Ornis Fennica 81:109–118. 2004

Habitat selection and patterns of distribution in a hierarchic forest owl guild

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Received 18 September 2003, accepted 20 March 2004

Patterns of segregation were studied in a size-structured forest owl guild with the largest Ural Owl *Strix uralensis*, intermediate Tawny Owl *Strix aluco*, and the smallest Tengmalm's Owl *Aegolius funereus*, by comparing habitat selection and patterns of distribution. Data on owl territories were collected between 1998 and 2003 on Mt. Krim, North Dinaric Alps, central Slovenia, using the playback method. The Ural Owl was the dominant species, occupying the largest part of its optimal habitat, i.e. its fundamental niche. The Tawny Owl had the widest habitat niche. Due to negative interactions it selected refugial areas free of Ural Owls, which were in lowlands only, where human influences prevent Ural Owls from settling. Tengmalm's Owl was the most specialised in habitat selection. Its territories were on high altitudes, within those of the Ural Owl. They inhabited similar habitats but we found no indications of interactions between them. In contrast, Tawny and Tengmalm's Owls were highly segregated in habitat and in space, due to distinctive negative interactions. Based on these results, we propose the following hypothesis: Tengmalm's Owl benefits from the presence of Ural Owls, which creates Tawny Owl free areas; this association does not affect the Ural Owl. This could be the first case of positive interactions in a predatory guild, i.e. a specific type of commensalism.

1. Introduction

A guild is a group of species that exploit the same class of environmental resources in a similar way (Root 1967). Interspecific competition is thus most likely to occur between guild members (Begon *et al.* 1996). In predator guilds, especially if the species differ considerably in size, the effects of negative interactions can be even more marked, and can be expressed as interspecific competition and intraguild predation (see e.g. Polis & McCromick 1987, Polis & Holt 1992, Fedriani *et al.* 1999, 2000, Sergio *et al.* 2003). Very few positive interactions have been observed within guilds (e.g. Elmberg *et al.* 1997). Their importance in natural communities has been little studied and is probably an underestimated phenomenon compared to negative interactions (Odum 1971, Begon *et al.* 1996, Forsman *et al.* 2002).

According to the simple theory of competition (Schoener 1982), guild species should shift their niche in order to coexist. There are three broad niche dimensions along which resource partitioning is developed: food, space, and time (Schoener

1974). In predator guilds, coexisting species reduce the predation risk and avoid direct agonistic interactions, rather than change their food habits (Jaksić & Braker 1983, Fedriani *et al.* 1999, Gerstell & Bednarz 1999). Segregation therefore often tends to be on temporal or spatial levels only (e.g. Jaksić 1982, Polis & McCromick 1987, Fedriani *et al.* 2000).

Spatial segregation can be understood as a specific form of habitat selection (Janes 1985), which results in a distinctive pattern of distribution of individuals. In predators, the dominant species occupy their preferred habitats, i.e. the fundamental niches, and the subordinate species suboptimal habitats, i.e. the realised niches (Polis & McCromick 1987, Newton 1998) which, on the local scale, act as refugia. In this way habitat segregation is actually, for subordinate species, a simple avoidance mechanism (Sergio *et al.* 2003).

We studied three sympatric owl species: Ural *Strix uralensis*, Tawny *Strix aluco*, and Tengmalm's Owls *Aegolius funereus*. All three belong to the same guild and are mainly nocturnal, vole eating predators (Mikkola 1983, König *et al.* 1999). Although their ranges in Europe overlap in several regions, only a few attempts to describe their mutual interactions have been made (e.g. Solonen 1993, Vrezec 2003). Studies of individual pairs have provided evidence of Ural Owl predation on Tawny and Tengmalm's Owls (Kohl & Hamar 1978, Mikkola 1983, Jäderholm 1987). Nevertheless, Hakkarainen and Korpimäki (1996) proved that Tengmalm's Owl can breed within Ural Owl territory, although this is supposed to be its suboptimal habitat. On the other hand, Tawny Owl is one of the most important predators on Tengmalm's Owl in Europe (Locker & Flügge 1998, König *et al.* 1999, Augst 2000), and the species are highly segregated (Vrezec 2003). Mikkola (1983) predicted the possibility of vigorous competition between them, as they show the highest similarity in hunting activity of all European owls. Ural and Tawny Owl also segregate in habitat use, indicating a competitive exclusion between them (Lundberg 1980, Korpimäki 1986, Vrezec & Tome in press).

