

Multi-scale habitat selection and foraging ecology of the eurasian hoopoe (*Upupa epops*) in pine plantations

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Abstract Bird conservation can be challenging in landscapes with high habitat turnover such as planted forests, especially for species that require large home ranges and juxtaposition of different habitats to complete their life cycle. The eurasian hoopoe (*Upupa epops*) has declined severely in western Europe but is still abundant in south-western France. We studied habitat selection of hoopoes in pine plantation forests using a multi-scale survey, including point-counts at the landscape level and radio-tracking at the home-range scale. We quantified habitat use by systematically observing bird behaviour and characterized foraging sites according to micro-habitat variables and abundance of the main prey in the study area, the pine processionary moth (*Thaumetopoea pityocampa*). At the landscape scale, hoopoes selected habitat mosaics of high diversity, including deciduous woods and hedgerows as main nesting sites. At the home-range scale, hoopoes showed strong selection for short grassland vegetation along sand tracks as main foraging habitats. Vegetation was significantly shorter and sparser at foraging sites than random, and foraging intensity appeared to be significantly correlated with moth winter nest abundance. Hoopoe nesting success decreased during the three study years in line with processionary moth abundance. Thus, we suggest that hoopoes need complementation between foraging and breeding habitats to establish successfully in pine plantations. Hoopoe conservation requires the maintenance of adjacent breeding (deciduous woods) and foraging habitats (short swards adjacent to plantation edges), and consequently depends on the maintenance of habitat diversity at the landscape scale.

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Introduction

The relevance of heterogeneous habitat mosaics for bird conservation has been recently highlighted with the emergence of the continuum model as a new paradigm in landscape ecology (Manning et al. 2004). This model considers landscape as a mosaic of habitats of different qualities instead of using a binary classification of habitat and non-habitat, as in the classical island biogeography theory (Kupfer et al. 2006). It also predicts that the effects of surrounding matrix habitats may be more important than processes occurring within habitat patches, as demonstrated for birds in different biogeographic areas (Wiens 1995; Wolff et al. 2002; Wethered and Lawes 2003; Tubelis et al. 2004). Edges between matrix and breeding habitats can have positive effects on bird populations because of differences in resource availability and microclimate at edges, and when food is taken outside the breeding habitat (McCollin 1998). In the latter case, species need the complementation of non-substitutable resources in the landscape mosaic to complete their life cycle (Dunning et al. 1992; Brotons et al. 2004; Quin et al. 2004). In western Europe, habitat complementation at the landscape scale is probably essential for the conservation of several bird species that have been declining at least in part of their European range through the past decades (Burfield and van Bommel 2004): turtle dove (*Streptopelia turtur*, Browne and Aebischer 2003), wryneck (*Jynx torquilla*, Freitag 2004), woodlark (*Lullula arborea*, Bowden 1990), red-backed shrike (*Lanius collurio*, Virkkala et al. 2004) or linnet (*Carduelis cannabina*, Eybert et al. 1995).

Habitat complementation has important implications for bird conservation in heterogeneous landscape mosaics with high turnover in space and time, such as plantation forests (Barbaro et al. 2005; Paquet et al. 2006). Some species of particular conservation concern need the juxtaposition of breeding and foraging resources found in semi-natural habitat patches that may no longer be available in landscapes composed entirely of commercial plantations. The identification of key foraging habitats, especially when distinct from the main breeding habitat, consequently arises as a major issue in bird conservation management. For example, the presence of adjacent semi-natural grasslands is beneficial to farmland birds in mosaic forest-agricultural landscapes, both in northern and southern Europe (Preiss et al. 1997; Pons et al. 2003; Virkkala et al. 2004). Managed grasslands are suitable foraging habitats for open habitat specialists, but also for species such as the eurasian hoopoe (*Upupa epops epops*) nesting in wooded habitats and foraging on grassland seeds or invertebrates.

Hoopoes preferably inhabit farmlands with trees or walls where they nest in hollows, and open habitats with short sward structures where they forage on large ground-living insects (Kristin 2001). They also occur in cleared and thinned forests (Campronon and Brotons 2006), and their bimodal distribution in bird-habitat ordination models suggest that they use multiple habitats (Preiss et al. 1997). The hoopoe is classified as declining in western Europe and France (Burfield and van Bommel 2004; Julliard and Jiguet 2005). Food quality and accessibility as well as the availability of suitable nesting cavities are major limiting factors (Martin-Vivaldi et al. 1999; Arlettaz et al. 2000). In western Europe, hoopoes occur in farmlands where they feed mainly on molecrickets (*Grylotalpa grylotalpa*) and Lepidoptera larvae (Fournier and Arlettaz 2001). They also inhabit pine plantations, where

they specialize in pupae of the pine processionary moth (*Thaumetopoea pityocampa*), which is a serious forest pest (Battisti et al. 2000; Kristin 2001). In south-western France, hoopoes breed in oak forest fragments embedded within a landscape matrix of maritime pine (*Pinus pinaster*) plantation forests (Barbaro et al. 2007).

Here, we examine habitat selection by hoopoes at the landscape-scale (i.e., distribution of breeding pairs), at the home-range scale (i.e., habitat use of individual birds), and at the micro-habitat scale (i.e., selection of foraging sites). Specifically, we ask if (i) landscape mosaics occupied by hoopoes show significant differences in habitat composition compared to unoccupied ones; (ii) hoopoe behaviour is different according to habitat within home range; (iii) hoopoe select foraging sites with particular micro-habitat attributes; and (iv) hoopoe foraging intensity is positively related to pine processionary moth abundance.

