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RESEARCH PAPER

Habitat suitability and nest-site selection of short-toed eagle *Circaetus gallicus* in Tolfa Mountains (Central Italy)

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Abstract. The availability of a suitable nesting site can be an important limiting factor for the reproduction of birds of prey, which are highly influenced by forest management and exploitation activities. Among them, the short-toed eagle (*Circaetus gallicus*) seems to tolerate logging activities carried out with traditional practices. This study aimed to investigate the habitat selection of 29 territorial pairs of this species in the Tolfa Mountains (Central Italy). Using Generalized Linear Models and the Information-Theoretic Approach, we compared the environmental features (i.e. land cover and topography) that characterize nesting sites in the study area. Additionally, we described the nest-site selection of the species by characterizing nine detected nests and comparing their characteristics with those of an equivalent number of nearby randomly selected sites. We found that, as expected, the short-toed eagle settles on hillsides covered by broad-leaved forests (both evergreen and deciduous) with open areas and away from agricultural areas. Moreover, the nests were found on steeper slopes, on trees extensively covered with climbing plants, possibly to hide them from predators and human disturbance. Our results suggest that, for the conservation of the short-toed eagle, careful management of woodland coppicing is required, as well as greater control of human disturbance.

Key words: habitat use, anthropogenic disturbance, Mediterranean forest, snake eagle, bird of prey

Introduction

The availability of a suitable nesting site can be an important limiting factor for the reproduction of birds of prey (Newton 1979, 1991), especially in relation to forest management and exploitation practices (Widén 1997, Kirk & Hyslop 1998, Bakaloudis et al. 2001, Bielański 2006). For instance, timber production may conflict with raptor conservation because large trees are the most valuable both for nesting raptors and the forest industry (Ewins 1997, Petty 1998). Moreover,

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medium-sized raptors, such as goshawk (*Accipiter gentilis*), common buzzard (*Buteo buteo*), and European honey buzzard (*Pernis apivorus*), are less likely to occupy their territory where a clear-cut has occurred in the proximity of the nest and only a small area of forest is retained (Santangeli et al. 2012). On the other hand, there is evidence that logging activities carried out with traditional practices (e.g. fell trees hauled out by mules) seem to be tolerated by the short-toed eagle (Bakaloudis et al. 2001).

The short-toed eagle (*Circaetus gallicus*) is a migratory bird of prey spending winter in sub-Saharan Africa, at least the Palearctic populations, although some individuals remain in the Mediterranean Basin (Ferguson-Lees & Christie 2001). It specializes in feeding on reptiles, mostly snakes, and requires heterogeneous landscapes with both open areas for catching prey and forests for nesting (Snow & Perrins 1998, Ferguson-Lees & Christie 2001, Sørensen & Herrando 2020). In Europe, the breeding population is estimated to number 17,600-20,900 pairs, and the population is considered stable (BirdLife International 2017). Nonetheless, it is listed in Annex I of the Birds Directive 2009/147/CE. The species suffered a marked decline in northern Europe in the 19th-20th centuries, due to habitat loss and persecution (Snow & Perrins 1998, Ferguson-Lees & Christie 2001). In Italy, it is a migrant breeder and a local winter visitor, with a patchy breeding distribution mainly located in the Alps and Prealps, coastal areas and mountains on the Tyrrhenian side, and along the Apennines (Brichetti & Fracasso 2018). The most recently published estimates show an increasing number of breeding pairs: 350-400 (Brichetti & Fracasso 2013), 480-520 (Baghino & Premuda 2005), 500 (Campora & Cattaneo 2006), 560 (Petretti 2008), 626-1,025 (Premuda et al. 2015). Over ten years (2004-2013) of counts in spring migration at the Apuane Alps observation site, which mainly involves the Italian population, an annual average increase of 10.3% was recorded (Premuda et al. 2015). Different hypotheses have been formulated to explain the increasing trend of the short-toed eagle population in Italy. Particularly, the high productivity rate of the Italian population, the increasing abandonment of agriculture and the consequent increase of hunting areas for the species, the higher availability of mature woodlands, with larger trees used as nesting sites than in the past and immigration from other areas due to the expansion of the species (Premuda & Belosi 2015). Short-toed eagle density has been calculated in suitable areas, both in Italy and in the Mediterranean Basin: 11.8 pairs/100 km^2 in Spain (Amores & Franco 1981), 2.1 pairs/100