Large species are usually dominant in interspecific aggression, and exclude smaller, subordinate species (Brown & Maurer 1986, Petty *et al.* 2003). We predicted an ecological hierarchy among sympatric owls in our study area, with the largest Ural Owl as the dominant and the intermediate Tawny and the smallest Tengmalm's Owl as subordinate species (for morphological characteristics see e.g. Glutz von Blotzheim & Bauer 1994). According to this prediction, (1) Ural Owl would occupy the largest part of the optimal habitat, i.e. its fundamental niche, (2) Tawny Owl, the first subordinate species, would use refugia not occupied by Ural Owl, while (3) Tengmalm's Owl, the second subordinate species, would occupy areas free of both Ural and Tawny Owls and, in addition, manage to use areas within the Ural Owl territory as well. The latter could constitute the first known case of positive interaction within a predator guild. We tested this scheme of heterospecific relations, comparing the habitats and distribution patterns of all three species in sympatry.

2. Study area and methods

2.1. Study area

The study was carried out on Mt. Krim (14°25'55''E, 45°58'15''N), 10 km south of Ljubljana city (central Slovenia). The area is 140 km^2, 77% of which is covered with forest and 20% is not forested, the remainder being urban areas (i.e. settlements) which are situated only in lowlands. Mt. Krim is a medium height mountain in the North Dinaric Alps with a broadly extended plateau range at an altitude around 800 m asl (Fig. 1), ranging from 290 to 1,108 m asl. The slopes of Mt. Krim are covered predominantly with mixed forest. The dominant tree species are Beech *Fagus sylvatica* and Silver Fir *Abies alba*. Most of the forest is in an old growth phase, with trees whose trunk diameter is more than 30 cm at breast height. This characteristic provides enough suitable natural nest tree holes for owls. Other more common tree species in the area are Norway Spruce *Picea abies*, Scots Pine *Pinus sylvestris*, Sycamore *Acer pseudoplatanus*, Hop Hornbeam *Ostrya carpinifolia*, Hornbeam *Carpinus betulus*, Flowering Ash *Fraxinus ornus* and Durmast Oak *Quercus sessiliflora*. Coniferous plantations of Norway Spruce are located mainly on lower parts of the mountain and around settlements, where forestry is most intensive. Clearings are small and dispersed, mostly

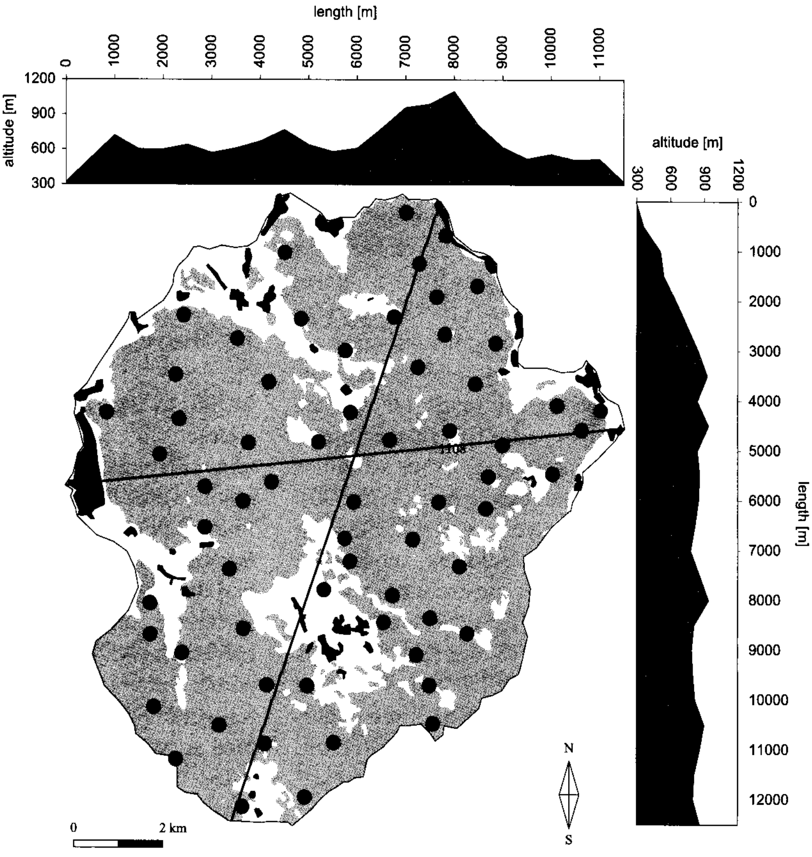

Fig. 1: The study area of Mt. Krim (140 km^2) with the distribution of survey points for identifying distribution patterns of sympatric owls (marked with dots). The light grey area is area covered with forest, dark grey areas are settlements, and white are clearings. Two cross-sections and graphs show the relief of the area. The highest peak is marked with cross (1,108 m asl).

around the settlements. (Furlan 1988, Slovenian Forest Service unpubl.)