Methods

Study area

The study took place in the Landes de Gascogne forest, south-western France, a region covering c.10,000 km² dominated by intensively managed maritime pine plantation forests. Climate, soil composition and current sylvicultural practices are described in Maizeret (2005). The distribution of breeding hoopoes was sampled at two nested scales within the study area. At the landscape-scale, the study site spans c.10000 ha (44°40'N to 44°44'N, 0°57'W to 0°46'W) and is composed of small (<5 ha) and isolated patches of oak (mainly *Quercus robur*) woodlands embedded in a matrix of pine plantations of different ages. At the home-range scale, we selected a part of the study site covering 180 ha, including pine stands, clearcuts and oak woodland patches bordered by large maize fields. Grasslands (with *Molinia caerulea*, *Pseudarrhenatherum longifolium*, *Agrostis curtisii* and *Ulex minor*) and heathlands (with *Pteridium aquilinum*, *Ulex europaeus*, *Erica cinerea*, *E. scoparia* and *Calluna vulgaris*) occur in recent clearcuts, firebreaks and sand track edges of the study area.

Bird surveys

The distribution of breeding hoopoes was surveyed at the landscape-scale in 2002–2003. Two observers performed 286 point-counts with unlimited distance using a sampling survey stratified by the main habitat types (see below). Points were established at least 400 m apart to avoid double counting (Sutherland et al. 2004). We conducted two 20-min visits before and after mid-May, within 5 h after sunrise and excluding rainy days.

Habitat use of individual birds in the 180 ha-area was investigated using the territory mapping method. Territory mapping is considered to be the standard method for birds showing territorial behaviour and not ranging widely (Bibby et al. 2000), such as the hoopoe (Kristin 2001). Between 2004 and 2006, hoopoes were monitored twice a week in the morning (9:00–11:00) or late afternoon (16:00–18:00) from mid-April to mid-July. We drove slowly along the dense network of tracks to survey the whole area, including the interior of pine stands typically distant of 50–100 m from the nearest track. Birds located inside the stands could be sighted from the tracks because stand understorey is regularly cut for management access. All stands were checked carefully with binoculars before driving along the tracks to locate hoopoes before they were disturbed and to avoid a bias on the

detection probability of birds between habitats. Driving was used because hoopoes were more closely approached by car, and because territory mapping involves locating individual birds as precisely and rapidly as possible to avoid double counting the same birds that may have moved from their initial locations (Bibby et al. 2000). The location and behaviour of every recorded bird were mapped on a Geographic Information System (ArcView, ESRI, Redlands, CA, USA), except birds seen in flight and those showing any change in behaviour because of the observer's presence. The coupling of territory mapping with colour-marking and radio-tagging (see below) allowed us to attribute a large majority of sightings to known individuals, as well as to distinguish adults from fledglings and additional non-breeding individuals (Bibby et al. 2000).

Nesting success

In the 180 ha-area, we established 13 specific nestboxes in 2002 to monitor breeding parameters. Nestboxes were located in deciduous tree patches to mimic natural conditions, and because male hoopoes were expected to aggregate in such habitats to sing and visit cavities (Martin-Vivaldi et al. 2002). At the beginning of the study, a breeding population of hoopoes was already established in the area. They nested only in large hollows in deciduous trees (mostly oaks) because cavities are lacking in pine plantations. This population bred continuously in natural cavities during the study with 3–4 pairs from 2004 to 2006. The provision of nestboxes provided nesting opportunities for additional pairs, which fluctuated from 4 pairs in 2004 and 3 pairs in 2005 to 6 pairs in 2006. Consequently, the total density of breeding pairs varied from 1 pair/20–45 ha during the study. We monitored breeding parameters (laying date, clutch size, brood size at hatching and number of fledged young) for 4 pairs in 2004, 4 pairs in 2005 (including 2 second clutches) and 9 pairs in 2006 (including 3 second clutches). Nestboxes were checked at the critical periods of egg laying, hatching and fledging, and nesting success was calculated only for the 14 successful clutches, by dividing the number of fledglings by clutch size (Martin-Vivaldi et al. 1999).

Ringling and radio-tracking

From 2004 to 2006, we caught 61 fledglings (c.20 days old) and 20 adults, and ringed them with a metal ring and Darvic plastic colour rings using combinations that allowed visual re-identification of individuals. In addition, 15 birds were radio-tagged using tail-mounted 1.3 g-tags (Pip-tags, Biotrack, UK), i.e., <2% of body mass, with a life of c.6 weeks and a range of c.1–2 km. Tags were glued on to the central tail feathers, but 8 out of the 15 hoopoes removed the tags by pulling out the rectrice within 24 h following the capture. The remaining 7 birds kept their tags between 2 and 46 days, and 6 were followed long enough to obtain more than 10 direct relocations (Table 1). Radio-tagged birds were relocated every day by approximate triangulation based on signal strength, until the bird was sighted and its precise location mapped (Browne and Aebischer 2003). We used interval sampling at more than 30-min intervals between two consecutive fixes to achieve independence of locations and to avoid bias by relocating birds disturbed by the observer (Sierro et al. 2001). Direct fixes were completed with additional, associated fixes when the bird identity could be confirmed visually (either by colour rings or by direct sighting of birds flying from foraging sites to the nest). This allowed an improved sample size for birds that had lost their transmitters early, and to estimate home ranges for two additional birds that were not tagged in 2005 (Table 1).

