



# Scale-sensitive landscape complementation determines habitat suitability for a territorial generalist

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Evaluating habitat suitability is often complex, as habitat effects may be scale-dependent, critical resources may be spatially segregated, and resource availability may also depend on intra- and inter-specific interactions. Using analyses that spanned multiple years and spatial scales, we investigated habitat requirements of a territorial generalist, the common raven *Corvus corax*, in a relatively pristine woodland, Białowieża Forest (E Poland). We compiled data from multiple raven surveys conducted between 1985 and 2001. Ravens were regularly distributed over the entire study area but declined in density over 50% within the 16 yr interval. In the same period game and forest management significantly reduced ungulate densities and likely diminished the habitat quality with regard to food supply, especially carrion. To better understand habitat requirements of ravens we studied breeding performance in relation to three different habitat types across multiple scales: open areas, coniferous-dominated forest, and deciduous-dominated forest. We found a prominent dissimilarity between raven nesting and foraging habitats highlighting the importance of resource complementation for ravens. On a fine scale, large old pines were exclusively selected as nesting trees and nesting areas were generally coniferous-dominated. However, at increasingly broader scales, coniferous habitats were negatively associated with raven reproductive success as those habitats likely provide a lower food supply. Only where the coniferous nesting areas at smaller scales were complemented with high percentages of deciduous forests and open areas at broader scales did the breeding performance increase. In addition to habitat composition, intra-specific interactions were important determinants of reproductive performance and very successful neighbors decreased reproductive performance of a focal pair. Most of previous studies have investigated resource complementation in terms of habitat edges or proximity of complementing resource patches. Our study demonstrates that the concept of landscape complementation also applies to gradients in landscape composition and emphasizes the importance of scales and intraspecific interactions in habitat analyses.

Classic habitat models assume that individuals are adapted to choose habitats with the highest reproductive value. This adaptation should lead to a distribution where the density of individuals is proportional to the resource density (the “ideal free distribution”, Fretwell and Lucas 1969). Based on these assumptions, habitat selection studies aim to reveal determinants of high reproductive success or abundance by comparing characteristics of areas that are used or occupied to areas that are potentially available (reviewed by Jones 2001 and Guisan and Thuiller 2005). However, patterns of area use alone can be misleading to assess suitability because habitat choices may be non-trivial with regard to several factors, including: 1) disconnects between habitat occupancy and quality: individuals may be located in inferior habitats, where they just can survive but not reproduce, or in apparently good habitats with abundant resources but high mortality and/or no reproduction. Animals may be

distributed in such sink habitats when either intra-specific competition may force some individuals to settle in less suitable areas or because their cues are mal-adapted due to rapid environmental change (“attractive sink”, Misenhelter and Rotenberry 2000, Delibes et al. 2001). Thus, the simple occupancy of a habitat alone may not be reliable to reveal its suitability and it may be more appropriate to consider reproductive performance rather than occupancy as a measure for habitat quality (van Horne 1983, Clark and Shutler 1999, Jones 2001, Sergio et al. 2003a, Johnson 2007, Kristan et al. 2007). 2) Scale dependency of habitat choices: animal preferences for or against habitat types may vary with scale and the scale at which essential resources occur may be critical to evaluate habitat suitability (Orians and Wittenberger 1991). Indeed many recent habitat studies do include more than one spatial scale in their analyses (Sergio et al. 2003b). However, choices of scales are

often arbitrary and thus far few studies have explored habitat selection across a continuous range of scales (Thompson and McGarigal 2002, Graf et al. 2005). 3) Multiple selection criteria: animal preferences for habitats are complex in that multiple habitat characteristics may be selected for simultaneously. Dunning et al. (1992) introduced the concept of landscape complementation to describe situations in which the series of critical resources required by an organism to complete its life cycle are contained not just in one habitat type but in multiple, spatially segregated habitat types. For example, amphibians require ponds for reproduction plus suitable terrestrial summer habitats (Pope et al. 2000). Likewise, many species require different habitats for refuge or shelter and for foraging (Petit 1989, Choquenot and Ruscoe 2003).

While many studies have focused on these three factors in isolation, little synthetic research exists that considers multiple factors in combination. For example, studies on resource complementation have typically focused on the proximity of the number of resources or habitat types that are essential for a particular species. However, very little research has attended to the importance of spatial scale for resource complementation (Haynes et al. 2007). In this study we ask whether resources need to co-occur at specific scales and suggest that these considerations are particularly relevant for territorial species (e.g. birds of prey; Newton et al. 1977, Nilsson et al. 1982). Their spacing behavior often leads to a homogeneous distribution across the landscape and maintaining a specific distance to neighbors that generally is believed sufficient to assure adequate food supply within the territory. Territorial animals usually don't venture inside territories of neighbors to seek limiting resources, but rather all resources need to be abundant in sufficient amounts within their own territory. Under these circumstances, it may not only be more revealing to test for habitat suitability using reproductive performance rather than occupancy (Sergio et al. 2003a, Johnson 2007), but also scale dependency of complementation may be particularly relevant since all habitat requirements need to be fulfilled within the confined space of a territory.

