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An approach to identify factors and levels of nesting habitat selection: a cross-scale analysis of Goshawk preferences

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Nest site selection may result from diverse agents that work on different spatial scales, and a multilevel analysis can offer a more realistic vision of the search image (proximate factors) and of the scale of nesting habitat selection by a species. Cross-scale analyses of nesting habitat preferences are scarce: in this respect, the Goshawk (*Accipiter gentilis*) is one of the most intensely investigated species, but most studies have focused only on a single habitat feature. This study, conducted in Burgundy (Eastern France), describes Goshawk nest site preferences by using a multilevel spatial scale analysis (nest tree level, stand level, landscape level), and identifies the habitat level that represents the supposed proximate factor for this species. We identified 57 active Goshawk nest sites (6.7 active nests/100 km^2). The stepwise logistic regression showed that 4 variables of the nest stand structure (high tree dbhs, high crown volumes, high flight space and short distance to trails) and 2 variables of the landscape surrounding nest trees (low avian prey richness for both 100–500 and 501–2000 g classes) were significant predictors of Goshawk nest site selection (98% of nests correctly reclassified). We hypothesised that Goshawk species choose nest sites on the basis of the overall structural features of the stand, and then focus on a particular nest tree.

1. Introduction

The selection of a specific nesting habitat presumably provides a more secure prospect for survival and reproduction than a random choice. The various determinants of avian habitat selection can be distinguished between proximate and ultimate factors. Proximate factors serve to quickly identify important habitat features (they act as immediate stimuli), and ultimate factors determine the success or failure of the individual choice and provide the evolutionary explanation (Hildén 1965). The impact of proximate factors on habitat selection is apparently demonstrated by the specific search images that birds supposedly use to select their habitat (James 1971). The proximate stimuli may work independently, hierarchically as a system of sequential decisions, or synergically in a complex fashion or "niche-gestalt", a combination of factors or aspects of the ecological niche that elicit a settling response from birds (Lack 1937).

In accord with Hall *et al.* (1997), we define "habitat selection" as the process an organism uses to choose a habitat, and "habitat preference" as the consequence of the habitat selection process, resulting in the disproportional use of some resources over others. For the past two decades, biologists have been studying bird habitat preference in a very detailed manner: quantitative studies on habitat features that relate to the settlement of a given species have become very common (Cody 1985). Keane and Morrison (1994) pointed out the need for habitat studies conducted on multiple spatial scales, from the micro-habitat (finer-scaled habitat features) through to the macro-habitat (landscape-scale features). Phenomenological models based on a wide array of spatial conditions more accurately address the ultimate causation, or "why" a species behaves or is structured as it is (Gavin 1991). Multilevel analyses of bird of prey habitat preference are scarce: in the most comprehensive studies, the habitat has been analysed at the nest stand structure and landscape levels (e.g., Santana *et al.* 1986, Anthony & Isaacs 1989, Sieg & Becker 1990, Cerasoli & Penteriani 1996, Penteriani & Faivre 1997, Sergio & Bogliani 2000), or at the landscape and food abundance levels (e.g., Ceballos & Donázar 1989, Schmutz 1989).

In terms of habitat preferences, the Goshawk (*Accipiter gentilis*) is one of the most intensely studied species. In the past two decades, given the vulnerability of this species to structural alterations of old-growth or mature forest stands (Crocker-Bedford 1990), research efforts have been targeted at developing a practical tool of forest management. Most studies have focused only on micro-habitat levels, such as the nest tree and nest stand (e.g. Moore & Henny 1983, Speiser & Bosakowski 1987, Lilieholm *et al.* 1994, Iverson *et al.* 1996) or on a macro-habitat level, such as the landscape surrounding the nest tree (e.g. Kimmel 1993, Bosakowski & Speiser 1994, Johansson *et al.* 1994). Studies on both the nest stand and landscape levels (Kostrzewa 1996, Squires & Ruggiero 1996, Penteriani & Faivre 1997) remain scarce, especially cross-scale analyses of the different habitat levels. However, a multilevel analysis of habitat preferences can offer a more realistic vision of the search image and the scale of the nesting habitat selection by a species.

Most studies on Goshawk habitat preferences have suffered from some biases in estimating nesting habitat preference. Few studies: 1) have quantified habitat availability, 2)have used stand level plots large enough to adequately describe stand structure, 3) have been conducted with a control plot system that was useful for nest stand management practices, and 4) relied on systematic nest searches in all forested areas, to avoid biased habitat characterisations due to an a priori selection of stands (Speiser & Bosakowski 1987, Squires & Ruggiero 1996, Penteriani & Faivre 1997, Daw *et al.* 1998).