Table 1 Radio-tracking parameters and home-range sizes for 17 hoopoes

Year	Sex	Age	Nestbox	Sighting period	Tracking days	Direct fixes ^a	Associated fixes ^a	Total fixes	Home range (ha) ^b	
									MCP	KER
2004	Fem	–	11	April 29–June 7	21	44	6	50	9.77	6.52
2004	Male	2nd year	5	April 9–June 2	2	2	28	30	7.52	7.79
2004	Male	2nd year	7	May 17–27	10	12	5	17	14.03	26.46
2004	Fem	–	7	April 29–May 27	10	15	4	19	17.37	24.27
2004	Male	2nd year	11	May 17–June 4	18	19	10	29	7.41	7.91
2005	Male	2nd year	–	June 2–3	1	3	1	4	–	–
2005	Male	2nd year	14	April 11–May 13	–	0	37	37	11.89	15.29
2005	Male	2nd year	7	April 12–July 20	–	0	40	40	12.29	16.90
2006	Male	2nd year	1	April 26–May 24	6	21	11	32	15.57	23.93
2006	Male	1st year	1	May 11–12	1	1	0	1	–	–
2006	Male	2nd year	14	April 28–July 20	1	1	39	40	16.63	22.47
2006	Male	2nd year	10	April 27–July 20	1	1	30	31	8.82	9.71
2006	Male	2nd year	11	April 27–June 14	1	1	27	28	9.46	10.89
2006	Fem	2nd year	11	April 26–May 31	12 ^c	30	7	37	30.76	21.98
2006	Fem	2nd year	14	April 26–June 13	1	6	11	17	7.97	10.43
2006	Male	2nd year	9	April 21–June 8	1	3	13	16	9.25	9.88
2006	Male	2nd year	–	April 18–June 2	1	6	10	16	12.99	20.99

^a Direct fixes were obtained by relocations of radio-tagged individuals and associated fixes by re-sightings of known individuals

^b Estimates of home-range sizes calculated by minimum convex polygons (MCP) and fixed kernel density functions (KER)

^c Transmitter failed after 12 days but was still on the bird when re-captured 46 days after

Habitat use and foraging ecology

Habitat maps were digitized on GIS from colour aerial orthophotographs at the scale 1:25,000. We used the following 7 habitat types, with field calibration: mature pine plantation (tree height >7 m), young pine plantation (tree height <7 m), deciduous woodland and hedgerow, shrubland and heathland, semi-natural grassland (including herbaceous firebreaks), hay meadow and crop (maize field). We calculated the percentage cover of each habitat and a set of landscape metrics within 400 m-radius buffers of 50.3 ha around point-counts using Fragstats software (McGarigal et al. 2002). Previous studies showed that the most significant landscape metrics related to bird distribution were mean patch size (in ha), edge density (total length of all edges between all habitat patches, in m ha⁻¹) and the Shannon index of habitat diversity (Barbaro et al. 2005). In the 180 ha-area, we measured micro-habitat variables in 1-m² quadrats located at 40 foraging sites and 40 random sites in May–June 2006. Foraging sites were located by direct observations of foraging hoopoes and the quadrats were centred on the empty cocoons left by the birds when extracting processionary moth pupae from the ground (Battisti et al. 2000). Control plots were established randomly within the same area using GIS tools to create random points. In both plots, we recorded the distance to the nearest occupied cavity, vegetation height, and percentage cover of the main plant species, bare ground, woody debris, litter, bryophyte, grass and shrub layers (Bowden 1990; Sutherland et al. 2004).

Prey availability

Previous observations of foraging hoopoes in the study area indicated that birds feed mostly on two prey species, which are typically extracted from the first cm of the ground (Kristin 2001): pupae of the pine processionary moth and adult field crickets (*Gryllus campestris*). As moth pupae seemed to be quantitatively the most important prey, we monitored moth populations by counting winter nests in tree crowns (Hodar and Zamora 2004; Battisti et al. 2005). Pine processionary moth larvae live gregariously and build a winter silk nest in the tree crown periphery. Density of winter nests is known to be maximal at pine stand edges because of female moth preference for trees standing out against clear sky (Démolin 1969). The short swards along stand edges allow the caterpillars to burrow themselves into the upper 5 cm of the soil for pupating, where they are exposed to hoopoe predation (Battisti et al. 2000). We assumed a significant relationship between moth nest density and below-ground pupae abundance per edge. To estimate moth abundance within the 180 ha-area, one observer counted all winter nests in the first two tree rows of pine stand edges in early spring of each study year. We did not sample the interior of pine stands because most feeding hoopoes used the herbaceous fringe between a track and a plantation, and food availability should only be measured in habitats where birds can actually forage (Wolda 1990).