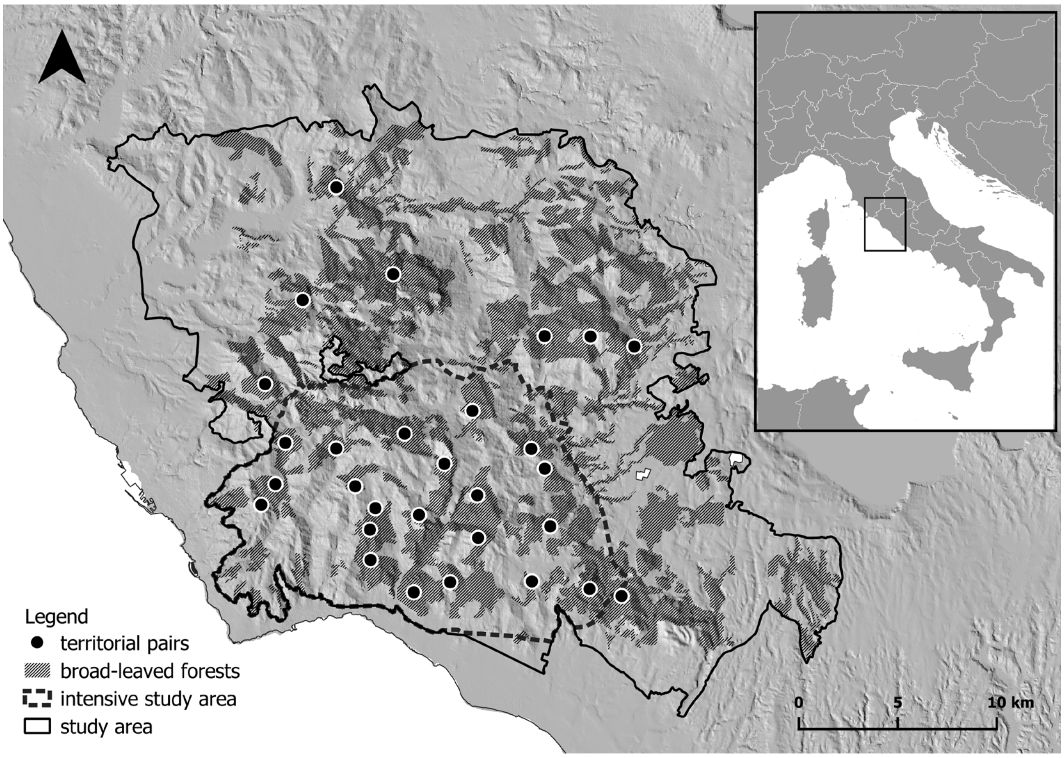

Fig. 1. The study area investigated to explain the occurrence of the short-toed eagle in central Italy. The sample area, broad-leaved forests, and the location of the short-toed eagle pairs are shown.

km^2 in Italy (Petretti 1988), 5.9-7.3 pairs/100 km^2 in Greece (Vlachos & Papageorgiou 1994, Bakaloudis et al. 2005).

The aims of this work were: 1) to determine the characteristics of the nesting site and, 2) to understand the main environmental variables affecting the spatial distribution of territorial pairs in an area of Central Italy. We hypothesized that, in accordance with its habitat requirements, the short-toed eagle settles in heterogeneous landscapes, in proximity to both woodlands and open areas. In particular, we expected a positive effect of evergreen forests, although the species may also select deciduous forest. In addition, based on field observation, we expected a negative effect of anthropogenic disturbance.

Material and Methods

Study area

The study area is located in "Monti della Tolfa" (Tolfa Mountains; WGS84, E 11.971°, N 42.150°), coinciding with the SPA (Special Protection Area) IT6030005 "Tolfetano-Cerite-Manziate District" designated in 1995 by the Italian National Authority (Ministry of Environment), thanks to the presence of several species of Community interest (Annex I of the Birds Directive 2009/147/CE), including the short-toed eagle. The area (676 km^2) is located in the north-western part of the Latium Region (Central Italy; Fig. 1); it ranges from the Tyrrhenian coast to about 25 km inland and is characterized by a central relief of volcanic origin (up to 633 m a.s.l.) surrounded by lower sedimentary formations. The hilly landscape is patterned by a dense hydrographic network of intermittent or ephemeral streams, with a marked seasonal regime, flowing either directly into the sea or into the River Mignone, which runs throughout the eastern and northern sectors of the study area. The land cover is composed mainly of farmland (314 km^2, 46.5%) and broad-leaved woodland (243 km^2, 35.9%), followed by shrubland (85 km^2, 12.6%), natural grassland (18 km^2, 2.6%), sparsely vegetated areas (15 km^2, 2.3%) and urban areas (0.4 km^2, 0.1%) (European Union 2018). The extent of urban areas is probably underestimated, due to the rapid increase in building activities leading to changes in land use from agricultural to residential. Extensive cultivation (wheat, corn) covers 87% of farmland, while vineyards, fruit trees and gardens cover most of the remaining agricultural area. Most of the woodlands are dominated by Turkey oak (*Quercus cerris*), sometimes in association with holm oak (*Quercus ilex*) or downy oak (*Quercus pubescens*) (82% of wooded areas). The remaining are composed of holm oak in warmer areas and by European beech (*Fagus sylvatica*) or chestnut (*Castanea sativa*) in cooler and wetter areas. Except for small portions of ancient forest and neglected coppice (woodlots left unmanaged), forested areas are managed for firewood production by stool shoot regeneration (coppice system) on a 20-30 yr rotation basis, where single mature trees are kept in the next rotation as seed bearers. Wooded areas form a mosaic with shrubs and grasslands (24% of the study area) where extensive livestock rearing (mainly cattle, horses and donkeys, with a few sheep, but only in open areas) is the main productive activity. The search for nests was carried out in an intensive study area (see Fig. 1; hereafter, sample area) represented by a sample area of 210 km^2 in the south-west part of the whole study area (about 1/3 of its total surface). The landscape is representative of the overall environment, being characterized mainly by farmland (30.9%), woodland (39.4%), shrubland (18.2%) and grassland (7.1%).

