forest area was systematically surveyed to locate all Goshawk nests (Pérez-Camacho *et al.* 2015, Rebollo *et al.* 2017a). Goshawk territories usually contain several nests that are used alternately over the years (Squires & Reynolds 1997). Each nest was visited periodically during the breeding season to determine its occupancy (presence of breeders or their signs), presence of eggs (incubating female) or nestlings. On the basis of these observations, nests were classified, respectively, as occupied nests, active nests and successful nests.

Nestlings of successful nests were counted, measured and banded when they were older than 20 days ($n = 263$; mean [±SD] nestling age at banding, 24.6 ± 4.2 days). The minimal width of the tarsus was used to sex the chicks (males, <6.5 mm; females, >6.5 mm; Kenward 2006) and the length of the seventh primary feather was used to estimate their age (Mañosa 1994). Laying dates were estimated by subtracting the incubation time for a single egg (38 days) from the hatching date of the oldest nestling (Kenward 2006). Earlier laying dates are related to greater reproductive success (Newton 1998, Byholm *et al*. 2002, Lehikoinen *et al*. 2012). The number of nestlings at banding was considered an indicator of fledging success (*i.e*. number of fully feathered young voluntarily leaving the nest for the first time; Steenhof & Newton 2007) since the highest mortality of chicks usually occurs around hatching (Kostrzewa & Kostrzewa 1990, Mañosa 1991, Byholm 2005).

We calculated G (*sensu* Brown and Rothery 1978) as an index of nest spacing regularity. This index ranges between 0–1, with values >0.65 indicating increasing regularity and suggesting the existence of territoriality.

2.4. Breeding habitat selection

Goshawk breeding sites (all active nests in 2004–2009, *n* = 64) and sites selected at random (reference plots representing habitat availability, *n* = 80) were compared at various spatial scales following a site-attribute design *sensu* Garshelis (2000). The reference plots were selected by generating random coordinates within the forest area, after excluding forest patches smaller than 4 ha because Goshawks in the study area do not use them for nest placement (Rebollo *et al.* 2017a). Reference plots that fell within occupied territories were not excluded. Based on the random coordinates, we located the closest appropriate tree to support a nest, which was defined as a tree with a diameter at breast height [DBH] ≥50 cm for Eucalyptus or ≥30 cm for Oaks and Pines. Goshawks in the study area rarely used smaller trees for placing the nest. Territory identity of the reference plots was assimilated to that of the nearest Goshawk territory in statistical analyses in order to prevent spatial autocorrelation.

Habitat selection occurs at multiple spatial scales, with each scale potentially showing functional significance and relation to fitness (Orians & Wittenberger 1991, Tapia *et al*. 2007). We considered the following spatial scales (Fig. 1): (1) the nest tree and its surroundings, including the nest site (sampled in a circular plot of radius 10 m around the nest tree) and nest stand (50 m radius, sampled in three circular plots of radius 10 m, averaging sampled habitat variables among the three plots.); (2) the post-fledging family area (PFA) surrounding the nest stand, which is the area used by the family group from the time the young fledge until they no longer depend on adults for food (Tapia *et al*. 2007). PFA size, which varies in the literature from 60 to 200 ha depending on the specific definition of PFA used and local environmental conditions (Squires & Kennedy 2006), was defined here to be 80 ha (~500 m radius around the nest tree) based on the high Goshawk breeding density in the study area. And (3) nesting territory, which is the area around the nest defended by the breeding pair against other Goshawks and showing little or no overlap with neighbouring territories (Squires & Reynolds 1997). Nesting territories were defined as circular territories with a radius of 1100 m around the nest tree, which roughly coincides with half the average distance between neighbouring active nests in the study area (2234 ± 162 m; Martínez- Hesterkamp *et al*. 2015, Rebollo *et al.* 2017a). Territoriality is a necessary component of any habitat model involving territorial breeding birds because it inhibits the use of areas around active nests (Reich *et al*. 2004).