Statistical analyses

For binary point-count data, we compared mean landscape attributes for occupied and unoccupied mosaics using two-sample *t*-tests, and Mann–Whitney *U*-tests when data had non-normal distributions. We used binomial Generalized Linear Models (GLM) with logit link to relate hoopoe occurrence and landscape variables. Stepwise backward model selection was performed with Akaike's Information Criterion using the 'stepAIC' procedure in R package (R Development Core Team 2006). For radio-tracking data, home-range sizes were calculated for the 15 individuals with more than 16 relocations (direct plus associated fixes). Among these birds, 8 had more than 30 relocations and thus allowed a reliable estimate of 70–80% of their maximum home-range area (Sutherland et al. 2004). We used two methods to estimate home-range sizes: minimum convex polygon (MCP) and fixed kernel density function with 95% of the fixes. For kernel functions, we used least-squares cross-validation for calculation of the smoothing parameter *H* (Worton 1989). For habitat use, we compared the proportion of relocations in each habitat within individual home ranges (used habitats) to habitat availability at two levels: within the 180 ha-area and within individual home ranges (Aebischer et al. 1993). For each individual, we calculated a forage ratio, using the B_{ij} index of Manly et al. (1972), by dividing the proportion of bird records in a given habitat by the proportion of habitat available, then by dividing the forage ratio for each habitat by the sum of forage ratios for all habitats (Sutherland et al. 2004). We tested for differences in mean forage ratios between habitats using the Kruskal–Wallis *H*-test. We then used compositional analysis to compare habitat use within home range to habitat availability within total study area, and within individual home ranges (Aebischer et al. 1993). Compositional analysis was performed using the R package 'adehabitat' with missing values replaced by 0.01%, and randomisation tests (1000 permutations) to assess for the significance of habitat selection (Calenge 2006). We compared the proportion of birds having a particular behaviour in each habitat to the proportion of each habitat available by means of χ^2 tests and non-parametric Kendall correlation coefficients (Robinet et al. 2003). Micro-habitat variables were log-transformed when necessary to improve normality and data recorded at foraging sites were compared with those measured at the nearest control

plot using a paired *t*-test. We used one-way ANOVA to test for a year effect on prey abundance (number of moth nests per stand edge) and nesting success, and linear regression to relate the log-transformed number of foraging hoopoes to prey abundance. To test for between-year variation in the regression slopes between foraging intensity and prey abundance, we performed an ANCOVA with the year as factor, the number of foraging hoopoes as response variable and prey abundance as covariate.

Results

Habitat selection at the landscape scale

Hoopoes were recorded in half of the 286 point-counts. There was a significant effect of habitat type on hoopoe mean abundance, with significantly higher abundance in deciduous woodlands compared to all other habitats (ANOVA, *F*-ratio = 5.662, *P* < 0.0001). Landscape mosaics occupied by breeding pairs had significantly higher habitat diversity and smaller mean patch size than unoccupied mosaics, thus hoopoes tended to select the most heterogeneous parts of the landscape (Table 2). They avoided areas that contained a high proportion of mature pine plantations and favoured areas with more deciduous woods, hedgerows and meadows (Table 2). In addition, the stepwise GLM selection using AIC retained four variables: deciduous woodland, grassland and meadow covers and Shannon index of habitat diversity, but only the latter showed a significant effect on hoopoe occurrence (coefficient = $1.09 \pm \text{SE } 0.34$, *z*-value = 3.21, *P* < 0.001).

Habitat selection at the home-range scale

Home-range sizes were estimated for 15 hoopoes (Table 1 and Fig. 1), of which 13 were radio-tagged birds. They measured on average 12.78 ha (SD ± 5.96 ; range 7.41–30.76 ha) when calculated with the MCP method, and 15.69 ha (± 7.07 ; range 6.52–26.46 ha) when calculated with the kernel method, a difference which was not significant (Mann–Whitney test, *U* = 86.0, *P* = 0.27). Similarly, for the 6 individuals with more than 10 direct relocations,

Table 2 Mean \pm SD values of landscape attributes measured within 50 ha-areas around point-counts for mosaics occupied or unoccupied by hoopoes (*t*-tests for landscape structure and Mann–Whitney *U*-tests for habitat cover)

Landscape attributes	Occupied	Unoccupied	<i>t</i> - and <i>U</i> -tests	<i>P</i>
<i>Landscape structure</i>				
Edge density (m/ha)	229.73 \pm 66.26	216.36 \pm 71.87	−1.636	ns
Mean patch size (ha)	2.16 \pm 1.23	2.61 \pm 1.57	2.676	*
Shannon index	1.71 \pm 0.37	1.54 \pm 0.51	−3.355	**
<i>Habitat cover (%)</i>				
Mature pine	37.81 \pm 20.66	45.93 \pm 24.69	12152.5	**
Young pine	17.99 \pm 17.06	17.11 \pm 18.43	9674.5	ns
Deciduous wood	9.47 \pm 12.11	8.05 \pm 12.72	8681.5	*
Hedgerow	0.32 \pm 0.74	0.14 \pm 0.43	8469.5	***
Shrubland	15.96 \pm 13.06	13.51 \pm 13.82	8856.5	ns
Grassland	4.73 \pm 5.62	6.24 \pm 8.37	11023.0	ns
Meadow	2.97 \pm 8.13	0.91 \pm 3.12	8821.0	**
Crop	2.29 \pm 8.20	2.00 \pm 8.29	9396.5	ns