Data collection

Short-toed eagle territories were located by observing the territorial behaviour of breeding pairs from high vantage points (Fuller & Mosher 1987, Bibby et al. 2000). All historically known traditional nesting sites were checked. The sample area was divided into squares of about 3 km each. Within each square, one or more strategic points were identified for observation, carried out with binoculars and a telescope. As the spring migratory movements of the adults range from February to April and pairs settle almost immediately, the census began in the first week of March and continued throughout the breeding season, until September. At each observation site, surveys were carried out from dawn to 12:00 or from 12:00 to sunset, sufficient to identify one or more significant events that would indicate the presence of a territorial pair. In 2019 and 2020, a total of 180 observation days were conducted, distributed in such a way to cover the whole grid. The minimum criteria for establishing the presence of a territorial pair were the following: courtship displays, mating, nest building, joint use of trees as a roost, and conflicts with neighbouring pairs (Fuller & Mosher 1987, Bibby et al. 2000, Bakaloudis et al. 2005). In order not to cause any disturbance in the more sensitive stages of reproduction, the search for nests inside the forest began no earlier

Table 1. Environmental variables used to investigate the habitat suitability and nest-site selection of the short-toed eagle in central Italy.

Variables		Unit
Habitat suitability	Elevation	m a.s.l.
	Slope inclination	°
	Slope exposition	-
	Terrain Ruggedness Index	-
	Solar radiation	kJ m^{-2}
	Arable lands	%
	Meadows	%
	Heterogeneous agricultural areas	%
	Holm oak forests	%
	Turkey oak forests	%
	Natural grasslands	%
	Shrublands	%
	Sparsely vegetated areas	%
	Habitat diversity (Shannon's Index)	-
	Edge forest/open areas	m
	Edge shrubland/open areas	m
Nest-site	Tree height	m
	Tree diameter at breast height (DBH)	cm
	Climbing plants	presence/absence
	Tree crown thickness (distance from the first live branch to the top of the crown)	m
	Height of the first live branch (distance between the ground and the first live branch)	m
	Inaccessibility index	low/medium/high
	Distance between tree and the nearest track/trail	m
	Distance between tree and the edge forest	m
	Tree elevation	m a.s.l.
	Slope inclination	°
	Length of the wooded slope	m
	Distance to the bottom of the wooded slope	m
	Tree position along the wooded slope	%
	Number of similar trees	-
	Years since the last coppice	-
	Shrub cover	%
	Tree cover	%
	Number of trees with DBH > 20 cm	-
	Number of trees with DBH < 20 cm	-
	Total number of all trees (with DBH ≥ 5 cm)	-
	Density of all trees (with DBH ≥ 5 cm)	n/100 m^2

than the first week of June, when juveniles would have been at least two weeks old. Pairs for which the nest was not found, but were observed for most of the breeding season, were however considered territorial and potentially nesting.

Environmental variables

Habitat suitability was investigated through Resource Selection Functions following a presence *vs.* availability approach (Boyce & McDonald 1999, Boyce et al. 2002), as described in the next section.