Although numerous Goshawk surveys have shown an association between bird presence and stand or landscape structure, they have not produced data on nesting habitat selection on the basis of prey abundance and richness.

Our approach to studying the factors and scale of birds' nesting habitat selection used an original three-level analysis ranging from micro-habitat (nest tree and nest stand) to macro-habitat (landscape level and prey abundance and richness). Our study quantifies nesting habitat preferences by Goshawks and, consequently, it identifies: 1) the elements that represent the proximate factor for this species, and 2) the habitat level at which the search image supposedly works.

2. Methods

This study was conducted from 1995 to 1998 in an area of about 900 km^2 (altitude range: 180–590 m) in Burgundy (47°40′N, 4°44′E; Eastern France). The area is dominated by wide and homogeneous tracts of broad-leaved trees, occasionally intercalated with small areas of cropland. Depending on soil conditions and microclimate, the forests may be locally dominated by *Quercus pedunculata*, *Q. petraea* or *Fagus sylvatica*. A subordinate but widespread species is *Carpinus betulus*.

2.1. Nest location and breeding density

Nest searches were based on a rigorous sampling protocol. Biases in the characterisation of nesting habitat may be due to the fact that researchers seek specific structural features of the stand before looking for the nest (Daw *et al.* 1998). The search for nests was systematic throughout the forested surface of the study area (without resorting to opportunistic searches or to any a priori knowledge of habitat structure) and relied on a combination of methods, including: 1) broadcasting of taped adult and young Goshawk calls along a grid of stations, by using the protocol developed by Kennedy and Stahlecker (1993); 2) listening sessions of dawn and morning adult vocalisations (Penteriani 1999a) during the pre-laying period (January–March).

Density was estimated with the nearest-neighbour distance method (Newton *et al.* 1977); regularity in nest spacing was tested by the G-test (Brown & Rothery 1978), calculated as the ratio between the geometric mean and the arithmetic mean of the squared nearest neighbour distances. This index ranges from 0 to 1: values close to 1 (> 0.65) indicate a uniform distribution of nests.

2.2. Nesting habitat analysis

To identify the elements involved in the process by which Goshawks select nesting habitats, we used 5 variables to characterise the nest tree, 8 variables to characterise the stand structure around the nest tree, 8 variables to characterise the landscape structure and 7 variables to characterise bird communities of potential preys (Table 1 + slope exposure, modified to run statistical analysis; for the description and computation of the variables, *see* Table 1 and Penteriani & Faivre 1997). The variables measured for the nest tree and the nest stand were chosen on the basis of their value as measures of the structure and architecture of forests and their common use in the Goshawk literature. Only one nest (active nest) for each nest stand was used (n = 50), in order to avoid biases due to pseudoreplication of the preferences of individual birds. Because Goshawks are often found to nest in one of the tallest trees of the nesting stand (Penteriani & Faivre 1997, Penteriani 1999b), each nest tree was compared with the biggest trees in the nest stand plot.

Nest stand plots, centred on the nest, covered 1 ha in a 56.4 m-radius circle. Our plots were larger than the standard 0.04 ha plot (11.28 m-radius), previously used in the majority of bird of prey stand evaluations. In our opinion, as noted also by Santana *et al.* (1986) and by Speiser and Bosakowski (1987), 0.04 ha plots are too small to give a representative image of the stand structure, because they often contain very few trees, sometimes only a single one (the nest tree, whose features may differ from those of the average trees of the stand, Penteriani & Faivre 1997). As a result, the structural image of the stand depends on a sample that is too small and whose trees are larger than average. Our plots contained 2 orthogonal axes (along which measurements were made) crossing the centre of the plot and pointing to the four cardinal points. Tree parameters were measured on the trees intercepted by the transects, based on the line intercept method (Bonham 1989). One control plot was used for each nest stand plot, centred on one, randomly-selected cardinal point, located 150 m from the nest (Fig. 1). We selected control plots close to the nest stand plot (in the same stand) in order to determine whether, inside a stand, the species choose only a limited portion characterised by a specific structure (*see* Penteriani & Faivre 1997, Penteriani & Faivre 2001). This element is of paramount importance in the management of the stands that the species selects.