Goshawk breeding habitat was described using 46 variables of forest composition and structure, topography, land cover types, and indicators of potential human disturbances (Tables A1 and A2 in the Appendix A). Forest sampling was carried out in January-February 2010, before the beginning of the breeding season, to avoid disturbances to breeding Goshawks. Variables at the PFA and nesting territory scales, and other landscape variables were acquired from a geographic information system (ArcGis 9.3, ESRI) with cartographic information from the Territorial Information System of Galicia (SITGA-IDEG, Xunta de Galicia). Additionally, a layer of land cover types was created from photointerpretation of satellite images (PNOA, 2009), from which 18 land cover types were defined (Table A1). We conducted a ground-truthing survey in April-May 2011 visiting all UTM 1×1 Km^2 grids of the study area to verify the classification of land cover types, paying special attention to the classification of forest types (200 grids, mean 36 minutes per grid). We also determined nearest-neighbour distance (NND) as an indicator of territorial behaviour (Newton *et al*. 1977, Rebollo *et al.* 2017a). The NND was measured as the distance from each nest/reference tree to the centroid of the nearest neighbour breeding territory, the centroid being the mean geographic position of the alternate nests of each breeding territory. This measure underestimates the NND of the active nests since all Goshawk territories are not occupied every year, but it allows comparing this variable between the nest and the reference plots. Additionally, it is a conservative measure because Goshawk territories can be defended even when egg laying is not achieved.

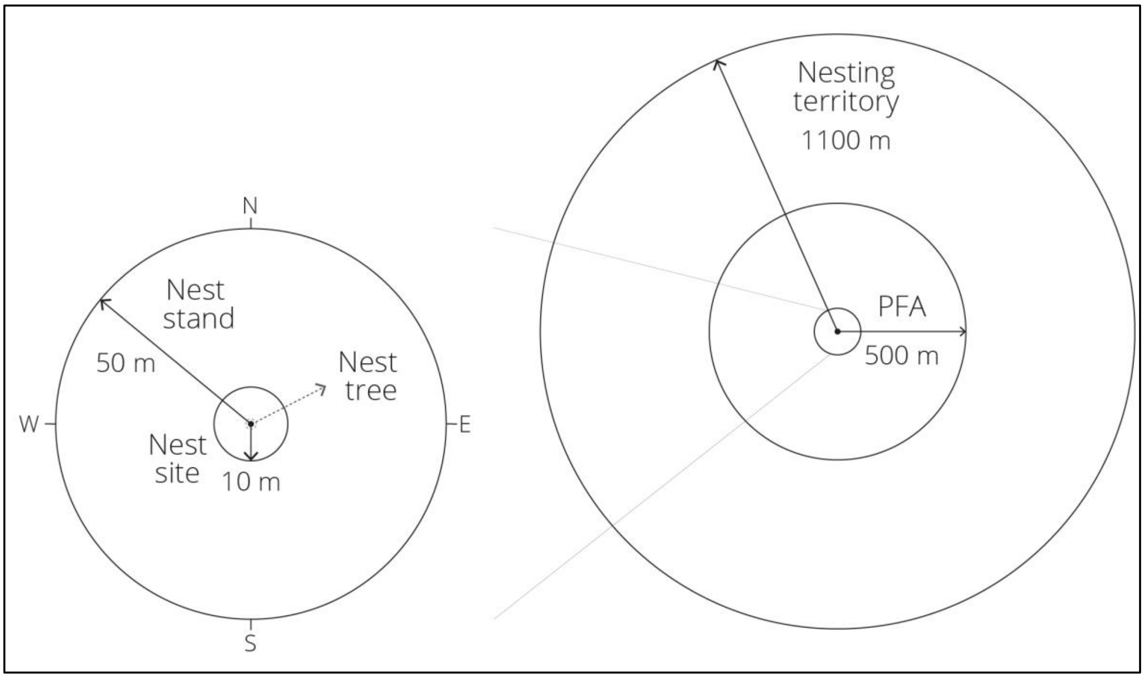

Figure 1. Scales of analysis of Goshawk breeding habitat preferences (right) and forest structure sampling design at the nest stand scale (left).

2.5. Statistical procedures

We used binomial (logit link) generalised linear mixed models (GLMMs) to determine patterns of Goshawk breeding habitat selection simultaneously at the three spatial scales (cross-scale analysis). Territory identity was specified as a random factor to control the lack of independence associated with the habitat preferences of the same breeding pairs in successive years.

We selected the predictor variables in the GLMMs using a three-step variable reduction procedure. In the first step, the mean of each habitat variable was compared between breeding sites and reference plots using the Mann-Whitney U test with a significance cut-off of $p \leq 0.05$. In the second step, variables satisfying this cut-off were included in principal component analysis (PCA), regardless of the scale to which they related. This early filtering of potential predictor variables was conducted to avoid, as much as possible, negligible information regarding nest location in the landscape. Discarded variables won't be thus interpreted lately in the subsequent regression analyses when considering PCA axes as complex predictor variables. We considered that a variable was summarised by a PCA component if the correlation between the two was associated with $r \geq 0.5$. In subsequent analyses, the first two PCA components were used as predictors in GLMMs. In the third step of variable reduction, Pearson's correlation analyses were performed with variables not summarised by PCA components. In the case of strongly correlated pairs of variables ($r > 0.6$), both variables were considered to estimate a single underlying factor (Green 1979), so only the variable showing greater significance in the Mann-Whitney U test of the first step was incorporated into subsequent analyses.