Other raptors, potential owl predators, such as Common Buzzard *Buteo buteo*, Goshawk *Accipiter gentilis,* and Sparrowhawk *Accipiter nisus*, are scarce on Mt. Krim (Vrezec 2000). The densities of potential mammal predators in the area, such as Stone Marten *Martes foina*, Red Fox *Vulpes vulpes*, and Wildcat *Felis sylvestris* (Kryštufek 1982, 1991), are not known, but they are evenly distributed all over the forests of Mt. Krim (pers. observ.), so we consider their influence on the distribution pattern of the owls as minimal.

2.2. Habitat selection analysis

We used the playback method to census owl territories on 41 survey points, selected randomly from the bottom of Mt. Krim to the top, and stratified according to the area of altitudinal belts. Survey points were spaced 700 to 2,150 m apart and were surveyed annually. Surveys were conducted during the breeding season, three times a month, from dusk to approximately midnight, under favourable weather conditions, in years 1998 to 2000. On any particular survey night, only one species' playback call was used, in order to avoid agonistic interactions between owl species. Playbacks were broadcast at each point for 10 min, followed by a 5-min listening period (see also Vrezec 2003). Each time an owl replied to the playback was considered as a positive response. Around each survey point an effective survey area (ESA) of radius 500 m was defined, as a representative part of an owl's territory. The territory was defined as occupied if we recorded an owl response within the ESA at least once in the three year period.

For each of 41 ESAs the following habitat variables were measured: (1) altitude (survey point), (2) maximal slope, (3) proportion of clearings (non-forested areas), (4) presence or absence of settlements (every permanently inhabited building in the ESA), (5) proportion of different forest types (coniferous, deciduous, and mixed, defined as a stand with 40 to 60% of coniferous trees), and (6) proportion of different forest growth phases. Forest growth phases were divided, according to the mean thickness of the tree trunks, into three categories: (1) young (diameter of the trunk at breast height, $D < 10$ cm), middle-aged ($10 < D < 30$ cm) and old ($D > 30$ cm). The proportions of forest types and forest growth phases in ESAs were defined from phytocenological maps on a scale 1:10,000 and assigned to one of five classes (upper limit: 0, 25, 50, 75 and 100%). Other variables were calculated from a landscape map (1:25,000). To define the representativeness of 41 ESAs for the whole study area, we selected another 52 points, each surrounded by a corresponding 500 m area. They were selected in a systematic grid (Gauß-Krüger coordinate of starting point: x 5457000, y 5092000) at every 2,000 m. For these systematically selected areas (SSA) we determined only habitat variables. Representativeness was determined by comparison of habitat variables values between ESAs and SSAs using Mann-Whitney U and χ^2 tests.

By comparing values of variables from ESAs used by certain owl species with those not occupied by it, we determined which features influenced habitat preferences of owls. For comparison we used Mann-Whitney U and χ^2 tests. For χ^2 calculations, classes with low frequency were summed with adjacent classes, and Yates correction was used where necessary. We employed multivariate discriminant function analysis, using the forward stepwise method (Manly 1994) to establish the degree of overlap between all three sympatric owls. Standardized coefficients determine the magnitude and direction of the contribution of each habitat variable to canonical functions. The ultimate measure of niche overlap was the squared Mahalanobis distance (D^2) between group centroids – a measure of how close or how far the species are in multi-variable space defined by discriminant functions (Manly 1994). When two species overlap completely, centroids are at the same point and $D^2 = 0$.

Niche breadth (B) in habitat selection was measured with Levins' index (1968), where p_i is the proportion of class i in a particular habitat variable:

$$B = 1 / \Sigma p_i^2 \qquad (1).$$

From the niche breadths of every habitat variable considered, the average (± standard deviation) niche breadth was calculated for each owl species.