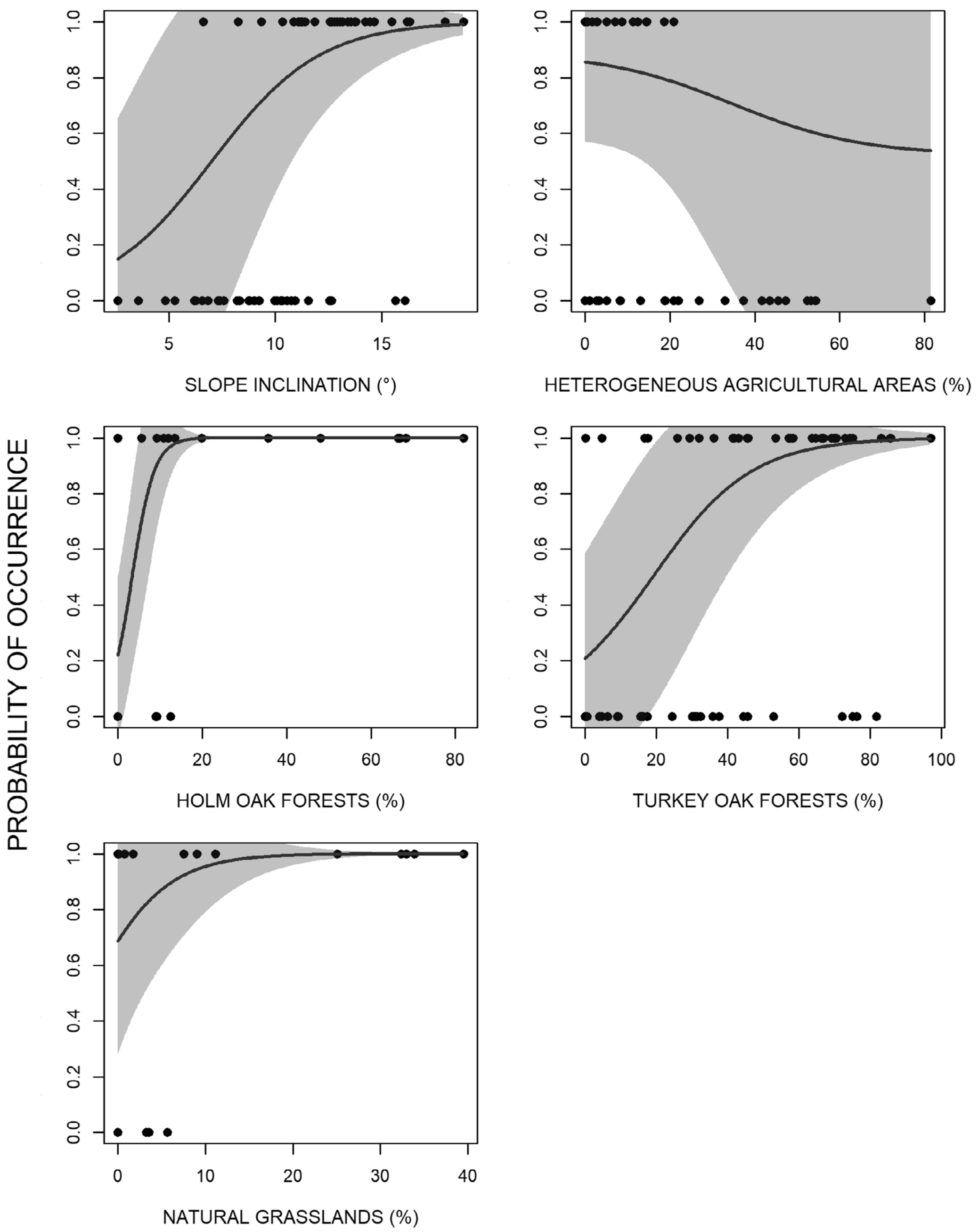

Fig. 2. Response curves of the environmental variables explaining the occurrence of the short-toed eagle in Central Italy.

We compared the environmental characteristics of sites where a reproductive pair was observed (i.e. "presence sites"; n = 29) with those of an equal number of available sites randomly chosen in the study areas (i.e. "availability sites"; n = 29). Specifically, we recorded topography, land cover, and other variables that could be involved in the species distribution (Table 1). Solar radiation was extracted from WorldClim 2.1 (Fick & Hijmans 2017), a dataset of spatially interpolated monthly climate data representative of the current climate for global land areas at a high spatial resolution (approximately 1 km^2). We measured habitat diversity using the Shannon-Wiener Index (Magurran 2004) and the length of edges between both forest/open areas and shrubland/open areas as the main habitat of snakes (Luiselli & Capizzi 1997, Scali et al. 2008). Presence sites were defined based on the territorial pairs identified during the field observations; specifically, we used both nest location or the mean centre of perch sites, in case the nest was not found. To take into account the ecology of the species, habitat suitability should be evaluated based on its spatial ecology and the distribution of pairs in the study area (Manly et al. 2002). The average distance between neighbouring

Table 2. Summary statistics (mean ± SE) of the environmental variables measured in "presence sites" and "availability sites" to investigate the habitat suitability of the short-toed eagle in Central Italy. Slope aspect is shown as the frequency in the main orientation. The significance of Mann-Whitney U test and χ^2 test (only for slope exposition) are shown (in bold are marked the variables with significant differences).

Environmental variable	Presence	Availability	*P*-value
Elevation (m a.s.l.)	**264 ± 14.27**	**223 ± 16.84**	**0.035**
Slope inclination (°)	**12.8 ± 0.45**	**8.9 ± 0.54**	**< 0.001**
Slope aspect	SW (n = 6, 20.7%) W (n = 8, 27.56%)	SE (n = 6, 20.7%) SW (n = 6, 20.7%)	0.891
Terrain Ruggedness Index	**12.1 ± 0.46**	**8.6 ± 0.52**	**< 0.001**
Solar radiation (kJ m^{-2} day^{-1})	19,664 ± 11.90	19,636 ± 14.48	0.052
Arable lands (%)	**4.58 ± 1.70**	**28.3 ± 5.37**	**< 0.001**
Meadows (%)	0.6 ± 0.34	3.1 ± 1.29	0.233
Heterogeneous agricultural lands (%)	**3.70 ± 1.10**	**21.3 ± 3.96**	**< 0.001**
Holm oak forests (%)	**13.7 ± 4.35**	**1.0 ± 0.54**	**0.005**
Turkey oak forests (%)	**52.9 ± 4.28**	**27.1 ± 4.31**	**< 0.001**
Natural grasslands (%)	**6.1 ± 2.14**	**1.7 ± 1.40**	**0.018**
Shrublands (%)	13.1 ± 2.39	9.6 ± 2.83	0.067
Sparsely vegetated areas (%)	**4.2 ± 1.24**	**1.5 ± 0.86**	**0.005**
Habitat diversity (Shannon's Index)	0.4 ± 0.02	0.42 ± 0.03	0.475
Edge forest/open areas (m)	5,496 ± 818.81	4,956 ± 810.01	0.541
Edge shrubland/open areas (m)	1,654 ± 403.56	903 ± 275.48	0.121

pairs was 2.1 km (see Results) so we measured the environmental variables within a 1 km radius of presence sites. Topographical data were obtained from the digital elevation model (DEM) of the study areas with a spatial resolution of 20 m. Land cover data were obtained from Corine Land Cover 2018 (European Union 2018).