GLMMs were built with all additive combinations of the former selected variables and a model selection procedure based on the Akaike information criterion corrected for small sample sizes (AICc). Models with ΔAICc ≤ 2 have substantial *a priori* support (set of confidence models). When no model in the set of confidence models was clearly better than the others based on Akaike weights (best model w < 0.9), a weighted model averaging procedure was used to discern the relative importance of each predictor variable (Burnham & Anderson 2002, Gibson *et al*. 2004).

To study the relationships between breeding habitat preferences and reproductive success, we used mixed models containing year and territory identity as random factors (Byholm & Kekkonen 2008). Habitat variables that received support in the analysis of habitat selection were used as predictors. Two indicators of reproductive success were tested as response variables: (1) laying phenology (in Julian days, with January 1 defined as day 1), which was evaluated using linear mixed models (LMMs); and (2) fledging success, defined binomially (logit link) as low (≤ 2 fledglings in the nest at banding) or high (≥ 3 fledglings) in GLMMs. We consider the cut-off point of 2 fledglings to be a biologically relevant indicator of reproductive success for the Goshawk in Europe given its optimal clutch size of 3-4 eggs, which leads to the highest proportion of young fledged (Kenward 2006). This, together with the facts that most clutches of a single egg are usually abandoned, and that clutches of 2 eggs often do not produce any fledgling (Kenward 2006) may indicate that the expectation of raising 2 or less fledglings has low adaptive value. With each response variable, a model selection procedure similar to the habitat selection analysis was performed.

Data were analysed using Statistica 8.0 (StatSoft, Tulsa, OK, USA) and the "lme4" package (Bates *et al*. 2015) in R 3.0.3 (R Development Core Team 2014)

3. Results

3.1. Breeding density

In the period 2004-2011 we detected 29 Goshawk nesting territories (15.8 territories 100 km^{-2}). The number of active nests per year ranged from 18 to 22 (mean ± SE, 19.1 ± 0.5; 10.4 egg-laying pairs 100 km^{-2}). The average distance between neighbouring nesting territories was 1933 ± 84 m (range 1367–3283 m) and between active nests each year was 2234 ± 48 m (range 1034–4590 m). The G index was 0.90 for the nesting territories and 0.83 for active nests, indicating a regular distribution of the nest sites. The mean laying date was April 7 (range, March 20 to May 5, SD = 10.7 days, n = 55). The average fledging success was 2.3 fledglings per active nest (SD = 1.2, n = 64). The number of egg-laying pairs decreased significantly during the period 2004–2011 (r = -0.74; p = 0.036; r^2 = 0.55).

3.2. Breeding habitat description

Goshawks built their nests on large trees (height = 36.6 ± 1.0 m, DBH = 73.7 ± 2.4 cm, n = 64). Ninety-two percent of the nests were on Eucalyptus, which were used above their availability (43.8%; chi-squared = 62.14; df = 3; $p < 0.001$; Table A3 in the Appendix A). The nests were located at a high average height (22.4 ± 0.7 m, range = 8–35 m), in the lower or middle third of the tree crown (91% of the nests), generally in the main central fork of the tree (54%) or in a thick lateral branch against the trunk (40%).

In comparison to reference sites, nest surroundings (nest site, nest stand) had a higher density of trees, higher density of large Eucalyptus trees (defined as DBH >50 cm in the nest site, >70 and >100 cm in the nest stand), higher canopy cover and height, greater number of tree strata and greater tree species richness. Thus nest surroundings attained higher structural complexity than reference sites. In fact, nest sites frequently presented a visually distinguishable forest structure within the nest stand. The number of trails was also higher in the nest stands than in the reference plots (Table A3 in the Appendix A).

At the PFA scale, the area of mixed Eucalyptus stands (Eucalyptus plantations enriched in large Eucalyptus trees, Oaks and Pines) was higher in breeding sites than in reference plots, and the area of fields and meadows with buildings was lower (Table A3 in the Appendix A). Ninety-seven percent of nests occurred in Eucalyptus stands, mainly in mixed Eucalyptus stands (92.2%), which were used above their availability (71.4%; chi-squared =15.8; df = 5; p = 0.007). Goshawks nested on the northern aspect above their availability. The number of built-up areas and total length of paved roads were lower in breeding sites than in reference plots. Goshawk nests were located at a mean distance from the forest edge greater than the reference plots (Table A3 in the Appendix A). Distances between 100 and 400 m were used above their availability; smaller or greater distances were avoided.