2.3. Distribution pattern analysis

In 2001 to 2003 a set of surveys were conducted on a larger scale in order to identify distribution patterns of sympatric owl territories. 21 new survey points were added to the existing 41 ESAs (Fig. 1). The additional points should provide the total number of territorial owls and a picture of their actual distribution in the whole study area. For this survey the same playback method was used as in habitat analysis. The exact locations of survey points were established using GPS system (Gauß-Krüger coordinates) and distances between occupied survey points were calculated from coordinates. If two owl territories were detected on the same survey point, the distance was 0 m, otherwise we considered the distance between two survey points. Distribution patterns were calculated according to the nearest neighbour distance method, using the standard normal deviate (Krebs 1989), where $z = 0$ indicates random, $z > 0$ uniform and $z < 0$ clumped distributions. We used distances only to the first nearest neighbour. To calculate the expected distance, we assumed that our survey method was sufficiently extensive to find almost all territorial pairs. Nearest neighbour distances were used for each year separately while the densities were averaged over all three study years. Thus we calculated the expected nearest neighbour distance from the average density as it would be if the distribution was random.

We investigated interactions by the type of joined two-species (heterospecific) distribution pattern in homogeneous space. A uniform distribution maximises nearest neighbour distances, indicating a type of negative interaction between species separated in the space (Odum 1971). On the other hand, random or clumped distribution shows that the two species are not segregated in the space, what indicates that there are no interactions

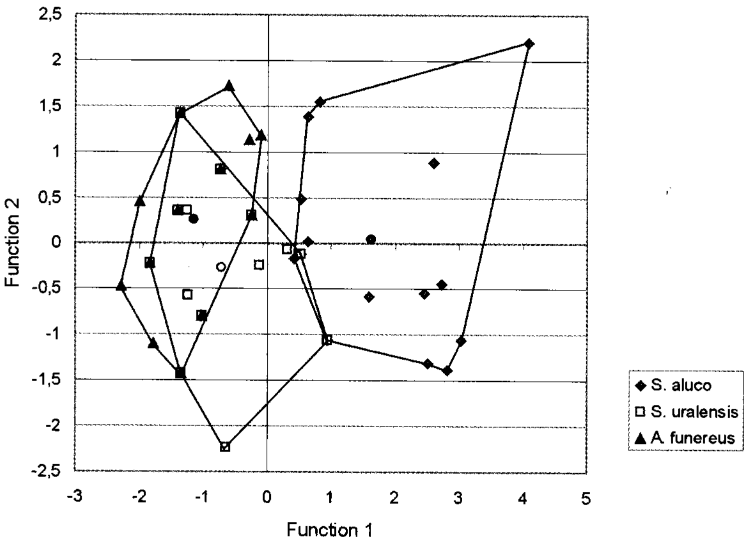

Fig. 2: Plot of the individual scores and group centroids (marked with circles) for the two functions, discriminating between Ural, Tawny and Tengmalm's Owls.

between them or there are even some positive interactions, where one species prefers staying close to the other more than staying just anywhere in a space.

3. Results

3.1. Habitat selection

In the 41 ESAs searched in 1998 to 2000, a total of 618 point counts were done. Our data on used habitat variables corresponded well to the actual habitat characteristics in the area of Mt. Krim, while we did not find any significant differences between ESAs and SSAs (Table 1). Ural Owl was detected in 15 (36.6%), Tawny Owl in 17 (41.5%) and Tengmalm's Owl in 13 (31.7%) of all ESAs. Tawny Owl significantly selected lower, and Tengmalm's Owl higher altitudes, while Ural Owl showed the greatest span in altitudinal distribution (Table 1). Tawny Owl occupied forest with lower proportion of mixed forest type and preferred areas in the vicinity of human settlements, while distributions of Tengmalm's and Ural Owl showed no statistically significant selection of forest type, forest growth phase, proportion of clearings or presence of settlements in the ESAs (Table 1).