Nest-site selection was defined by comparing the environmental variables (Table 1) between "nest trees" (n = 9) and an equal number of "random trees" (Bakaloudis et al. 2001, Barrientos & Arroyo 2014). "Random trees" were chosen by generating random points in the same wooded patches within which the nests were found. Specifically, "random trees" were located 70-400 m from the "nest trees" to avoid spatial overlap with the nest sites while guaranteeing their representativeness within the study area (Bakaloudis et al. 2005, Barrientos & Arroyo 2014). The environmental variables were measured in the field at the end of the breeding season (September), in a circular zone with a radius of 17.8 m (0.1 ha) (Barrientos & Arroyo 2014). Tree heights were calculated with a laser rangefinder and with trigonometric formulas (van Laar & Akça 2007). Diameters at breast height (DBH) were measured with a ruler (± 0.01 m) and vegetation cover was visually estimated in 10% increments (0-10%, 10-20% and so on). The position of "nest/random trees" along the slope was calculated as the ratio between the distance from the tree to the bottom of the slope and the total distance from the bottom of the slope to the ridgetop × 100 (Folliard et al. 2000). We also calculate the number of similar trees in the plot, i.e. those trees having the same DBH ± 10% as the "nest tree". We defined a tree following the IUCN's Global Tree Specialist Group (GTSG) definition: "a woody plant with usually a single stem growing to a height of at least two meters, or if multi-stemmed, then at least one vertical stem five centimetres in diameter at breast height" (Beech et al. 2017). Further, a categorical inaccessibility index was recorded, as difficulty in accessing the nest/random area on foot depending on the relief and density of the understorey (three levels: high, medium, low). The spatial analyses were carried out with Quantum GIS v.3.14.16 "Pi".

Statistical analyses

The habitat suitability of the study area for the short-toed eagle was explored preliminarily by testing for significant differences in the environmental variables measured in "presence sites" and "availability sites" with the Mann-Whitney U test and the χ^2 test. We then computed a Generalized

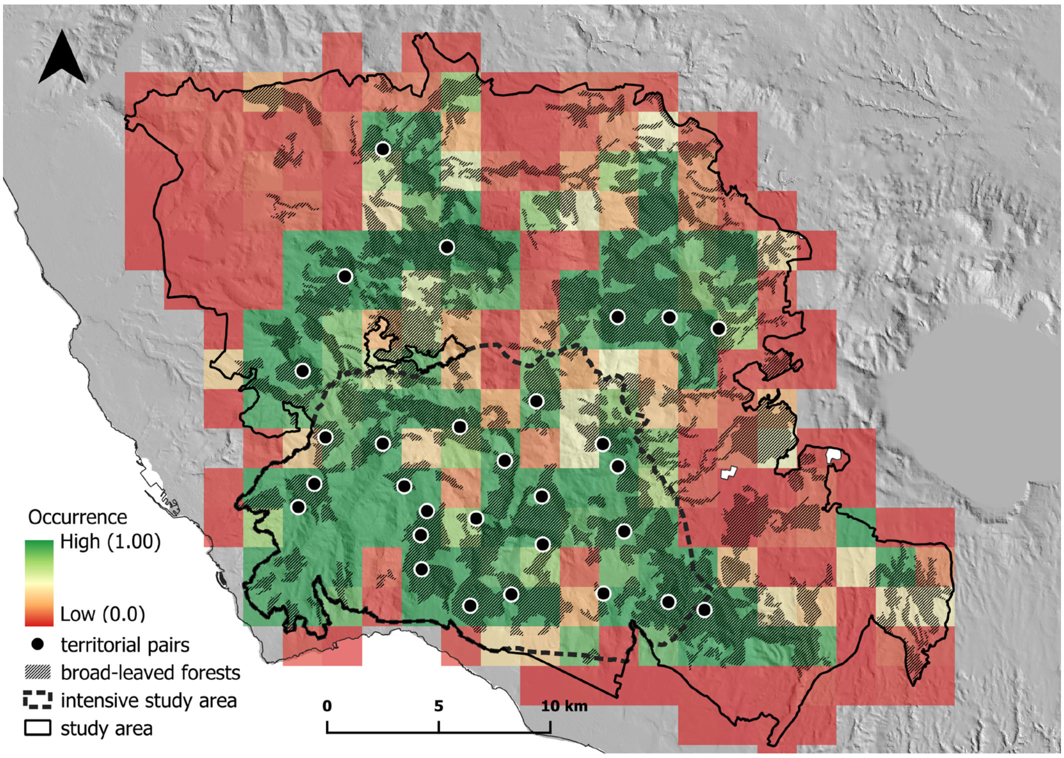

Fig. 3. Predicted probability of occurrence of the short-toed eagle in the study area located in Central Italy.