Most Goshawk nests occurred peripherally within the main mass of forest plantations, maintaining a certain distance to the forest edge (average 177 ± 12 m), with only a few territories (7 out of 29) established in isolated forest patches within the agricultural matrix (Figure A1 in the Appendix A). The nesting territories did not differ from the reference plots in the proportions of land cover types, topographic features, or other variables indicative of human disturbance. Conversely, active nests showed significantly longer distances (NNDs) than reference trees to the centroid of the nearest neighbour breeding territory (Table A3 in the Appendix A). There were no active nests within 1000 m of any other active nest. NNDs between 1000–1500 m were used in proportion to their availability, and those between 1500–2500 m were used well above their availability.

3.3. Principal component analysis

The first two components of PCA accounted for, respectively, 24% and 16% of the variance, and included variables related to the forest structure (Table 1). The first component (PCA1) represents a gradient of size (age) and density of Eucalyptus trees at the scales of nest tree, nest site and nest stand, which we called *age-and-density of Eucalyptus trees in the nest surroundings*. The second component (PCA2) represents a gradient of tree species richness and structural complexity in the nest surroundings and PFA, which we called *structural complexity-maturity of the nesting forest patch*.

Table 1. Principal component analysis (PCA) of the habitat variables showing significant univariate differences between breeding sites and reference plots.

PCA1	Factor loadings*	PCA2	Factor loadings*
Nest tree		***Nest site***	
Height	0.77	Tree strata	-0.50
Crown height	0.71	Total Eucalyptus	0.66
DBH	0.64	Eucalyptus DBH 7.5-15	0.64
Crown volume	0.55	Total trees DBH >7.5	0.51
Nest site		***Nest stand***	
Maximum height	0.81	Tree strata	-0.53
Eucalyptus DBH > 50	0.66	Tree species richness	-0.49
Total Eucalyptus	0.57	Eucalyptus DBH 7.5-15	0.59
Total trees DBH >7.5	0.50	Total Eucalyptus	0.57
Eucalyptus DBH 7.5-15	0.49		
Nest stand		***PFA***	
Eucalyptus DBH 15-50	0.70	Total mixed Eucalyptus stand cover	-0.63
Total Eucalyptus	0.69	Total Eucalyptus stand cover	-0.52
Total trees DBH >7.5	0.69		
Maximum height	0.63		
Eucalyptus DBH 7.5-15	0.60		
Total trees DBH >15	0.58		

Note: Factor loadings refer to factor-variable correlations.

3.4. Breeding habitat selection

In the end, 7 variables were analysed in binomial GLMMs (Table 2). The set of confidence models (ΔAICc <2) comprised 11 models, and all variables analysed were included in at least one of the models. Model averaging indicated that territoriality

(NND), age-and-density of Eucalyptus in the nest surroundings (PCA1), and structural complexity-maturity of the nesting forest patch (PCA2) were the most influential variables in the process of breeding habitat selection. Standardised estimates suggest that territoriality (NND) was the most important variable, followed by PCA1. These two variables were roughly 3 times more important than PCA2 (Table 3). The best-fitting model explained R^2_m = 91% of the variance using only the three most important variables (NND, PCA1, PCA2). This high goodness of fit should allow reliable predictions of the probability of occurrence of Goshawk nests.

Table 2. Highest-ranked generalised linear mixed models using AICc-based model selection for Goshawk breeding habitat selection.

Ni	Model	log (L)	k	AICc	ΔAICc	w_i	R^2m	R^2c
1	NND + PCA1 + PCA2	-21.99	3	54.41	0	0.15	0.91	0.95
2	NND + PCA1 + PCA2 + CANOPY + DFE	-19.82	5	54.46	0.05	0.15	0.91	0.98
3	NND + PCA1 + PCA2 + CANOPY	-21.08	4	54.78	0.37	0.13	0.90	0.97
4	NND + PCA1 + PCA2 + ASPECT	-21.41	4	55.43	1.01	0.09	0.90	0.95
5	NND + PCA1 + PCA2 + DFE	-21.43	4	55.48	1.06	0.09	0.91	0.97
6	NND + PCA1 + PCA2 + CANOPY + ASPECT + DFE	-19.32	6	55.71	1.30	0.08	0.90	0.98
7	NND + PCA1 + PCA2 + CANOPY + ASPECT	-20.51	5	55.84	1.43	0.07	0.90	0.97
8	NND + PCA1 + PCA2 + TRAILS	-21.74	4	56.09	1.67	0.07	0.91	0.97
9	NND + PCA1 + PCA2 + CANOPY + TRAILS	-20.69	5	56.20	1.78	0.06	0.90	0.98
10	NND + PCA1 + PCA2 + CANOPY + DFE + TRAILS	-19.62	6	56.31	1.89	0.06	0.91	0.98
11	NND + PCA1 + PCA2 + ASPECT + DFE	-20.75	5	56.33	1.91	0.06	0.91	0.96