d.f. = 284, ****P* < 0.001, ***P* < 0.01, **P* < 0.05, ns = not significant

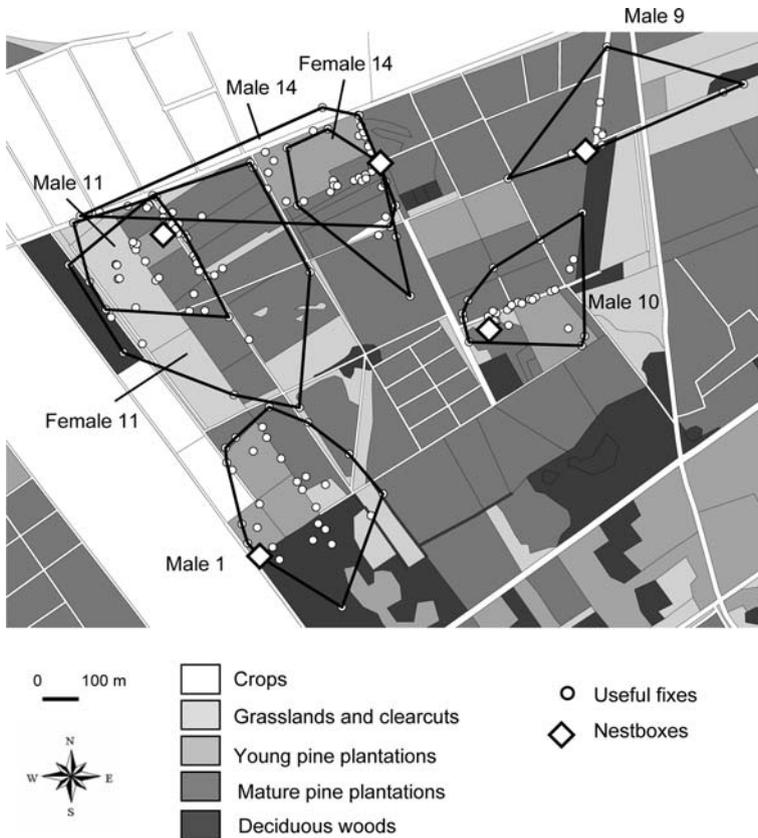


Fig. 1 Home ranges of 7 radio-tagged hoopoes in 2006 (white dots indicate fixes used to calculate home-range sizes by means of minimum convex polygons)

home-range sizes estimated with total fixes and with direct fixes only were not statistically different ($U = 15.5$, $P = 0.69$), and the estimates strictly identical for 4 birds. Home ranges overlapped largely within breeding pairs but generally not between pairs, with few exceptions (Fig. 1). Within home ranges, forage ratios differed significantly among habitats (Kruskal–Wallis test, $H = 49.0$, $d.f. = 5$, $P < 0.0001$). Mean forage ratios were higher for sand tracks and deciduous woodlands and hedgerows than for the other habitats, demonstrating positive selection of these two habitats as compared to their availability (Fig. 2). Compositional analysis showed that habitat selection for the 13 tagged hoopoes differed significantly from random at both levels of habitat availability within total study area ($\Lambda = 0.026$, $P < 0.001$) and individual home ranges ($\Lambda = 0.025$, $P < 0.001$). At the home range level, the ranking matrix of preferred used habitats gave the following order (>>> indicating significant differences): Sand tracks > Deciduous woods and hedgerows >>> Mature pines > Grasslands >>> Crops > Young pines.

Habitat use according to behaviour

A total number of 711 hoopoe observations were made between 2004 and 2006 ($n = 225$ in 2004, $n = 142$ in 2005 and $n = 344$ in 2006). Half of the birds were recorded in sand tracks

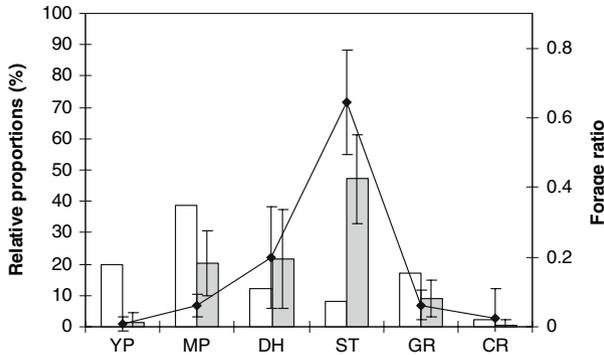


Fig. 2 Relative proportions (%) of habitat types available within the study area (white bars), mean (\pm SD) proportion of hoopoe relocations per habitat type within home ranges (grey bars) and mean (\pm SD) foraging ratio per habitat type (black line). YP = young pine, MP = mature pine, DH = deciduous woods and hedgerows, ST = sand tracks, GR = grasslands, CR = crops

and their herbaceous edges (51%), 17% in mature pine plantations, 14% in oak woods, 9% in hedgerows and 8% in grasslands. Habitat use differed between years ($\chi^2 = 30.22$, d.f. = 8, $P < 0.0001$), with grasslands being less used in 2004 than in 2005–2006 and sand tracks more used in 2004–2005 than in 2006. The most common behaviour noted was roosting, either in a tree or on the ground (47% of sightings), then foraging (34%), singing (11%) and feeding chicks (8%). Hoopoe behaviour varied significantly among habitats ($\chi^2 = 455.43$, d.f. = 12, $P < 0.0001$) and among years ($\chi^2 = 60.09$, d.f. = 6, $P < 0.0001$), with more foraging birds in 2005–2006 than in 2004. Singing hoopoes were recorded in all wooded habitats, including pine plantations (Fig. 3a), while foraging birds were mainly recorded from sand tracks and secondly from grasslands (Fig. 3b). The proportion of birds having a particular behaviour in each habitat was compared to habitat availability in the 180 ha-area. We find significant habitat selection for all behaviour categories, according to the non-significant Kendall correlation coefficients ($\tau = -0.359$ for breeding behaviour, $\tau = 0.105$ for singing, $\tau = 0.200$ for foraging and $\tau = -0.200$ for roosting, all $P > 0.05$).