Here we investigate habitat suitability for common ravens *Corvus corax* in Białowieża Forest (E Poland). Białowieża Forest is one of the most pristine woodlands in Europe featuring a mosaic of coniferous stands, deciduous stands, and open areas. Ravens are resident and territorial birds with relatively large area requirements and a pair usually occupies the same territory for their entire life. Habitat quality for ravens usually depends on two components: food supply and nest sites (Ratcliffe 1997). Ravens are generalist consumers; however, when carrion is available they are often highly specialized as scavengers (Heinrich 1989, Stahler et al. 2002, Selva and Fortuna 2007). In Białowieża Forest, the diet of adult ravens consists mainly of rodents and ungulate carcasses (Rösner et al. 2005, Selva et al. 2005). Here, carcasses are more abundant in deciduous-dominated forest, and rodent densities are higher in open areas and deciduous forest, whereas coniferous-dominated areas provide less of both resource types (Aulak 1970, Jędrzejewski and Jędrzejewska 1996, Jędrzejewska and Jędrzejewski 1998, Selva 2004). Ravens are also generalists regarding the nest site. They can build their nests on cliffs, various tree species and human-derived

structures such as electricity pylons, buildings or even abandoned cars (Ratcliffe 1997, Boarman and Heinrich 1999, Bednorz 2000). Nesting platform choices differ regionally and probably depend on cultural traditions within populations (Bednorz 2000). Previous research indicates that in Białowieża Forest ravens prefer large pines as nesting platforms (Pugacewicz 1997). At first glance, Białowieża Forest appears as generally suitable for ravens. The entire area is occupied by raven territories and, since in the forest mosaic habitat types are finely distributed, any of the main habitat types occurs at least to some extent in any of the relatively large territories. To better understand determinants of habitat suitability for ravens, we ask whether in such seemingly suitable habitat significant variation in breeding performance persists and whether the concept of scale-dependent complementation may provide new insights explaining this variation. Is there a discrepancy between hypothesized good foraging areas and nest-site locations (i.e. deciduous and open areas vs coniferous areas); and is that discrepancy scale dependent (i.e. broad scales for foraging and fine scales for nesting)?

To assess habitat suitability we compiled data sets of several raven surveys across a 16-yr period from 1985 to 2001 that provided information on the distribution of territories, the type and height of nesting tree, and the reproductive success. In addition, we used satellite remote sensing to compile habitat information at varying scales around the nest site. We used these data to research three aspects of raven ecology in Białowieża Forest that together allow assessing complementarity and scale dependency of resources. First, we examined the density and distribution of raven territories. We compared nest densities in 1985 and 2001 and asked whether within each survey period nests are indeed regularly spaced, as expected for a territorial habitat generalist. Secondly, we examined habitat selection at the scale of the nest site to test ravens preference for tall pines as nesting platform. Thirdly, we investigated habitat effects across scales on raven breeding performance. We ask whether breeding performance was related to habitat characteristics around the nest site and whether potential associations between breeding performance and habitat types vary with spatial scale. In addition to habitat, intraspecific interactions such as competition or nest predation may be important factors for raven breeding success and we included reproductive performance of neighbors as a proxy for competitive strength in our analyses.

## Methods

### Study area

The study was conducted in the Polish part of Białowieża Forest (ca 600 km<sup>2</sup>) which is located on the Polish-Belarusian borderland and represents the best preserved woodland in lowland temperate Europe. The forest includes a protected part, the Białowieża National Park (100 km<sup>2</sup>), and a larger part which is commercially managed for timber extraction and game hunting. The National Park itself is divided into a strictly protected area (47 km<sup>2</sup>) and a section

of previously commercial forest that was added as buffer zone in 1996.

Białowieża Forest is characterized by a mosaic of deciduous and coniferous forest (Faliński 1986). The most characteristic association is the oak-lime-hornbeam forest *Quercus robur*, *Tilia cordata*, *Carpinus betulus*. Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* dominate the coniferous forests. Forestry practices have favored coniferous species and the area covered by deciduous forest has been declining for a century (Jędrzejewska et al. 1994). The only open areas (4% land cover) within the forest are marshes of sedges and reeds in narrow river valleys and village glades. The forest harbors a rich animal community, including five ungulate species (Jędrzejewska and Jędrzejewski 1998). Most common are red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and wild boar *Sus scrofa*. In the early 1990s, the Polish Forestry Administration started an intense hunting campaign to reduce ungulate numbers and facilitate forest growth. As a result, the ungulate population declined by 2 to 3 fold (Jędrzejewski et al. 2002). Large predators include wolves *Canis lupus* and Eurasian lynx *Lynx lynx*. For further details on the study area see Jędrzejewska and Jędrzejewski (1998) and Faliński (1986).