Note: The table shows model number (Ni), maximised log-likelihood function [log (L)], number of estimated parameters (K), AICc, AICc differences (ΔAICc), Akaike weights (wi), and marginal and conditional R-squared values (R^2_m, R^2_c). Abbreviations: ASPECT, nest stand aspect; CANOPY, nest site canopy cover; DFE, distance to forest edge; NND, nearest-neighbour distance; PCA1, age-and-density of Eucalyptus in the nest surroundings; PCA2, structural complexity-maturity of the nesting forest patch; TRAILS, nest stand trails. R^2_m and R^2_c are R-squared values for mixed-effects models indicating the proportion of total variance explained, respectively, by fixed effects alone or by the combination of fixed and random effects, as defined by Nakagawa & Schielzeth (2013).

Table 3. Relative importance (w+) and model-averaged parameter estimates for variables in binomial GLMMs describing Goshawk breeding habitat selection.

Variable	w+	β-Estimate	Adj. SE
Intercept		-2.382	1.502
NND	1	6.502	3.324
PCA1	1	5.629	2.957
PCA2	1	-1.975	1.153
CANOPY	0.55	1.406	1.195
DFE	0.43	1.376	1.302
ASPECT	0.30	0.747	0.797
TRAILS	0.19	-0.592	0.905

Note: Before analysis, variables were standardised to an average of zero and a standard deviation of one in order to obtain beta estimates. This allows direct comparison of the strength of the selection coefficients of the variables as well as comparison of the importance of variables across scales, thereby allowing the hierarchy of the habitat selection process to be inferred. See Table 2 for abbreviations.

Using the model showing the best fit, we estimated the probability of occurrence of Goshawk nests under three theoretical forest scenarios: mixed mature Eucalyptus stands with high structural complexity (P0), stands with the mean characteristics of age and structural complexity in the study area (P1), and young plantations with low structural complexity (P2) (Fig. 2). These scenarios typify a gradient of breeding habitat suitability based on observed habitat preferences. NNDs were predicted to increase as the forest structure departed from the preferred breeding habitat characteristics. Thus, forest structure influenced the local density of Goshawks: higher density (shorter NNDs) occurred in the preferred habitat, corresponding to Eucalyptus stands with larger trees, higher tree species richness and greater structural complexity (mature-like patches).