Linear Model (GLM) with binomial error distribution (Keating & Cherry 2004, Rushton et al. 2004) where the response variable was "presence/availability" (1/0), and the predictors were the environmental variables. We selected the variables to be included in the model using an Information-Theoretic Approach (Burnham & Anderson 2002). Specifically, we defined *a priori* a set of models using the environmental variables. For each of these we calculated the second-order Akaike Information Criterion (AIC_c) (Burnham & Anderson 2002) and based on the difference between the AIC_c of each model and the lowest AIC_c (ΔAIC_c) we defined the best set of models explaining the occurrence of the species. Finally, we used the best set of models (only those with $\Delta AIC_c \leq 2$) to perform model averaging, calculating both the coefficients and the importance of the variables selected (Burnham & Anderson 2002). The variables used in the models were standardized (Legendre & Legendre 1998) and to verify the absence of multicollinearity we used the Variance Inflation Factor (VIF) with three as a threshold value (Zuur et al. 2010). The explained deviance D^2 was used as a measure of variance explained by the models and we tested the spatial correlation of residuals with the Moran *I* test (Zuur et al. 2007). The discriminatory ability of the average model was measured via the area under the curve (AUC) of the ROC plot (Pearce & Ferrier 2000, Fawcett 2006) after a leave-one-out cross-validation (Fielding & Bell 1997). Finally, based on the average model we predicted the habitat suitability of the study area for the short-toed eagle.

We explored nest-site selection comparing the characteristics of the environment surrounding "nest/random trees" through the non-parametric Exact Wilcoxon signed-rank test and the Cochran *Q* test for paired data (Legendre & Legendre 1998). The statistical analyses were carried out with R

Table 3. The best-fitting models explaining the occurrence of the short-toed eagle in Central Italy. For each model, the model covariates, log-Likelihood (logLik), AIC_c and ΔAIC_c, Akaike weight (w_i) and deviance explained (D^2) are shown.

Model	logLik	AIC_c	ΔAIC_c	w_i	D^2
Slope inclination + holm oak forests + Turkey oak forests + natural grasslands	–15.04	41.11	0.00	0.63	66.1
Slope inclination + heterogeneous agricultural lands + holm oak forests + Turkey oak forests + natural grasslands	–14.35	42.18	1.07	0.37	67.6

Table 4. Summary statistics of the average model explaining the occurrence of the short-toed eagle in central Italy. The estimate (β) and its standard error (SE), lower (LCI) and upper confidence intervals (UCI), variable importance (w) and variance inflation factor (VIF) are shown. The VIF is shown as the average between the two models in the best set.

Environmental variable	β	SE	LCI	UCI	w	VIF
Intercept	1.667	1.124	-	-	-	-
Slope inclination	1.345	0.742	–0.110	2.800	1.00	1.091
Heterogeneous agricultural lands	–1.215	1.220	–3.607	1.177	0.37	0.803
Holm oak forests	7.051	3.394	0.400	13.703	1.00	2.131
Turkey oak forests	1.970	0.779	0.442	3.496	1.00	2.142
Natural grasslands	2.364	1.792	–1.223	5.950	1.00	1.053

Table 5. Characteristics of the nests and the "nest trees" (n = 9) of short-toed eagle in Central Italy. For the forest types covering the slope we show the exact values.

Variable	Mean ± SD	Range
Nest height (m)	11.4 ± 3.88	7.5-16
Tree height (m)	14.2 ± 5.0	8-21.5
Nest position (nest height/tree height; %)	81.5 ± 12.3	57-94
Tree DBH (cm)	35.4 ± 11.6	20-47
Tree crown thickness (m)	8.8 ± 2.5	5.5-11.5
Tree position along the wooded slope (%)	67.8 ± 17.4	38.9-88.2
Years since the last coppice	27 ± 18.3	3-47

v.3.6.1 (R Core Team 2019) with the packages *MuMIn* (Bartoń 2018), *verification* (NCAR – Research Applications Laboratory 2015) and *spdep* (Bivand et al. 2015).

Results

Habitat suitability

In the study area, we found 29 territorial pairs of short-toed eagle (21 in the sample area), for nine of which we also found the nest. Neighbouring pairs were located at an average distance of 2,114 m ± 1,091 (SD), with a minimum of 1,115 m and a maximum of 5,243 m. Preliminary analyses showed that presence sites were characterized by higher slope and terrain ruggedness than "availability sites" (Table 2). The species occurred in areas with more forest (of both holm oak and Turkey oak), natural grassland, and sparsely vegetated areas. Conversely, the species seemed to avoid arable land and heterogeneous agricultural land (Table 2). Habitat diversity and edges between forests/shrublands and open areas showed no significant differences between "presence sites" and "availability sites" (Table 2).

Two models best explained short-toed eagle presence (Table 3). Specifically, it occurred on hillsides with holm oak and Turkey oak forests, and some natural grasslands (Table 4, Fig. 2). Additionally, it avoided heterogeneous agricultural lands, even though the effect of this variable is less evident (Table 4, Fig. 2).