## Field procedures

We analyzed data from three different raven surveys in Białowieża Forest spanning a time period of 16 yr: 1) in 1985–1987, Pugacewicz (1997) performed a systematic search that identified 86 territorial or breeding pairs, 2) between 1988 and 2000 Selva and Pugacewicz opportunistically monitored known territories, but did not search the area systematically, and 3) in 2001 Mueller performed another systematic search yielding 30 territorial or breeding pairs.

In Białowieża Forest, ravens start breeding in February–March and fledglings are leaving the nest in the end of April/early May. We searched for raven nests from February to April, prior to leaf-out of deciduous trees. For the systematic searches we monitored the entire area by patrolling regularly the grid of forest roads and paths; additionally raven activities and presence were noted the whole year round during other fieldwork. Ravens are very vocal and their general presence is easily detected. In addition to listening to calls we located territorial pairs by looking at territorial displays, transfer of nest material etc. Whenever we noticed ravens we searched the area intensively to find the nest. We also checked all nest sites that were known to be occupied during previous years. However, since the area is densely forested, sometimes we were unable to find the exact location of the nest while being well aware that a territorial raven pair was present in that particular area. Only within a restricted core survey area of 430 km<sup>2</sup> (Fig. 1) we found every nest during the surveys in 1985–1987 and 2001 ( $n = 48$  in 1985–1987, and  $n = 20$  in 2001).

In all surveys (1985–2001) we visited breeding pairs systematically during the breeding season and evaluated if the pair was successful (a minimum of 1 fledgling observed) or not (no signs of fledglings). Overall 139 breeding

attempts were monitored in 12 different years across 66 different territories in the entire study area. In 2001, Mueller additionally determined the number of fledged chicks via repeated long-term observations with a telescopic lens for 20 breeding pairs. For all raven nests extant in 2001 (regardless whether they were actually occupied that year or used only in previous years, total  $n = 38$ ), Mueller also recorded the species and the height of nesting trees with a clinometer.

## Remote sensing and GIS-related analyses

To analyze raven foraging habitats on a broader scale, we used a Landsat TM scene taken in July 1997. The image was classified into 41 vegetation classes using an unsupervised classification. The labeling of the land cover classes was carried out based upon field verification in June 1998 (for further details see Prins 1999). We focused on differentiating among the three major habitat types (deciduous-dominated forest, coniferous-dominated forest and open areas) that provide different food supply for ravens (i.e. rodents and ungulate carcasses, Aulak 1970, Jędrzejewski and Jędrzejewska 1996, Jędrzejewska and Jędrzejewski 1998, Selva 2004). The 41 vegetation classes were merged according to these three habitat categories (Fig. 1). We did not consider areas delineated as water bodies and mixed forest ( $\leq 8\%$  of the landscape), as they could not be assigned to any of the above categories. Forestry practices consist mainly of small clear-cuts which are reforested later on, preferentially with conifers. Between 1985 and 1999,  $< 2300$  ha, i.e. ca 3% of the study area, were clear-cut. Thus, for the purpose of our study the Landsat image of 1997 represented the main habitat types across the entire survey period reasonably well (see Prins 1999 for more details).

From the classified map we calculated the extent of the 3 landcover classes at different scales around each nest site (buffers of 150, 500, 900, 1500 and 2000 m radii). Larger radii did not seem appropriate given a parallel study that estimated the territory size of ravens in Białowieża Forest to be 13.1 km<sup>2</sup>, which corresponds to a radius of 2040 m (Rösner and Selva 2005).

## Statistical analyses of spatial distributions and breeding performance

Within the core survey area (Fig. 1) we calculated the density of raven nests for the surveys in 1985–1987 and 2001 including all territorial and breeding pairs. We then characterized the spatial regularity of these nests using nearest neighbor distances (NND), correcting for edge effects with a boundary strip (Fig. 2, Krebs 1989), and calculated the index of aggregation (R, values above 1 indicate regularity; Clark and Evans 1954, Krebs 1989). We used logistic mixed models (lmer function in MASS library in R; Bates 2005, R Development Core Team 2006) to test the effects of habitat composition on breeding success for all breeding attempts observed (surveys from 1985 to 2001;  $n = 139$ ). We tested the effects of the proportion of open areas and deciduous forest (and in alternative models, the proportion of coniferous forest) at different scales using