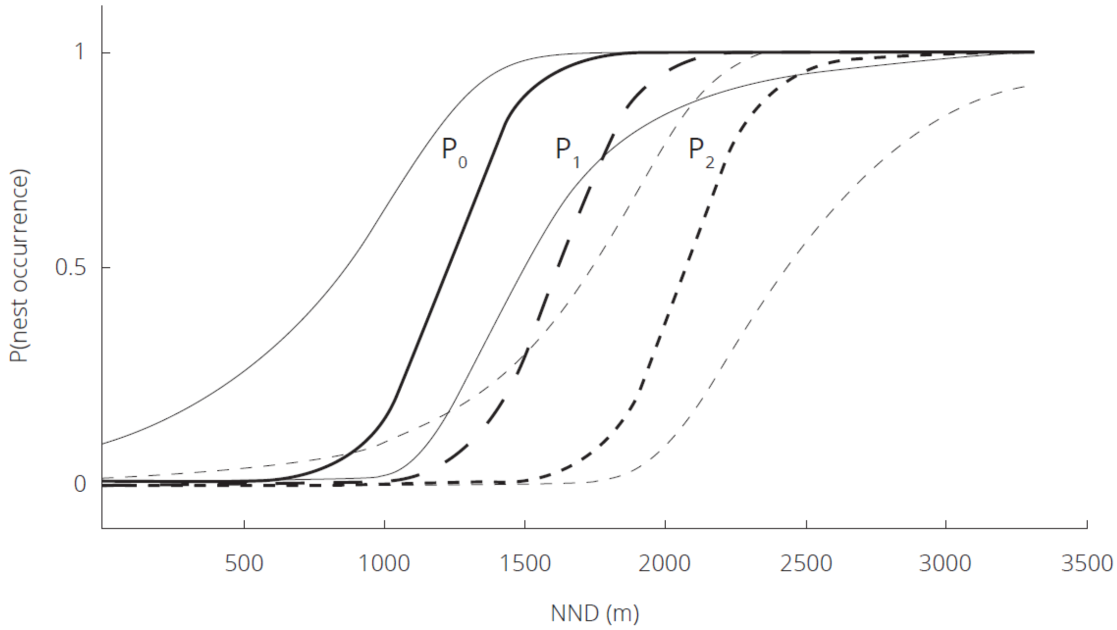

Figure 2. Probability of occurrence of Goshawk nests as a function of NND under three theoretical forest scenarios: mixed mature Eucalyptus stands with high structural complexity (P0), stands with the mean age and structural complexity in the study area (P1) and young plantations with low structural complexity (P2). Predictions were calculated using the most parsimonious model of the set of confidence models (Model 1, Table 2). Theoretical forest scenarios were simulated using the 10th percentile, mean and 90th percentile values of PCA1 and PCA2. Grey curves represent 95% confidence intervals of predictions based on the residual variance of the model. For clarity the confidence intervals associated with P1 were not drawn.

3.5. Relationship between breeding habitat preferences and reproductive success

We analysed the relationship between the three most important variables shaping breeding habitat selection (NND, PCA1, PCA2) and reproductive success. Territoriality (NND) was inversely related to both breeding phenology and fledging success (Tables 4 and 5): as the distance between Goshawk breeding pairs decreased, laying dates occurred later and the number of fledglings produced per active nest decreased. Habitat preferences detected at smaller scales (PCA1 and PCA2) did not show a significant relationship with reproductive success.

Table 4. Highest-ranked linear mixed models using AICc-based model selection for Goshawk reproductive success in relation to breeding habitat preferences.

Response variable	N_i	Model	log (L)	k	AICc	ΔAICc	W_i	R^2_m	R^2_c
Laying phenology	1	NND	-204.9	1	421.0	0.0	0.45	0.10	0.34
Fledging success	1	NND	-39.8	1	88.3	0.0	0.72	0.16	0.27
	2	NND + PCA1	-39.6	2	90.2	1.91	0.28	0.17	0.29

Note: See Table 2 for statistics and variable abbreviations.

Table 5. Goshawk reproductive performance in relation to breeding habitat preferences, based on parameter estimates in LMMs (laying phenology), relative importance (w+) and model-averaged parameter estimates in GLMMs (fledging success).

Response variable	Variable	w+	β-Estimate	Adj. SE
Laying phenology	Intercept		97.6	2.5
	NND		-3.527	1.485
Fledging success	Intercept		0.342	0.423
	NND	1	0.863	0.373
	PCA1	0.28	0.219	0.325

Note: See Table 2 for abbreviations. See also footnote in Table 3.

4. Discussion

Our results suggest that the studied exotic Eucalyptus plantations were a suitable breeding habitat for Goshawks, presenting a dense breeding population with a regular spatial distribution and high reproductive success. Goshawks showed marked breeding habitat preferences at various spatial scales. Territoriality greatly influenced habitat selection and reproductive success. Large Eucalyptus trees were a key structural element, providing the nest tree as well as appropriate structure in their immediate surroundings. The particular architecture of Eucalyptus, the prevailing forest smallholding regime, and the old age and low intensity of exploitation of these plantations likely help to explain the dense Goshawk breeding population, its regular spatial distribution, and its high reproductive success. The clear preference of the Goshawk for structurally mature-like patches argues for using this top predator as a forest management indicator species in order to promote biodiversity in these exotic plantations.

4.1. Breeding habitat preferences

Goshawks showed a hierarchical breeding habitat selection at various spatial scales in the Eucalyptus plantations. Goshawk territoriality was the primary determinant of the breeding habitat selection process. This selection is believed to begin with the detection of a free space between occupied territories, allowing the breeding pairs to acquire their own trophic resources, reduce interference competition and avoid extra-pair fertilisations (Newton 1979, Reich *et al*. 2004, Rutz 2005, Kenward 2006). Klaver *et al*. (2012) found that breeding sites were primarily determined not by territoriality but by the structural characteristics of the habitat. Our results and those of others (*e.g.*, Reich *et al*. 2004) suggest that when suitable breeding habitats are abundant and widespread, breeding pairs are regularly distributed and territorial behaviour becomes the main factor constraining breeding habitat selection.