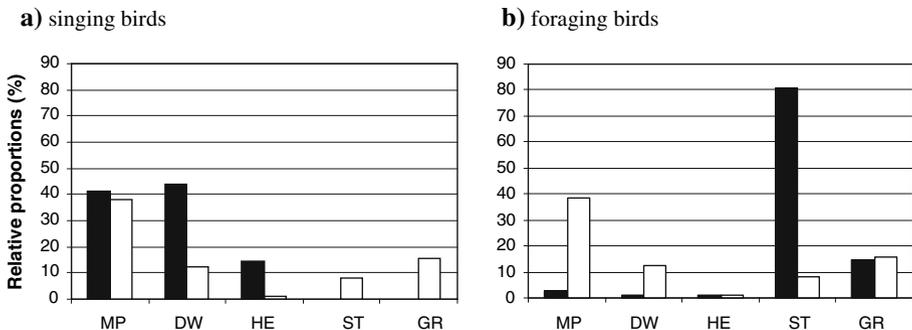


Fig. 3 Relative proportions (%) of hoopoe behaviour category per habitat type (black bars), compared to habitat availability (white bars) in the 180 ha study area: (a) singing birds and (b) foraging birds (data are pooled over the three study years). MP = mature pine, DW = deciduous woods, HE = hedgerows, ST = sand tracks, GR = grasslands

Small-scale selection of foraging habitats

The mean distance between foraging sites and nests was 271 ± 143 m (range 8–600 m), which was not significantly different from the distance measured between the randomly located plots and the nearest nest (Table 3). Foraging sites were all located in sand track edges adjacent to pine plantations, except one located in a mature pine plantation and four located in grasslands far from plantation edges. Vegetation was significantly shorter ($7.4 \text{ cm} \pm 7.1$) in foraging sites compared to control plots ($23.8 \text{ cm} \pm 15.7$). Bare ground ($25.7\% \pm 26.7$ versus $12.1\% \pm 29.3$) and bryophytes ($17.1\% \pm 18.2$ versus $5.3\% \pm 13.2$) had significantly higher cover in foraging sites than in control plots (Table 3). Vegetation composition at foraging sites also differed from control plots, with cover of bracken *Pteridium aquilinum*, gorse *Ulex europaeus* and deciduous shrubs being significantly higher in control plots, and cover of short annual graminoids, dicots and dwarf gorse *Ulex minor* being higher in foraging sites.

Prey abundance, foraging and nesting success

Moth abundance non-significantly decreased during the study (ANOVA, $F = 1.58$, d.f. = 2, $P = 0.21$, $n = 90$), from an average of 62.3 (SD ± 38.2) nests per edge in 2004 to 53.8 (± 31.2) in 2005 and 47.5 (± 26.3) in 2006. There was a significant year effect on hoopoe nesting success ($F = 5.21$, d.f. = 2, $P = 0.03$, $n = 14$), which decreased in line with moth abundance from 0.81 (± 0.09) in 2004 to 0.67 (± 0.17) in 2005 and 0.52 (± 0.15) in 2006. In all 3 years, the log-number of hoopoes observed foraging at a pine plantation edge was significantly and positively correlated to the number of moth winter nests per edge (Fig. 4). This relationship was stronger in 2004 ($n = 30$ edges, $r^2 = 0.452$, $P < 0.0001$) than in 2005 ($n = 39$, $r^2 = 0.273$, $P < 0.001$) and 2006 ($n = 40$, $r^2 = 0.218$, $P < 0.002$). Results of ANCOVA showed a significant prey abundance effect ($F = 43.19$, d.f. = 1, $P < 0.0001$) on

Table 3 Mean \pm SD values of micro-habitat attributes measured in 1-m² quadrats centred on 40 hoopoe feeding locations and 40 randomly distributed plots

Micro-habitat variables	Foraging sites	Random sites	<i>t</i> -test	<i>P</i>
Distance to the nearest nest (m)	271.5 \pm 143.0	254.4 \pm 133.7	-0.881	ns
Vegetation height (cm)	7.4 \pm 7.1	23.8 \pm 15.7	4.271	***
Bare ground (%)	25.7 \pm 26.7	12.1 \pm 29.3	-6.139	***
Woody debris (%)	1.8 \pm 3.9	2.5 \pm 2.9	1.828	ns
Litter (%)	8.1 \pm 12.2	20.5 \pm 27.3	1.966	ns
Bryophyte cover (%)	17.1 \pm 18.2	5.3 \pm 13.2	-3.756	***
Grass cover (%)	34.0 \pm 24.8	41.8 \pm 30.9	-0.270	ns
Shrub cover (%)	11.3 \pm 14.3	17.2 \pm 22.4	1.123	ns
<i>Pteridium aquilinum</i> (%)	0.3 \pm 0.5	6.3 \pm 10.3	4.392	***
<i>Molinia caerulea</i> (%)	3.5 \pm 12.2	6.2 \pm 16.6	1.159	ns
<i>Pseudarrhenatherum longifolium</i> (%)	7.9 \pm 14.4	11.3 \pm 11.8	1.751	ns
Short annual graminoids (%)	11.0 \pm 15.6	6.4 \pm 15.9	-2.204	*
Dicots (%)	2.0 \pm 3.2	0.6 \pm 2.2	-3.156	**
<i>Calluna vulgaris</i> (%)	6.2 \pm 14.1	4.5 \pm 12.8	-1.281	ns
<i>Erica cinerea</i> (%)	2.7 \pm 5.3	4.0 \pm 10.3	-0.924	ns
<i>Erica scoparia</i> (%)	0.7 \pm 3.2	1.6 \pm 3.6	1.784	ns
<i>Ulex minor</i> (%)	2.2 \pm 3.4	1.2 \pm 5.2	-2.962	**
<i>Ulex europaeus</i> (%)	0.3 \pm 1.6	4.9 \pm 12.1	4.177	***
Deciduous shrubs (%)	0.4 \pm 0.9	5.1 \pm 8.1	3.607	***