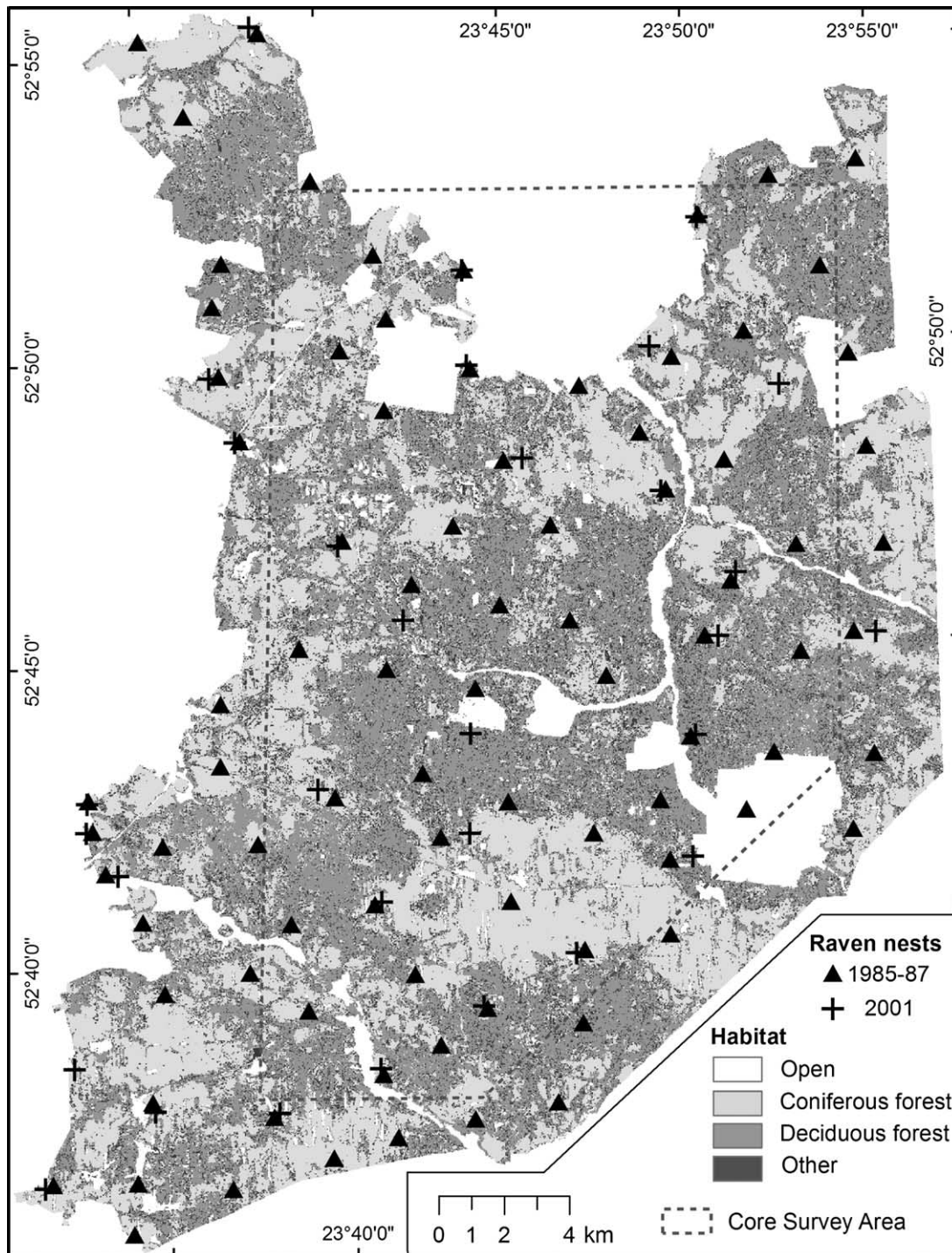


Figure 1. Map of the study area (Białowieża Forest, eastern Poland) showing the main habitat types and the location of raven nests in the 1985–1987 and 2001 surveys. Habitat category “other” refers to mixed forests and water bodies.

buffer sizes from 150 to 1500 m. Due to the higher density of ravens in the 1980s, and consequently smaller NNDs and territories, we did not include the largest radius (2000 m) for this analysis. We included the territory ( $n = 66$ ), year ( $n = 12$ ) and observer ( $n = 3$ ) as random factors. For breeding pairs of the 2001 survey ( $n = 20$ ), for which we had the exact numbers of fledged chicks, we performed analyses with the same explanatory variables (the percentage of open areas and deciduous forest in buffers from 150 to

2000 m) but with the number of fledglings as response using generalized linear models with Poisson errors. For these analyses we included two additional explanatory variables to check whether they could explain additional variance in breeding performance: nest height and intraspecific interactions. We accounted for intraspecific interactions by considering the success of the nearest neighbor as a proxy of its competitive ability. Since the distribution of fledglings (min = 0, max = 5, mean = 2.6) was divided into