The landscape level involved the analysis of circular plots centred on the 50 active nest trees used in the two other levels. Plots had a diameter equal to the minimum distance between neighbouring occupied nest trees (2 km, *see* Fig. 1), to avoid plot overlap and double counting of landscape features. Each plot had two orthogonal axes from the plot centre. The number of ecotones, the relief index and the interspersion index were calculated along these axes. For each nesting habitat plot, a control plot was randomly established: to qualify as a control plot, the plot centre had to lie within a forested area (defined as a patch of > 5 ha homogeneously covered by trees: this size represents the minimum extension of forest used by Goshawks to nest in the study area) and not overlap with neighbouring plots.

In the centre of each landscape plot, bird abundance and richness were estimated by using the I.P.A. count method (Blondel *et al.* 1970). As this method requires, we did a double-count (March and May) of all the birds we observed and heard, giving a score of 0.5 points when observed only or alarming, and of 1 point when singing. Newton (1986) and Beier and Drennan (1997) showed that prey abundance comparison via point counts is a method powerful enough to detect differences between areas. Only bird communities were sampled to evaluate potential prey abundance, considering the high percentage of birds in the Goshawks' breeding diet in the study area (prey items = 204; bird percentage = 89.7%, bird biomass = 85.5%; mammal percentage = 10.3%, mammal biomass = 14.5%; Penteriani 1999b). For the statistical analysis we used all bird species, sepa-

Table 1. Variables used in the stepwise logistic regression analysis of the Goshawk nesting habitat (mean ± SD) at the three spatial scales (nest tree, nest stand and landscape surrounding nest tree). The values in bold proved to be significant in logistic regression analysis (P ≤ 0.05).

Variables	Goshawk nesting sites (n = 50)		Control plots (n = 50)	
	mean ± SD	range	mean ± SD	range
Nest tree level				
Diameter at breast height (m)	0.5 ± 0.1	0.3–0.74	0.5 ± 0.1	0.1–0.7
Tree height (m)	27.9 ± 4.2	20.0–36.0	28.0 ± 4.2	18.0–37.0
Trunk without limb height (m)	10.3 ± 3.3	4.0–16.0	11.7 ± 3.0	7.0–22.0
Crown volume (m^3)	3986.9 ± 1421.5	1080.1–8160.9	3932.3 ± 1350.7	1780.4–6420.7
Distance between trunks (m) [a]	8.7 ± 2.7	3.4–17.7	7.2 ± 2.2	3.8–12.4
Nest stand level				
Diameter at breast height (m)	**0.3 ± 0.1**	**0.2–0.5**	**0.2 ± 0.1**	**0.1–0.3**
Tree height (m)	25.5 ± 4.6	15.2–33.7	19.6 ± 5.9	6.0–29.2
Trunk without limb height (m)	10.5 ± 2.6	6.1–15.5	7.7 ± 2.3	3.0–13.3
Crown volume (m^3)	2716.2 ± 1319.1	188.0–5333.6	1349.1 ± 964.2	22.4–3738.7
Distance between trunks (m) [b]	7.2 ± 2.2	3.8–12.4	4.6 ± 1.7	1.9–10.7
Flight space (m^3) [c]	**83.3 ± 32.8**	**25.5–180.4**	**34.3 ± 16.7**	**3.4–73.3**
Slope gradient (°)	7.2 ± 10.9	0.0–45.0	5.6 ± 7.7	0.0–25.0
Tree distance to nearest trail (m)	**26.8 ± 26.3**	**0–100**	**72.7 ± 27.9**	**20–150**
Landscape/bird community level				
Woodland patches (%)	84.8 ± 11.7	60.0–100.0	82.5 ± 11.1	60.0–100.0
Number of ecotones [d]	10.3 ± 8.0	1.0–29.0	8.5 ± 5.3	1.0–18.0
Patch interspersion index [e]	1.1 ± 0.7	0.2–2.8	0.9 ± 0.9	0.2–3.3
Relief index	15.9 ± 9.8	3.7–35.0	14.7 ± 7.4	2.5–35.0
Distance to nearest wood edge (m)	1002.5 ± 1042.2	75.0–4750.0	629.2 ± 422.2	75.0–1600.0
Distance to nearest built-up area (m)	2791.2 ± 1179.1	775.0–5500.0	2791.2 ± 1179.1	775.0–5500.0
Distance to nearest paved road (m)	1037.5 ± 842.9	200.0–2925.0	1102.5 ± 821.0	50.0–700.0
Distance between 2 nearest Goshawk sites/2 nearest control plots (m) [f]	3162.5 ± 376.9	2650.0–4000.0	4100.0 ± 1988.6	50.0–7500.0
Mean IPA 1–100 g	1.7 ± 0.2	1.3–2.2	1.6 ± 0.2	1.1–2.1
Mean IPA 101–500 g	1.5 ± 0.3	0.8–2.0	1.4 ± 0.4	0.8–3.0
Mean IPA 501–2000 g	0.3 ± 0.3	0.0–1.0	0.5 ± 0.4	0.0–1.2
Richness	18.9 ± 2.6	15.0–26.0	19.3 ± 3.9	12.0–26.0
Richness 1–100 g	14.0 ± 1.9	10.0–18.0	14.2 ± 2.9	9.0–18.0
Richness 101–500 g	**4.0 ± 1.2**	**3.0–7.0**	**4.6 ± 1.4**	**2.0–7.0**
Richness 501–2000 g	**0.5 ± 0.7**	**0.0–2.0**	**0.9 ± 0.7**	**0.0–2.0**