paired *t*-tests, d.f. = 39, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns = not significant

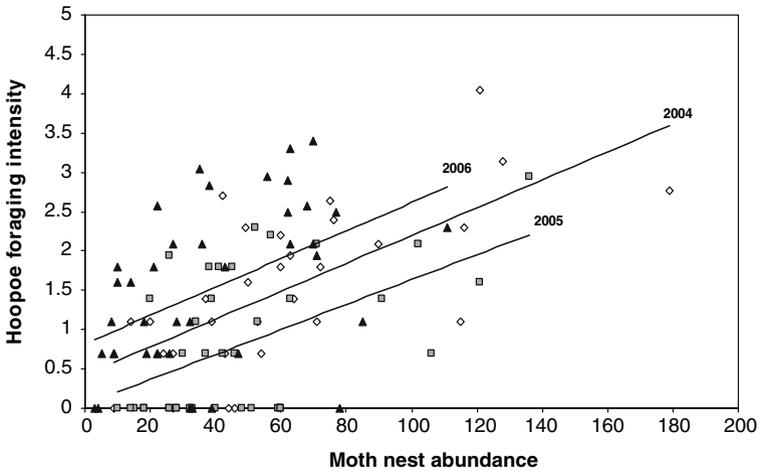


Fig. 4 Relationship between the log-number of foraging hoopoes and moth nest abundance per edge from 2004 to 2006 (black triangles: 2006, $r^2 = 0.22$, $n = 40$, $P < 0.002$; grey squares: 2005, $r^2 = 0.27$, $n = 39$, $P < 0.001$; white diamonds: 2004, $r^2 = 0.45$, $n = 30$, $P < 0.0001$)

hoopoe foraging intensity when taking into account the covariation between year and prey abundance. However, the interaction effect between year and prey abundance was not significant ($F = 0.06$, d.f. = 2, $P = 0.94$), i.e., the slopes of the three regression models were not significantly different. The overall year effect was however significant ($F = 10.91$, d.f. = 2, $P < 0.0001$), indicating that the intercepts differed according to year, in parallel to the variations in hoopoe density (Fig. 4).

Discussion

Habitat use and landscape complementation

The present study demonstrated that resource complementation between habitats at the landscape-scale was an important mechanism of habitat selection for this breeding population of hoopoes. Birds showed a preference for landscape mosaics with high habitat diversity. They selected particularly deciduous woodlands and hedgerows for the availability of deep nesting cavities in old oaks. At the home-range scale, hoopoes likewise showed a preference for habitat mosaics combining mature pine plantations, deciduous woods, hedgerows, grasslands and sand tracks, but only sand tracks and deciduous woods and hedgerows were selected more than expected from their availability. Deciduous woods and hedgerows were typical breeding sites, while foraging birds occurred mostly on sand track edges, and sometimes on grasslands. At a finer scale, foraging hoopoes selected microsites with short and sparse vegetation dominated by bryophytes, annual graminoids, dicots and dwarf gorse.

Habitat selection in birds is known to be a hierarchical process acting at multiple scales (Wiens 1995). For instance, owls choose their habitats according to trophic resources at a large scale, and according to breeding and roosting requirements at a smaller scale (Martinez and Zuberogoitia 2004). Similarly, choughs (*Pyrrhonorax pyrrhonorax*) use grazed habitats at a coarse scale and, at a finer scale, areas with the shortest swards for foraging (Whitehead et al. 2005). Our results suggest multi-scale habitat selection at three nested spatial scales:

(i) at the landscape scale, breeding hoopoes select oak woodlands embedded in a matrix of pine plantations and open habitats, (ii) at the home-range scale they prefer areas with breeding and foraging habitats in close vicinity, and (iii) at the micro-habitat scale, foraging birds select short and sparse swards along plantation-track edges. Thus, landscape mosaics with high habitat diversity are favoured because they fulfil both breeding and foraging requirements. As landscape complementation and supplementation are widespread mechanisms of multi-habitat use, they have important implications for bird conservation in mosaic landscapes (Wiens 1995; Brotons et al. 2004; Tubelis et al. 2004). In pine plantation forests of western Europe, several other threatened insectivorous birds would benefit from increasing habitat diversity at the landscape-scale through supplementation or complementation of resources, including nightjar (*Caprimulgus europaeus*, Sierro et al. 2001), wryneck (Freitag 2004), woodlark (Bowden 1990), or mistle thrush (*Turdus viscivorus*, Pons et al. 2003).