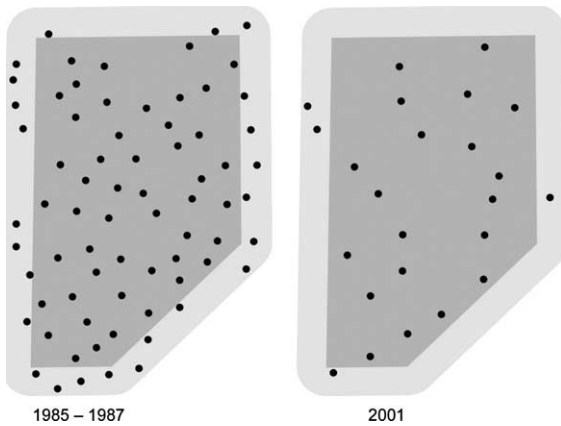


Figure 2. Distribution of breeding and territorial pairs in 1985–87 and 2001 within a core census zone (440 km<sup>2</sup>); boundary strip in light gray.

two almost equally-sized groups (one group had 0, 1, or 2 chicks (n = 11) and another 4 or 5 chicks (n = 9), no brood fledged 3 chicks in 2001), we defined a 2-level factor that distinguished very successful neighbors from less successful neighbors (>3 fledglings versus <3 fledglings). We used maximum likelihood and the Akaike information criterion for model selection.

## Results

### Density and spatial distribution of nests

Within the core survey area, we recorded a density of 11 pairs 100 km<sup>-2</sup> in 1985–1987 (n = 48) compared to only 5 pairs 100 km<sup>-2</sup> in 2001 (n = 20, Fig. 2). Thus, the number of raven pairs declined more than 2 fold over the 16-yr period between the two surveys. Longevity of some nest sites was high, as approximately 50% of the nest sites found in 2001 were already in use 16 yr earlier. For both surveys, 1985–1987 and 2001, the index of aggregation

showed that raven nests were spatially dispersed rather than clumped or randomly distributed (for the 1985–1987 survey: n = 48, mean NND = 2.22 km, SD = 0.31 km, R = 1.48, p < 0.001; for the 2001 survey: n = 20, mean NND = 3.26 km, SD = 0.59 km, R = 1.38, p < 0.001).

### Habitat selection

Raven nests were distributed over the entire forest area and occurred at the ecotone as well as in the forest interior (Fig. 1). Nests were almost exclusively located in the top of large old pine trees. The only exceptions (6 of 139 monitored breeding attempts) were built in spruce trees. These exceptions happened only where the nest site was located far (>1 km) from the nearest stand of old pines. The average height of the nests was 28.38 m (n = 38, SD = 4.89 m, min. = 14.5 m, max. = 37 m).

In the immediate proximity of nesting trees, territories were dominated by coniferous rather than deciduous forest. Within the 150 m buffers around nests, forests had a median of 74% coniferous areas. Such conifer-dominance exceeded the nearly equal mix of coniferous and deciduous forest in the study area as a whole (51% coniferous forest; open areas were excluded for comparisons in the direct neighborhood of nests; Wilcoxon test: n = 66, V = 1681, p < 0.001). On increasingly larger scales, the dominance of coniferous forest decreased, and relatively more habitat around each nest was covered by deciduous forest and open areas (Fig. 3A).

### Habitat effects on breeding performance

At the smallest scale (the nesting tree itself) we did not find any significant relationship between habitat characteristics and breeding performance. Nest height did not affect breeding performance in any of the models we tested and was excluded based on AIC. We could not test for any effect of nesting tree species because pines were almost exclusively chosen as nest sites.