In the discriminant function analysis the following habitat variables were included: altitude, presence or absence of settlement, proportion of clearings, slope, proportion of young forest growth phase, and proportion of mixed forest type (Table 2). Others were excluded as redundant as they did not contribute significantly to discrimination. The first discriminant function contributed 97% to the explanation of variation. The function was weighted most by the proportion of clearings, presence of settlement and proportion of young forest growth phase (Table 2). It discriminated well between Tawny Owl and the other two owls (Fig. 2). The second function contributed the remaining 3% of the explanation and had no power to discriminate between the owls (Table 2, Fig. 2). There was a marked niche overlap between Ural and Tengmalm's Owl ($D^2 = 0.57$, ns, df = 6, 37), while niches between Tawny and Ural ($D^2 = 5.82$, $P = 0.0002$, df = 6, 37), and Tawny and Tengmalm's Owl ($D^2 = 8.18$, $P = 0.0002$, df = 6, 37) differed significantly. On average, Tawny Owl had the greatest niche breadth (B = 2.80 ± 1.214), while Tengmalm's Owl appeared to be the most specialized species in its habitat selection (B = 2.09 ± 0.565), and Ural Owl intermediate (B = 2.43 ± 0.84).

3.2. Distribution patterns

In the period 2001 to 2003, 43 Ural, 63 Tawny and 18 Tengmalm's Owl territories were recorded from a total of 665 point counts made on Mt. Krim.

Table 1. Habitat characteristics of all the effective survey areas (ESA) compared with systematically selected areas, showing that the ESAs are representative of the whole study area, and the habitat selection of Ural, Tawny and Tengmalm's Owl. Data were tested using Mann-Whitney U and χ^2 test (Q_1–Q_3-interval between the 1st and 3rd quartiles).

	Med	Min–Max	Q_1–Q_3	Test	P	df
ESA (n = 41)						
Altitude	710 m	320–1060 m	520–820 m	U = 866.5	ns	
Slope	16.7°	5.8–33.2°	12.2–20.8°	U = 1040.5	ns	
Clearings	25%	0–100%	0–25%	$\chi^2 = 0.3$	ns	3
Mixed forest	75%	25–100%	75–100%	$\chi^2 = 1.7$	ns	2
Coniferous forest	0%	0–75%	0–0%	$\chi^2 = 0.0$	ns	1
Deciduous forest	0%	0–75%	0–25%	$\chi^2 = 0.3$	ns	2
Young growth phase	0%	0–25%	0–25%	$\chi^2 = 0.0$	ns	1
Medium growth phase	25%	0–75%	0–50%	$\chi^2 = 1.0$	ns	2
Old growth phase	75%	25–100%	50–75%	$\chi^2 = 3.8$	ns	2
Ural Owl (n = 15)						
Altitude	790 m	410–1060 m	595–840 m	U = 144.0	ns	
Slope	16.5°	10.1–27.0°	11.8–18.3°	U = 152.0	ns	
Clearings	0%	0–100%	0–25%	$\chi^2 = 0.9$	ns	3
Mixed forest	75%	50–100%	75–100%	$\chi^2 = 0.1$	ns	1
Coniferous forest	0%	0–25%	0–0%	$\chi^2 = 0.2$	ns	1
Deciduous forest	0%	0–50%	0–25%	$\chi^2 = 0.1$	ns	1
Young growth phase	0%	0–25%	0–25%	$\chi^2 = 0.9$	ns	1
Medium growth phase	25%	0–75%	13–38%	$\chi^2 = 0.0$	ns	2
Old growth phase	50%	25–100%	50–75%	$\chi^2 = 0.0$	ns	2
Tawny Owl (n = 17)						
Altitude	540 m	320–850 m	410–660 m	U = 108.0	0.007	
Slope	17.9°	8.1–33.2°	12.9–21.2°	U = 163.5	ns	
Clearings	25%	0–50%	0–25%	$\chi^2 = 1.9$	ns	3
Mixed forest	75%	25–100%	50–75%	$\chi^2 = 4.3$	0.040	1
Coniferous forest	0%	0–75%	0–0%	$\chi^2 = 0.4$	ns	1
Deciduous forest	25%	0–75%	0–25%	$\chi^2 = 1.8$	ns	1
Young growth phase	0%	0–25%	0–0%	$\chi^2 = 2.4$	ns	1
Medium growth phase	50%	0–75%	25–50%	$\chi^2 = 0.1$	ns	2
Old growth phase	50%	25–100%	50–75%	$\chi^2 = 2.1$	ns	2
Tengmalm's Owl (n = 13)						
Altitude	800 m	700–940 m	790–850 m	U = 83.0	0.004	
Slope	14.4°	5.8–20.2°	11.7–17.6°	U = 126.0	ns	
Clearings	25%	0–100%	0–25%	$\chi^2 = 0.3$	ns	3
Mixed forest	100%	75–100%	75–100%	$\chi^2 = 0.6$	ns	1
Coniferous forest	0%	0–25%	0–0%	$\chi^2 = 1.1$	ns	1
Deciduous forest	0%	0–25%	0–25%	$\chi^2 = 0.0$	ns	1
Young growth phase	0%	0–25%	0–25%	$\chi^2 = 3.5$	ns	1
Medium growth phase	25%	0–50%	0–25%	$\chi^2 = 0.9$	ns	2
Old growth phase	75%	25–100%	50–75%	$\chi^2 = 2.0$	ns	2
Settlements	Proportion of ESAs with settlements					
ESA (n = 41)		26.8%		$\chi^2 = 3.1$	ns	1
Ural Owl (n = 15)		13.3%		$\chi^2 = 2.0$	ns	1
Tawny Owl (n = 17)		58.8%		$\chi^2 = 10.3$	0.001	1
Tengmalm's Owl (n = 13)		7.7%		$\chi^2 = 3.3$	ns	1