Foraging and prey availability

Foraging habitat selection results from an interaction between food abundance and accessibility, mediated by vegetation structure (Morris et al. 2001). As a result, the question arises if hoopoes feed on habitat edges because of higher prey abundance or higher accessibility compared to stand interiors? For example, nightjars did not use pine plantations as much as oak scrublands despite similar moth abundance in the two habitats because dense understorey in plantations prevent birds from foraging in flight (Sierro et al. 2001). Like other ground gleaners or probers, hoopoes feed preferably in short sward structures with c.25% bare ground. They generally avoid the interior of plantations stands because of dense understorey, but they can use them when mechanical cutting creates short vegetation or small gaps (Campronon and Brotons 2006). Dense vegetation and impenetrable soils make arthropods inaccessible by probing or gleaning (McCracken and Tallowin 2004), and shorter and sparser swards are therefore preferred by most ground insectivores (Bowden 1990; Browne and Aebischer 2003; Whitehead et al. 2005). Hoopoes are able to use foraging sites located far from nesting cavities (Arlettaz et al. 2000; Kristin 2001). In our study area, the distance between the nest and suitable foraging sites did not seem to be a limiting factor since hoopoes undertook foraging trips of up to 600 m from the nest. Mean foraging distance was 272 m, larger than that observed in other ground insectivorous birds such as wryneck (115 m, Freitag 2004) or woodlark (118 m, Bowden 1990).

The hoopoe is a brood reduction strategist able to adjust clutch size to prey availability by selective starvation of the youngest chicks (Martin-Vivaldi et al. 1999). The influence of food availability and its accessibility on breeding success is therefore critical (Fournier and Arlettaz 2001). As a specialist predator, the hoopoe is likely to respond to fluctuations in prey abundance (Crawford and Jennings 1989; Sherry 1990), as suggested by nesting success decreasing in line with moth abundance. Lepidopterous pupae and larvae are the main preys of many insectivorous forest birds (Glen 2004). The distribution of pine processionary moth is the main factor for the occurrence of another specialist predator, the great spotted cuckoo (*Clamator glandarius*, Hoyas and López 1998). However, in western Europe, only the hoopoe can feed on buried moth pupae during the breeding season, because of its long curved bill and unique foraging technique among forest insectivorous birds (Kristin 2001). Although hoopoes commonly feed on pine processionary moth in Spain and Italy, the main prey in Switzerland is the molecricket (Arlettaz et al. 2000; Battisti et al. 2000). The decrease in moth abundance observed during the study coincided with an increase in grassland use and foraging time, which suggests that hoopoes may switch to alternative

orthopteran preys (field crickets), in years of low moth density. However, as the nutritional value of moth pupae compared to field crickets is not documented, the relative importance of the two preys in the study area and their among-years variations remain to be investigated (Fournier and Arlettaz 2001).

Implications for conservation

The long-term conservation of the hoopoe in mosaic landscapes dominated by pine plantations depends on the maintenance of habitat diversity or its restoration by planting or regenerating oak woodland patches embedded in the pine plantation matrix. An appropriate management of the fringes between tracks and pine stands by regular cutting is also critical to allow hoopoes to access their preys (either moth pupae or field crickets) and will benefit other ground foraging birds (McCracken and Tallwin 2004), as well as plants and arthropods (Mullen et al. 2003). Edges between mature plantations and clearcuts may also provide suitable foraging sites if they are bordered by a short herbaceous strip both favourable to caterpillar burrowing and hoopoe probing. Moreover, previous studies have shown that clear-cutting in plantation forests lead to the establishment of a specific bird assemblage involving several threatened species (Barbaro et al. 2005; Paquet et al. 2006).

As nest site availability, together with prey availability, is a limiting factor for the hoopoe in plantation forests, we advocate the use of nestboxes to increase breeding density or restore populations in areas where cavities are lacking. Hoopoes generally respond to the establishment of nestboxes within a few years (Arlettaz et al. 2000; Kristin 2001). Moreover, breeding pairs tend to aggregate in the study area (Barbaro et al. 2007), although spatial aggregation may be caused by potentially confounding factors such as environmental heterogeneity (Cornulier and Bretagnolle 2006) or intra-specific social interactions (Martinez and Zuberogoitia 2004). In the hoopoe, displaying males tend to aggregate spontaneously where they expect to find females, and non-paired males frequently help to feed incubating females and chicks of other males (Martin-Vivaldi et al. 2002). We therefore suggest that the establishment of a dense network of nestboxes will allow the clumping of breeders in loose colonies and would increase social interactions in hoopoe populations.

In addition, the use of nestboxes may also be a tool for promoting biological control of pest insects in pine plantation forests. Predation of pine processionary moth by insectivorous birds may maintain moth populations at low densities, despite interactions with other causes of mortality such as parasitoid insects (Crawford and Jennings 1989; Battisti et al. 2000; Glen 2004). The increase of pine processionary moth populations with climate warming and the consequent potential threats to forest health and biodiversity (Hodar and Zamora 2004; Battisti et al. 2005) may be therefore mitigated by an increase in the density of functional insectivores such as the hoopoe (Jones et al. 2005). Conservation management in production forests should aim at maintaining or restoring native vegetation patches and corridors within a complex landscape matrix to enhance the functional diversity of species (Fischer et al. 2006). The hoopoe is an emblematic example of a threatened keystone species that may be favoured by such management recommendations in plantation forests.

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