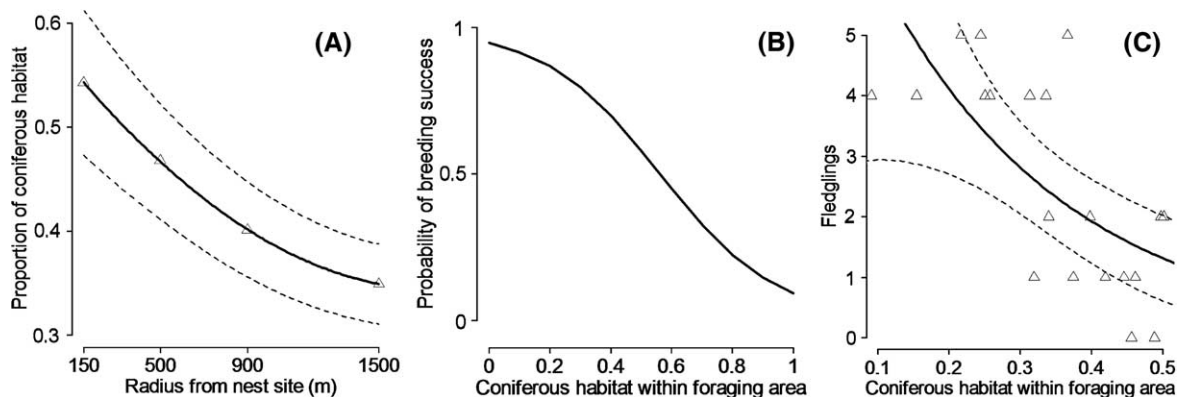


Figure 3. Landscape composition of raven territories at different spatial scales and its effect on breeding performance. (A) Site selection of 66 raven territories in relation to coniferous areas at increasing scales around nests. Triangles display the mean values, whereas lines give the smooth fit of means and 95% confidence intervals. (B) Logistic mixed model predicting the effects of the proportion of coniferous forest within 1500 m around nests on the probability of raising chicks vs no chicks (n = 139 broods in 66 territories monitored between 1985 and 2001, for model details see Table 1B). (C) Model prediction and 95% confidence intervals of the Poisson model of the effects of the proportion of coniferous forest within 2000 m around nests on the number of fledged chicks (n = 20 broods monitored in 2001, for model details see Table 2B).

In contrast, habitat composition of the area surrounding a nest had a significant impact on raven breeding performance, with stronger effects observed at larger scales. Coniferous-dominated forest, the typical nesting habitat, negatively affected the probability of breeding success (data from all surveys 1985–2001, Fig. 3B). Open areas and deciduous forests had a positive effect on breeding success (Table 1). Larger scale models (including habitat within 900 and 1500 m buffers around nests) had a better fit compared to models with smaller radii (150 and 500 m buffers; Table 1A). The best fit model (1500 m buffer) predicted that areas entirely covered by coniferous habitats resulted in a probability of breeding success close to zero, while territories that comprised <50% coniferous areas usually yielded fledglings (Table 1B, Fig. 3B).

We obtained similar results when examining the number of fledged chicks in 2001 ( $n=20$ , mean number of chicks = 2.6,  $SD=1.73$ , min. = 0, max. = 5). Deciduous stands and open areas had a positive effect on the number of fledglings, explaining about 45% of the deviance, whereas coniferous areas negatively affected breeding performance (Table 2, Fig. 3C). The explanatory value of the habitat variables increased with increasing buffer sizes around nests, with a best fit of the 2000 m model (Table 2A, Fig. 4). When intra-specific interactions, represented as very successful neighbors, was added to this model, the explanatory value increased significantly, explaining up to 65% of the deviance (Table 2C).

## Discussion

Here we have taken a synthetic approach towards habitat suitability analyses, studying habitat preferences and breeding success of common ravens with regard to multiple selection criteria across a range of spatial scales. Our work highlights the importance of scale-dependent resource complementation since ravens selected conifers as nest sites but were dependent on deciduous and opens areas at the broader scales of the foraging habitat. In addition to habitat related factors, intraspecific interactions appeared to be important determinants of breeding success.

Understanding complex habitat selection behavior may have considerable implications to better predict population

dynamics under changing management scenarios. This may be particularly relevant for ravens in Białowieża Forest since over the 16 yr time span of our study we found that raven densities declined more than 50%. Previous studies have shown that worsening conditions of foraging habitats and the subsequent decrease of food supply may cause population declines in ravens. For example, the expansion of coniferous forest had a negative influence on raven abundance and breeding success in other areas (Newton et al. 1982, Gibbons et al. 1995). In Britain, the disappearance of critical foraging habitat (“sheep walk”) due to afforestation together with the reduction of available carrion due to improved sheep management were the main causes of raven population decline (Marquiss et al. 1978). In Białowieża Forest, the substitution of deciduous stands for fast growing conifers has been a common forestry practice for the last century (Jędrzejewska et al. 1994). However, these changes happened over time frames much longer than the 16 yr interval between our raven surveys.

More recently though, from 1991 to 1995, the Polish Forestry Administration conducted an intense reduction of ungulate numbers to promote forest growth. Total ungulate densities fell from 16 ungulates  $\text{km}^{-2}$  in winter 1991–1992 to 6 ungulates  $\text{km}^{-2}$  in 1997–1998 (Jędrzejewski et al. 2002). These practices may have significantly reduced carrion availability (Selva 2004) and may be related to the decline of ravens we observed in Białowieża Forest. Ungulate carrion is an extremely important food resource for ravens in temperate and northern latitudes in general (Heinrich 1989) and its relevance has been particularly well documented for Białowieża Forest (Selva 2004, Rösner et al. 2005, Selva et al. 2005). Carrion is especially critical during the breeding season, starting in February, when most other food resources are depleted or unavailable but carrion resources peak (Jędrzejewska and Jędrzejewski 1998, Selva 2004, Selva et al. 2005). In this context, the shortage of ungulate carrion in other central European forests (mainly due to the absence of top mammalian predators) could partly explain why ravens there do not breed in the forest interior, but only close to the forest edges, where agricultural land is in close proximity and other food sources are available (Grünkorn 1991a, b).