[a] mean distance between the nest tree and the nearest four trees pointing to the four cardinal points.
[b] mean distance between each tree intercepted by the paths of the transects and the nearest four trees pointing to the four cardinal points.
[c] volume inside the stand and available for Goshawk flights near the nest, assimilated to square based parallelepiped, where major sides are represented by trunks without limb heights and the basal sides are the distances between trunks.
[d] calculated as the number of ecotones encountered along two orthogonal axes from the plot centre.
[e] calculated as the number of habitat patches along two orthogonal axes from the plot centre.
[f] we compared the distance between the centre of two nearest Goshawk nesting plots with two nearest control ones to verify if the nest site distribution was different from a random one.

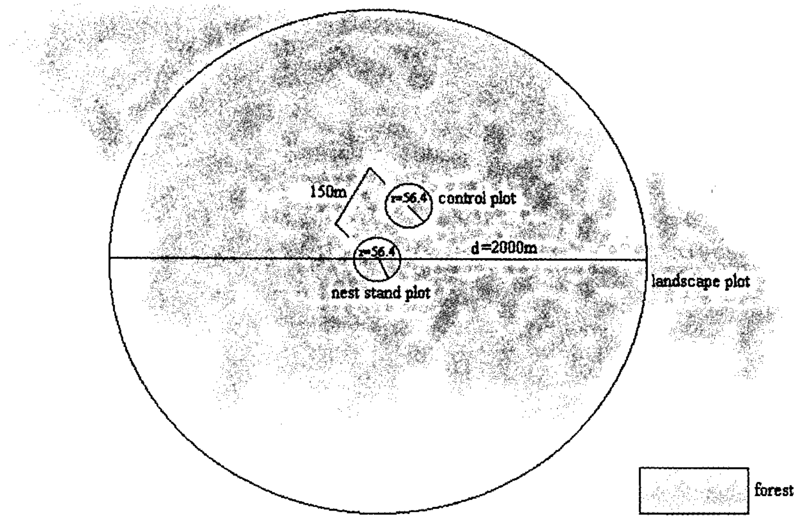

Figure 1. The 3 levels of analysis of the nesting habitat of the Goshawk *Accipiter gentilis*: the nest tree level, the nest stand level and its control plots (both with r = 56.4m, with a distance of 150m between their centres) and the landscape level (d = 2000m). The nest stand and the landscape plots are centred on the nest tree.

rated into three weight classes: 1–100 g, 101–500 g and 501–2000 g. We separated them by weight using direct measurement estimates of the live biomass, weight data from the study area and bibliographic material (Géroudet 1946–1957).

To compare relative strengths of the selection coefficients among the 3 spatial scales (nest tree, nest stand and landscape surrounding the nest tree), we conducted a cross-scale analysis putting all the habitat variables (from micro- to macro-habitat level) into a single logistic regression model. A forward stepwise logistic regression procedure was used to create the model of habitat preferences, because this multivariate statistical technique permits the prediction of binary attributes such as presence/absence. The P-value for entering variables in the model was $P \leq 0.05$, whereas the value to remove a variable was $P \geq 0.10$. To avoid using intercorrelated independent variables in the analysis, and to reduce the number of variables presented in the model, pairs of strongly intercorrelated variables ($r > 0.7$) were considered as estimates of a single underlying factor: only one of the two variables was employed in the analysis. The chosen variable was the one that seemed most likely to be perceived as important by the Goshawks (e.g., crown volume versus crown length), or the easier one to record. When necessary, variables were transformed to better meet the assumptions of normality.

Variables were selected based on the statistical significance of their effect (Wald statistic, $P < 0.05$ for individual tests). The logistic regression was performed by using SPSS 10.0 software.