Structural characteristics of the habitat were the secondary determinant of the breeding habitat selection process. For nest placement, Goshawks selected a very large Eucalyptus tree, well above its availability, more than 1100 m from other breeding pairs. Eucalyptus reach a greater height than other tree species, allowing the Goshawk to place the nest very high above the ground (22.4 m, range = 8–35 m), a nest height amongst the highest in the world (9–25 m; Kenward 2006). Large Eucalyptus trees provide good support to build a relatively large nest, which is important in an area where rain and wind storms are frequent (Cabalar 2005, Jimenez-Franco *et al*. 2014). A nest located at a tall height, on the lower part of the tree crown, hidden under abundant canopy cover in a Eucalyptus tree with a straight trunk, smooth bark and no low branches, should be well protected against human plundering of nests, as well as against terrestrial and avian predators (Newton

1979). During the study period, we did not detect any cases of nest plundering or of nestling predation by other raptor species and we detected only one event of nestling predation by the Common Genet (*Genetta genetta*).

The nest tree was predominantly located in forest patches with high structural complexity: high tree density, high average tree height, high tree species richness, high number of tree layers and dense canopy cover. These mature-like patches in the nest tree surroundings conceal the nest from predators and offer more favourable microclimatic conditions than more open, exposed forest environments (Newton 1979, Penteriani 2002, McGrath *et al*. 2003).

At the larger PFA spatial scale, Goshawks selected areas with greater forest cover, predominantly Eucalyptus stands enriched in native or semi-native tree species (mainly Oak, Pine, Chestnut and Laurel). The greater forest cover provides protection for the family group during the extended breeding period, in which most Goshawk activities occur in the vicinity of the nest: courtship, nest building, incubation, prey delivery to the female and nestlings, and training of fledglings in flight and hunting before they disperse (Penteriani *et al*. 2001).

Goshawks nested preferentially in abrupt areas showing lower road density and lying away from the forest edge, suggesting that they actively avoid potential human disturbances in an area with a high human population density. Goshawks are persecuted in the study area because they often hunt prey species of economic interest, including game species, racing pigeons and domestic poultry (García-Salgado *et al*. 2015). In fact, we have observed their capture with pigeon-baited Swedish Goshawk traps, and this illegal killing may be one of the main factors explaining the marked population decline of Goshawks in the study area in recent years (Rebollo *et al*. 2017b).

The preference of Goshawks for nesting in mature-like patches may make them useful as an indicator of biodiversity within exotic Eucalyptus plantations, as other authors have suggested in other forest ecosystems (Sergio *et al*. 2006, Burgas *et al*. 2014, 2016). Therefore, the habitat preference of this top predator may provide guidance for developing and selecting forest management strategies to enhance biodiversity on exotic plantations. Nevertheless, further research is required to confirm the biodiversity indicator role of this habitat-generalist in Eucalyptus plantations before implementing any management recommendations (Sergio *et al*. 2008, Ibarra & Martin 2015).

4.2. Habitat preferences and reproductive success

Territoriality, measured here as NND, was the only variable found to be related to reproductive success. Egg laying occurred earlier and fledgling production was greater as NND increased, *i.e.*, as the size of the nesting territory increased. Larger territories may be associated with more prey and with less interference competition between neighbouring breeding pairs (see Bretagnolle *et al*. 2008). Other authors have observed a positive relationship between Goshawk breeding density and the frequency of intraspecific nest intrusions and extra-pair fertilisations (Rutz 2005). Studies carried out during the pre-laying and incubation period in Osprey in Corsica showed that higher local density increased interactions between conspecifics and mate guarding behaviour, and reduced prey deliveries, copulation rates and reproductive success (Mougeot *et al*. 2002, Bretagnolle *et al*. 2008).

The smallest NNDs were observed in habitat stands preferred by Goshawks, *i.e.* old mixed Eucalyptus stands. These preferred habitats likely act as density traps, *sensu* Rodenhouse *et al*. (1997), because the density of breeding pairs approximates the carrying capacity of the system. However, the negative density-dependent effects observed in our study do not necessarily imply that these habitats are of lower quality for Goshawks.

Reproductive success may actually be greater in the long term if these territories are occupied and produce fledglings more regularly.

Habitat preferences detected at smaller scales, *i.e*. age-and-density of Eucalyptus in the nest surroundings (PCA1) and structural complexity-maturity of the nesting forest patch (PCA2) did not show a significant relationship with reproductive success. On the contrary, other authors have reported such relationships at these scales. For example, Bijlsma (1993) showed that although Goshawks preferred to nest in larches, nests in these trees were less successful than those in pines, spruces and firs (cited in Kenward 2006). In other examples, McGrath *et al*. (2003) found positive correlations between fledging rate and tree basal area within 1 ha of the nest, and Krüger (2002) found that nests were most successful in stands with large trees (greater DBH) and in areas with more woodland. Our failure to observe relationships between habitat preferences and reproductive success may reflect high availability of suitable nest sites in our study area, reflected in the fact that we were always able to find a nest-appropriate tree closer than 50 m from the random coordinates. Such a high number of nest sites would ensure that most breeding pairs could nest effectively. We cannot rule out the possibility that nesting in preferred sites improved reproductive success, but this improvement was counteracted by interference competition in the crowded, preferred breeding habitats.