To better understand raven habitat requirements we used a multiscale approach and found a pronounced

Table 1. Multi-model inference based on logistic mixed models predicting the effects of habitat types at areas of different radii around nests on the probability of breeding success ( $n=139$  broods, null deviance = 175). The territory, observer, and year were included as random factors. Models include the proportion of coniferous forest (deviance: 157.2, DF: 138) or alternatively, the proportion of open and deciduous-dominated areas (deviance: 158.4, DF: 137) as fixed effects. Results of the analysis are shown for the best model. Signif. codes: “\*\*\*\*”  $p < 0.001$ , “\*\*\*”  $p < 0.01$ , “\*\*”  $p < 0.05$ .

(A) Model selection (AIC)	150 m	500 m	900 m	1500 m	
coniferous	175.6	172.2	169.6	167.2	
deciduous and open	174.8	174.2	171.2	170.4	
(B) Model (1500 m)	Fixed effects	Estimate	SE	Random effects	SD
coniferous	(Intercept)	2.952***	0.815	Territory	0.839
	Coniferous	−5.251**	1.642	Year	0.000
				Observer	0.806
deciduous and open	(Intercept)	−1.660	1.053	Territory	0.872
	Deciduous	5.742*	2.158	Year	0.000
	Open	4.619*	1.597	Observer	0.826

Table 2. Effects of the proportion of coniferous forest or, alternatively, of the proportion of open and deciduous areas on the number of fledglings observed in 20 nests monitored in 2001. Generalized linear models were fitted using a Poisson error distribution and log link. Null deviance for both models: 26.542, DF: 19. (A) model selection, (B) best model including habitat variables, (C) model including habitat as well as intraspecific competition (as factor distinguishing very successful neighbors). Significance codes: "\*\*\*\*"  $p < 0.001$ , "\*\*\*"  $p < 0.01$ , "\*\*"  $p < 0.05$ , "\*"  $p < 0.1$ .

(A) Model selection (AIC)	150 m	500 m	900 m	1500 m	2000 m
coniferous	79.759	78.332	78.417	74.195	70.249
deciduous and open	81.324	79.858	77.948	74.549	71.096
(B) Model (2000 m)	Fixed effects		Estimate	SE	Dev. exp.
coniferous	(Intercept)		2.176***	0.363	0.406
	Coniferous		-3.806***	1.145	
deciduous and open	(Intercept)		-1.399.	0.749	0.450
	Deciduous		4.327**	1.403	
	Open		3.995***	1.162	
(C) Model (+competition)	Fixed effects		Estimate	SE	Dev. exp.
coniferous	(Intercept)		2.448***	0.382	0.614
	Coniferous		-3.873**	1.192	
	Competition		-0.691*	0.306	
deciduous and open	(Intercept)		-1.331.	0.796	0.653
	Deciduous		4.897**	1.523	
	Open		4.000***	1.212	
	Competition		-0.715*	0.319	

disparity across scales. On a small scale, coniferous stands were selected as nesting areas, but on larger scales coniferous-dominated areas had a negative effect on breeding success. Large Scots pines were almost exclusively selected by ravens as nest sites in Białowieża Forest, which is also the case in several other areas (Ratcliffe 1997). Such large pines provide good visibility; due to their height and morphology they may be more difficult for humans to access (Ratcliffe 1997), and they rarely uproot or fall in windstorms (Peltola et al. 2000, Mueller et al. unpubl.). In our study, we only once recorded a brood loss due to falling of the nesting tree and it was a spruce. This is an important consideration because Pugacewicz (2005) found that in north-eastern Poland, where ravens breed not just in pines but in various tree species, 47% of brood losses were associated with nest or tree falling. In Białowieża Forest, nesting trees were usually tall and we could not find any relationship between nest height and breeding performance. However in areas where nesting trees are generally smaller, broods in lower nests tended to be less successful (Davis and Davis 1984, Dombrowski et al. 1998).

While we did not find any relation between nest site characteristics and reproductive success on a small scale, habitat composition at broader scales had strong effects on breeding performance. In all analyses, the largest buffer radius had the greatest explanatory value of habitat effects on reproductive performance. The scale that best predicted habitat effects on number of fledglings in 2001 (2000 m) almost exactly coincided with estimates of raven territory size obtained from experimental allocation of marked carrion in the same year and area (2040 m, Rösner and Selva 2005), suggesting that the birds use their territories up to the boundary with high efficiency. Such explorative approaches towards scale sensitivity are seldom pursued in bird habitat modeling analyses (but see Thompson and McGarigal 2002, Graf et al. 2005), but may be critical to determine appropriate estimates for ecological meaningful

units (e.g., scale of nesting habitat versus scale of foraging habitat).