There was no collinearity among variables (Table 4) and the discriminatory ability of the average model was excellent (AUC = 0.939, P-value < 0.001). The deviance explained by both models was good (average D^2 = 66.9%) and the residuals were not spatially correlated (Moran I test, I = 0.357, P-value = 0.361). The model predicted an average probability of occurrence in the study area of 0.46 ± 0.42 (SD) (Fig. 3).

Nest-site selection

Although we identified 29 territorial pairs in the study area, we only located nests for nine of them. Nests were located on inclined slopes covered with Turkey oak (77%) or holm oak forests (23%) coppiced on average 27 years previously. However, the species also nests in recently coppiced woods (only three years, in one case), particularly on mature seed bearers left after coppicing. Nests were situated in trees with an average height of 14.2 m (8 m in holm oaks), usually in the highest part of the canopy. "Nest trees" were located

Table 6. Comparison between the environmental variables measured around "nest trees" and "random trees" to investigate the nest-site selection of the short-toed eagle in Central Italy. The significance of the Exact Wilcoxon signed-rank test and Cochran *Q* test (only for "Climbing plants" and "Inaccessibility index") are shown (boldface denotes significant differences).

Environmental variable	Nest tree	Random tree	*P*-value
Tree height (m)	14.2 ± 5.0	13.1 ± 4.1	0.672
Tree DBH (cm)	35.4 ± 11.6	33.3 ± 11.7	0.625
Climbing plants	**presence (n = 7)** **absence (n = 1)**	**presence (n = 3)** **absence (n = 6)**	**0.049**
Tree crown thickness (m)	8.8 ± 2.5	8.3 ± 2.5	0.523
Height of the first live branch (m)	5.1 ± 2.8	4.9 ± 2.0	0.938
Inaccessibility index	Low (n = 4) Medium (n = 1) High (n = 4)	Low (n = 4) Medium (n = 4) High (n = 1)	0.251
Distance tree-nearest track (m)	262.8 ± 125.2	244.1 ± 115.6	0.469
Distance tree-edge forest (m)	391.4 ± 218.3	413.9 ± 244.8	0.496
Tree elevation (m a.s.l.)	260.1 ± 84.9	240.0 ± 100.8	0.516
Slope inclination (°)	**31.1 ± 12.2**	**15.9 ± 8.4**	**0.016**
Length of the wooded slope (m)	842.0 ± 227.9	853.6 ± 188.4	1.000
Distance to the bottom of the wooded slope (m)	581.2 ± 217.8	595.9 ± 154.7	0.652
Tree position along the wooded slope (%)	67.8 ± 17.4	70.1 ± 14.6	0.820
Number of similar trees	7.2 ± 5.9	9.4 ± 9.3	0.637
Years since the last coppice	27 ± 18.3	27 ± 18.3	1.000
Shrub cover (%)	52.2 ± 27.7	58.3 ± 31.6	0.898
Tree cover (%)	77.2 ± 22.8	70.6 ± 24.0	0.500
Number of trees with DBH > 20 cm	20.2 ± 25.5	31.0 ± 23.1	0.551
Number of trees with DBH < 20 cm	1,134.9 ± 1,535.5	1,142.7 ± 1,359.3	0.461
Number of trees with DBH ≥ 5 cm	1,155.3 ± 1,526.7	1,172.6 ± 1,354.5	0.570
Density of trees with DBH ≥ 5 cm (n/100 m^2)	115.3 ± 152.3	116.9 ± 135.0	0.461

between the intermediate third and the upper third of the hillside (Table 5). Statistical analyses showed that only a few variables were significantly different between "nest trees" and "random trees". Particularly, "nest trees" more frequently had climbing plants on their trunks (especially *Hedera helix*) and were located on steeper slopes than "random trees" (Table 6).

Discussion

The short-toed eagles in the study area settled in broad-leaved forests, mainly composed of Turkey or holm oak, with a few open areas of sparse vegetation and natural grassland. The selection of broad-leaved forests is in accordance with previous knowledge of the species (Snow & Perrins 1998, Ferguson-Lees & Christie 2001), as well as the selection of holm oak forests, confirming that in Italy evergreen broad-leaved forest is the most widely used forest type (Brichetti & Fracasso 2018). However, in Italy the species also breeds both in coniferous and mixed forests (Campora & Cattaneo 2006, Brichetti & Fracasso 2018), as in Greece (Vlachos & Papageorgiou 1994, Bakaloudis et al. 2000, 2001) and Spain (Barrientos & Arroyo 2014).