4.3. High Goshawk breeding density and implications for forest management

With 15.8 nesting territories per 100 km^2 and 10.4 active pairs per year per 100 km^2, the breeding density of this Goshawk population during the study period is among the densest in Europe, where it averages 3.4 active pairs per 100 km^2, with most of the populations below 10 active pairs per 100 km^2 (Kenward 2006). The observed average reproductive success (2.3 fledglings per active nest) is also high in the European context, where the corresponding values are 1.8 in northern, central and western Europe, and 1.6 in southern

Europe (Rutz *et al*. 2006). We think that these exotic Eucalyptus plantations present a high density of breeding pairs for three main reasons related with the home range scale mosaic of habitats that provides high-quality feeding and breeding habitats for Goshawks. First, these plantations are part of an agricultural matrix that makes up an agroforestry system providing high prey availability at the scale of nesting territory (Rebollo *et al*. 2017b). This allows compression of the territories, which explains why the distances between neighbouring active nests are among the shortest in the literature (Martínez-Hesterkamp *et al*. 2015, Rebollo *et al*. 2017a). Unfortunately, we are not certain about where the Goshawks are hunting because we did not track them. However, our own diet studies show that both forest prey species and non-forest species are similarly important in the Goshawk breeding diet (García-Salgado *et al*. 2015, Rebollo *et al*. 2017b). These findings suggest that Goshawks both hunt in and out of the forest plantations, or in the intersection of these habitats (forest edge), where they have been observed to hunt disproportionally in other studies (*e.g*. Kenward 1982). This is consistent with the fact that most Goshawk territories in the study area include a considerable amount of woodland edge (simply bear in mind that the average distance from the nests to the forest edge is relatively short, 177 ± 12 m). Mature Eucalyptus plantations might be important habitats for hunting during the breeding season. Especially at the beginning of the breeding season male Goshawks need to provide as many preys as possible to their partners, while staying close to them and their nests to avoid territory intrusions and extra-pair fertilizations. We have indirectly observed that male Goshawks providing more forest prey to their broods enjoy greater reproductive success than those providing more non-forest prey (Pérez-Camacho *et al*. 2015; see also Penteriani *et al*. 2013), which would highlight the importance of these mature Eucalyptus plantations as a hunting habitat for the Goshawk. Second, characteristic forest management has helped create abundant, suitable nesting places well distributed spatially. The small-scale, low-intensity forest exploitation in the study area has allowed the growth and maturation of planted and native tree vegetation, leading to wide, regularly distributed mature stands preferred by Goshawks. This translates to several suitable nest sites at different places within the nesting territories. The small size of the clear-cuttings in the study area means that Goshawks can respond to disturbances by switching to nearby alternative nests. In fact, these characteristics of Eucalyptus plantations are favourable for other forest raptors (Sparrowhawk – *Accipiter nisus*, Common Buzzard – *Buteo buteo*) that can also reach densities among the highest in Europe (Martínez-Hesterkamp *et al*. 2015, Rebollo *et al*. 2017a). Third, Goshawks in the study area can nest in very large Eucalyptus trees, which provide very stable nest support out of the reach of practically all terrestrial predators.

Forest plantations must play an increasingly important role in the conservation of biodiversity (Brockerhoff *et al*. 2008, Brockerhoff *et al*. 2013, Trumbore 2015) in response to widespread decline of forest biodiversity. Plantations must fulfil this role while still ensuring necessary exploitation of wood resources. This necessitates a trade-off between economic profitability and conservation, which can be achieved through various options, ranging from intensive exploitation of plantations, with negative effects on biodiversity, to the elimination of exotic plantations and restoration or protection of native forests, at the expense of economic benefits. Using surrogate species such as the Goshawk to provide important information for plantation management may provide more options for striking efficient and balanced trade-offs favourable for both economics and biodiversity. Our results suggest that one should proceed gradually when replacing Eucalyptus plantations with native tree species in order to guarantee the availability of tall trees and mature forest patches regularly distributed across the landscape. The goal is to offer good conditions for the Goshawk and for the biodiversity potentially associated with it, as Suárez *et al*. (2000) and Olano *et al*. (2016) have suggested for other raptor species and forest plantations.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://..

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