3. Results

3.1. Breeding density

We identified 57 active nest stands, with a total of 126 nests. Minimum distances between active nests averaged 2.84 km (n = 23, range 2.0–3.8 km, SD = 0.58). The density calculated throughout the 900 km^2 study area was equal to 6.7 active nests/100 km^2 (n = 25, range 2–3.9, SD = 0.63). The values of 0.98 for the G-statistical test indicated a regular distribution of nests within the study area.

3.2. Nesting habitat preferences

When compared with the biggest tree inside the nest stand plot, the nest tree proved to be similar in size to the largest trees in the nest stand plots (Table 1). The nests were found solely on north-, east- and west-facing slopes: W = 9 (7.2%), NW = 42 (33.3%), N = 3 (2.4%), NE = 59 (46.8%) and E = 13 (10.3%).

The logistic regression model quantified the linear combination of independent variables best discriminating between Goshawk and control plots, and showed 6 significant predictors at the nest stand and landscape levels. At the nest stand level, 4 variables entered the forward stepwise logistic regression model: tree distance to nearest trail (B = –0.191, Wald = 6.1, df = 1, P = 0.014), flight space (B = 0.002, Wald = 5.9, df = 1, P = 0.015), diameter at breast height (B = 0.779, Wald = 4.9, df = 1, P = 0.026) and crown volume (B = 0.001, Wald = 4.8, df = 1, P = 0.028). All variables, except tree distance to nearest trail, showed higher values at nest stand level (Table 1). At the landscape level, 2 variables entered the model: species richness of medium-sized birds (101–500 g) (B = –9.507, Wald = 5.6, df = 1, P = 0.018) and species richness for large birds (501–2000 g) (B = –2.22, Wald = 4.1, df = 1, P = 0.042). Both values were lower in Goshawk plots (Table 1). The other landscape features and prey abundance/richness values showed relatively similar values between Goshawk and control plots (Table 1). The model correctly reclassified 49 of both Goshawk and control plots, for an overall classification rate of 98% (–2 Log likelihood = 16.57). No nest tree level variables entered into the model.

4. Discussion

Our cross-scale approach to the analysis of nesting habitat preferences mainly indicated that stand structure could guide the species in the selection of nesting habitat. Within the stand, the Goshawk seems to choose one of the biggest trees to build its nest. Such chosen stands appeared to have surroundings with lower values of prey richness than neighbouring control areas. The results of this study are consistent with those reported by Hall (1984) and Penteriani and Faivre (1997). These authors hypothesised that the species choose nest stands on the basis of their overall structural features and then focus on a particular nest tree, a landmark in the forest. A favourable stand structure is assumed to trigger the settling reaction.

In all the studies on Goshawk nest stand preferences, the structure of the nest stand seems to differ from that of the control stands and is characterised by tall trees, high canopy cover and low stem density (Moore & Henny 1983, Hall 1984, Speiser & Bosakowski 1987, Hargis *et al.* 1994, Lilieholm *et al.* 1994, Squires & Ruggiero 1996, Penteriani & Faivre 1997, Daw *et al.* 1998). The intensity of activity in the vicinity of the nest tree (nest building, vocal duets and copulations, prey delivery by the male for female and nestling, and by male and female for nestling and fledgling, fledgling activity near the nest before dispersing; Kenward *et al.* 1993a, b) probably explains the importance of the nest stand structure as a proximate factor in selection of nesting places.

The considerable differences shown by some studies in the characterisation of landscape, prey abundance and territory use may result from local factors and from the adaptability of the species to those levels. By contrast, the nest tree and the nest stand always have some recurrent constants. This is another finding that supports stand structure as a proximate factor in the selection of the nesting habitat. The elements that are most often regarded as important in nest stand structure are: 1) nest and stand accessibility (high values of distance between trunks, as in proximity of trails, and flight space); 2) microclimate factors and protection from predators (dense canopy and north exposures); and 3) ample support for a large nest.