In addition to habitat effects and despite a regular spacing, intra-specific competition was an important determinant of breeding success which has been also shown for other bird species (Denac 2006). Such negative effects could arise when neighbors displace conspecifics from food resources in adjoining territories, or, alternatively, when they predate other ravens' nests. However, little evidence exists regarding the importance of intra-specific nest predation in raven populations, and raven pairs very rarely trespass neighbor territories (Rösner and Selva 2005). Nevertheless, some studies show that pairs breeding too

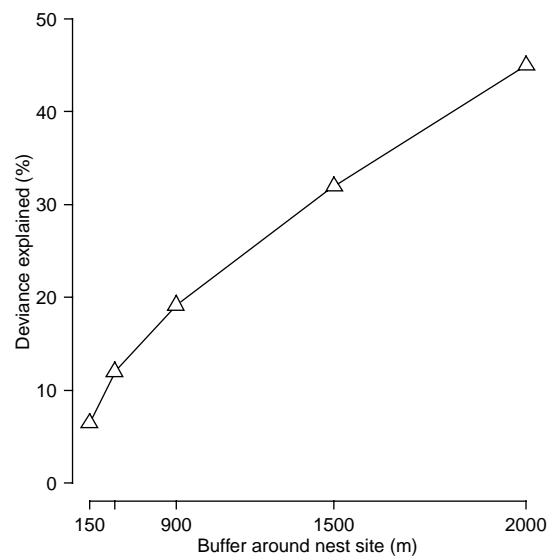


Figure 4. Effect of scale on predicting breeding performance (number of fledglings) within a single year (2001) using a Poisson model and deciduous and open habitats as predictor variables ( $n = 20$  broods).

close to each other (for example at dumps) experience low reproductive success (Grünkorn 1991a, b). Thus far, few studies have incorporated intra-specific competition in bird habitat models (Doligez et al. 1999); we suggest that this aspect may deserve more attention in future research. As an additional component that affects breeding performance, other studies have found the occupation rate of territories to be important (e.g. in black kites *Milvus migrans*; Sergio and Newton 2003). In our study, we found some nest sites in 1985 and 2001 at the same location. Ravens form life-long bonds and are long lived, so that at least theoretically it is possible that some pairs were present at the same site for over 16 yr. However, we could not confirm whether these nests had been continuously occupied by the very same raven pairs, and we did not focus on the effect of occupation rate on breeding performance in this study.

We conclude that intraspecific factors together with a combination of complementary resources at their respective scales – deciduous forests and open areas as good foraging habitat together with coniferous-dominated forests as nesting areas – constitute suitable raven habitat in Białowieża Forest. Thus far, resource complementation studies have focused on 1) complementary edge effects and 2) landscape complementation in patchy landscapes, both of which are related to the scale-dependent complementarity we have focused on here. In the context of habitat edges, Ries and Sisk (2004) built a framework that includes positive edge response via complementary resource distributions in adjacent habitats. Many examples within the edge literature exist that document complementary edge effects for birds including corvids (references in Ries et al. 2004). For instance, edge habitats between suburban and forested areas provide opportunities for both foraging and roosting in Torresian crows (*Corvus orru*, Everding and Montgomerie 2000). On a broader scale, landscape ecologists use the term “landscape complementation” to describe multiple, spatially disjunct patches that together constitute the resources an organisms depends on to fulfill its lifecycle (Dunning et al. 1992). In this context, ecologists have focused on the distance between patches as a criterion whether resources complement each other (e.g. breeding ponds and summer habitat for frogs, Pope et al. 2000; thermal refuges and food resources for pigs, Choquenot and Ruscoe 2003). Scale-dependent resource complementarity for ravens in Białowieża Forest is different in that the forest is an interwoven mosaic in which the different habitat types are never far apart. Neither the presence/absence of habitats edges nor the distance between different habitat patches would have been useful to reveal complementarity of resources. We addressed this issue by considering gradients in landscape composition at varying scales to reveal resource complementation.

Our results show that a systematic analysis of the relative abundance of the different habitat types as a function of spatial scale provides new insights in habitat suitability studies and a better understanding of species requirements and habitat selection processes. Scale sensitive landscape composition may be an important concept to understand resource complementation and guide future studies that try to discern important habitat components across varying scales (Haynes et al. 2007). Considering multiple scales of habitat characteristics in combination with reproductive

parameters may considerably increase our understanding of the processes that determine the distribution and abundance of species in complex landscapes.

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