Open areas are important as the main foraging habitat of the species (Bakaloudis et al. 1998, Campora & Cattaneo 2006, Bakaloudis 2009), where it can most easily locate and catch snakes. The only significant negative effect was found for heterogeneous agricultural areas, although the wide confidence intervals make this effect uncertain. However, the negative effect could be a result of the selection of quiet sites for nesting. This result is in agreement with findings in Israel, where the species avoids agricultural areas (Hadad et al. 2015). In fact, the species cannot nest in these areas because of the lack of suitable nesting sites but might use them as foraging areas. Indeed, in Greece agricultural areas, both intensively and non-intensively cultivated, were considered important as foraging sites (Bakaloudis et al. 1998, Bakaloudis 2009). In fact, these areas hold higher densities of the grass snake (*Natrix natrix*), which is the main prey of the short-toed eagle in north-eastern Greece (Bakaloudis & Vlachos 2011). In Italy, including in our study area, the main prey is the western whip snake (*Hierophis viridiflavus*) (Petretti 1988, Campora & Cattaneo 2006), which lives mainly in natural grasslands and edge habitats (Filippi & Luiselli 2006, Scali et al. 2008). This difference in prey species could explain our finding of the selection of natural grasslands and avoidance of heterogeneous agricultural areas, confirming previous research showing that short-toed eagle rarely uses cultivated areas for hunting in our study area (Petretti 1988).

Interestingly, neither habitat diversity nor the extent of edge between forests or shrublands and open areas were key factors explaining the presence of the species. Similar results were found in another study carried out in central Italy showing no relationship between the presence of the species and edge extent (Cecere et al. 2018). However, other studies have reported that ecotonal and heterogeneous habitats are the preferred hunting areas for the short-toed eagle (Petretti 1988, Sánchez-Zapata & Calvo 1999, Ontiveros 2016). As Cecere et al. (2018) hypothesized, we argued that the importance of landscape heterogeneity for the species might arise at higher spatial scales than we analysed, therefore we did not find any significant effect.

Slope gradient also seems to be important, with a higher probability of occurrence on steeper slopes. This effect could be an artefact, given that forests are mainly located on hillsides, but our nest-site analysis showed the same effect, although data were collected only in woodlands. Therefore, we believe that this is a genuine relationship and that steeper slopes might enable eagles to reach the nest more easily (Petretti 1988). Alternatively, eagles could select these sites to take advantage of rising thermal updrafts, which are used for soaring and searching for food, as has also been concluded by other researchers (Lopez-Iborra et al. 2011, Cecere et al. 2018).

We found an average nearest distance between neighbouring active nests of 2.1 km, which was similar to those found in Greece (2.2-2.7 km) (Vlachos & Papageorgiou 1994, Bakaloudis et al. 2005), but unlike those found in Israel (0.9-1.4 km), where pairs nest as close as 50 m from one another (Hadad et al. 2015).

As regards nest-site selection, we acknowledge that the few data collected must be interpreted with caution; nonetheless they provide some useful information. The nests we found were at an average height from the ground of 11.4 m, on trees 14.2 m high, and with a DBH of 35.4 cm. These values are different from those previously measured by one of the authors in the same study area (Petretti 1988). Indeed, he found nests built at an average height of 7 m and on trees with an average diameter of 28 cm. Considering that in recent decades forest management has not changed, the current selection of higher "nest trees" than in the past could be a consequence of the search for safer places for nesting due to the increase in anthropogenic disturbance. Nevertheless, the characteristics of both nests and "nest trees" we analysed are within the range found for the species (Vlachos & Papageorgiou 1994, Bakaloudis et al. 2000). Furthermore, in our study area, "nest trees" were located between the intermediate third and the upper third of the slope, partially in agreement with past findings in the same areas. Indeed, Petretti (1988) found a positive correlation between nest altitude and top slope altitude, perhaps because these sites offer better views of the surrounding areas. Likewise, in Greece, the "nest trees" were located in the upper third of the slope (Bakaloudis et al. 2001). In general, we did not detect any differences between "nest trees" and "random trees" in terms of their main characteristics, similarly to Bakaloudis et al. (2000). Raptors typically select larger trees (Barrientos & Arroyo 2014) because they provide more stable nest support (Newton 1979, Penteriani 2002), as well as protection against predators and other sources of disturbance (Moreno-Opo et al. 2012). We found a positive relationship between "nest tree" and the presence of climbing plants, particularly ivy, as also highlighted in the past (Petretti 1988). This finding agrees with preferences of another raptor, the common buzzard, whose nests were built on trees fully covered with ivy so that the nest itself was completely surrounded by ivy and often impossible to see from the ground (Sergio et al. 2005). Building concealed nests high above the ground, as well as in areas with a high density of trees, has been previously reported for raptors as strategies to hide the nest from predators (Jędrzejewski et al. 1988, Hubert 1993, Bakaloudis et al. 2001). It is possible that some territorial pairs will not be able to start or complete nesting because of the lack of suitable forest for nesting, or from the impact of anthropogenic disturbance, which negatively affects the species (Bakaloudis et al. 2001, Lopez-Iborra et al. 2011). The preference for nesting on the intermediate third of slopes, and higher from the ground than in the past, could arise from a preference to stay as far away as possible from tracks illegally travelled by off-road motorcycles. Likewise, the choice of trees abundantly covered with climbing plants and in areas that are difficult to reach could testify to active selection of safer sites (Sergio et al. 2005). In future, to allow the nesting of all potentially reproductive pairs, the importance of correct management of forest areas is emphasized. This could be accomplished with more careful management of woodland coppicing and greater control of the growing anthropic disturbance, especially the presence of off-road motorcycles.

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