A similar multilevel approach was adopted by Beier and Drennan (1997) to evaluate the influence of vegetation structure and prey abundance on selection of foraging habitat. As in our results, in which species richness of the main avian preys of Goshawks (101–500 and 501–2000 weight classes, Penteriani 1999b) was lower in nest stands and their surroundings than in control areas, their results fail to suggest that prey abundance was important in site selection. The only significant feature was that Goshawks seemed to prefer sites with more numerous and larger trees. Selection of nesting habitat on the basis of structural features, rather than prey abundance, was also observed by Hargis *et al.* (1994). For a species that hunts mainly by making short flights between perches (Kenward 1982, Widén 1984), the choice of hunting areas is probably a compromise between prey abundance and habitat structure that facilitates prey capture. On the other hand, Kenward and Widén (1989) and Ward and Kennedy (1996) showed that food was the main factor determining habitat use; in local conditions of high abundance and availability of a prey species, this factor can probably become dominant over habitat features. Moreover, it is well known that Goshawks are opportunistic foragers; they are adaptable to different hunting situations and to changes in abundance and vulnerability of prey species (Kenward & Widén 1989, Tornberg & Sulkava 1991, Olech 1996), but less so to changes in nest stands and are typically dependent on mature forests (Reynolds *et al.* 1992).

At the landscape level, Goshawks use a variety of habitats for hunting (Iverson *et al.* 1996, Penteriani & Faivre 1997), and their habitat preferences at this level, when proven for certain macro-habitat features (Kimmel 1993, Bosakowski & Speiser 1994), seem to be opportunistic and not to be dependent on particular landscape features, as for the stand structure.

The results of our analysis do not lessen the importance of prey abundance in the ecology of this species. Many studies have clearly demonstrated that raptor population density, breeding performance, home range size, and nestling behaviour vary with prey abundance (Newton 1979, Kenward 1982, Kenward & Widén 1989, Kenward *et al.* 1993a, b), the ultimate factor determining the success or failure of the settlement of a species. This is consistent with the view that habitat selection proceeds in a stepwise fashion, the various criteria of selection being hierarchically ordered (Klopfer & Ganzhorn 1985). Studies like ours seem to indicate that Goshawks apparently do not pay much attention to prey density in selecting their nest stand within their home range. It must be noted that prey abundance is not necessarily a good measure of prey availability (Hutto 1990): when measuring abundance, we cannot evaluate the food source with the same perception as a predator, or prey's crypticity and difficulty of capture. Moreover, prey animals may actively avoid Goshawk nest stands: there is evidence that preys can adjust their density and distribution in function of those of their predators (Ferrer 1993, Forsman *et al.* 1998).

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Selostus: **Kanahaukan pesimäaikainen elinympäristönvalinta Ranskassa: monimittakaavainen lähestymistapa**

Lintujen pesimäpaikan valintaan vaikuttavat monet tekijät. Eri tekijät voivat operoida lisäksi eri mittakaavatasoilla. Jotta lintujen elinympäristönvalintaan vaikuttavia tekijöitä ymmärrettäisiin paremmin, tarvitaan monimittakaavaista lähestymistapaa. Monimittakaavaisessa lähestymistavassa arvioidaan sekä pienemmän mittakaavan tekijöiden (esim. habitaatin laatu) että suuremman mittakaavan tekijöiden (esim. maiseman rakenne) vaikutusta lintujen pesimäpaikanvalintaan. Artikkelin kirjoittajat tutkivat kanahaukan pesimäpaikanvalintaa Ranskassa monimittakaavaisesti: pesäpuutasolla, pesimämetsikkötasolla ja pesimämaisematasolla. Aineisto koostui 126 kanahaukan pesästä, jotka sijaitsivat 57 metsäsaarekkeessa (6.7 pesää/100 km^2). Käytössä olleiden pesien välinen keskimääräinen minimietäisyys oli 2.8 km. Askeltavan regressioanalyysin mukaan neljä metsikkötason muuttujaa (puiden läpimitta rinnankorkeuden tasolla, kuutiomäärä, lentoala sekä pesäpuun etäisyys lähimmästä polusta) ja kaksi maisematason muuttujaa (100–500 g painoisten ja 501–2000 g painoisten saalislintujen lajimäärä alueella) selittivät kanahaukan pesimäpaikanvalintaa. Kanahaukan havaittiin suosivan metsäsaarekkeita, joissa puiden läpimitta rinnankorkeuden tasolla, puiden kuutiomäärä, avoin lentoala ja pesimäpuun etäisyys lähimmästä polusta oli suuri. Kanahaukalle sopivien saalislintujen lajimäärä oli pienempi kanahaukan pesimäalueilla kuin kontrollialueilla. Artikkelin kirjoittajat päättelevät, että kanahaukka valitsee pesimäpaikkansa ensin metsikön yleisen rakenteen perusteella ja tämän jälkeen lintu valitsee pesimämetsästä sopivan pesäpuun. Pesäpuu on yleensä yksi metsikön suurimmista puista.

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