Table 2. Values of standardized coefficients for six ecological factors in two discriminant functions and the significance of these functions.

Habitat variables	Function 1	Function 2
Altitude	–0.587	0.793
Settlement	1.109	0.627
Clearings	–1.494	–1.319
Slope	0.532	–0.135
Young forest growth phase	0.822	1.065
Mixed forest type	–0.573	–1.015
Wilks' lambda	0.366	0.953
χ^2	38.678	1.835
Df	12	5
P	0.0001	ns
Eigen value	1.604	0.049
Proportion	97%	3%

Tengmalm's Owl was excluded from calculations for year 2001, since only one territory was found in this year. The smallest nearest neighbour distances were observed for Tengmalm's Owls, while the largest were between territories of Ural Owls. According to the nearest neighbour distance method, Ural Owl was distributed randomly, but both others in clumps (Table 3). The smallest heterospecific nearest neighbour distances were between Ural and Tengmalm's Owl territories, and the largest between Tawny and Tengmalm's Owl territories. Joint Ural and Tawny Owl, and Tawny and Tengmalm's Owl distributions were uniform, while the results indicated a random distribution of joint Ural and Tengmalm's Owl territories (Table 3).

4. Discussion

The study area, Mt. Krim, is covered with more or less continuous forest, with many large tree holes, which are the most frequently used nest-sites of Ural Owls in Slovenia (Vrezec & Kohek 2002). Settlements are scarce and stands of old forest growth phase are common. According to Mihelič *et al.* (2000) this kind of montane forest is the most suitable habitat for Ural Owls in Slovenia. Since the habitat selection of Ural Owl on Mt. Krim did not differ significantly from average habitat characteristics in the area (Table 1), and since the species distribution in space was random, we suggest that our first prediction was correct – Ural Owl occupied the major part of its optimal habitat, i.e. its fundamental niche.

Tawny Owl had the widest niche of all the owls studied, confirming the findings of Sánchez-Zapata and Calvo (1999), that it is very flexible with regard to habitat selection. Nevertheless, in three out of ten habitat variables, it showed a significant preference, contrary to expectations for a generalist species. The preference for low altitudes in Slovenia has been noted before (Tome 1996, Vrezec 2003). Tawny Owl is capable of inhabiting urban areas (e.g. Galeotti 1994, Ranazzi *et al.* 2000), while Ural Owl is not (Table 1). On the other hand, Ural Owl is known to exclude Tawny Owl from its territories (Vrezec and Tome in press). Since settlements on Mt. Krim are situated in lowlands, we see the preferences only as a consequence of the avoidance mechanism against Ural Owl. This is also confirmed by data on the

Table 3. Mean con- and heterospecific nearest neighbour distances (in metres) between sympatric Ural, Tawny, and Tengmalm's Owls. Distribution patterns were investigated using standard normal deviate (z), where z = 0 means random, z > 0 uniform, and z < 0 clumped distribution.

In meters	Observed	Expected	z	P
Conspecific				
Ural Owl (n = 43)	1,365	1,563	–0.92	ns
Tawny Owl (n = 63)	899	1,291	–2.66	0.007
Tengmalm's Owl (n = 17)	1,252	2,029	–2.20	0.028
Heterospecific				
Ural – Tawny	1,687	947	8.87	< 0.001
Ural – Tengmalm's	1,235	1,220	0.11	ns
Tawny – Tengmalm's	2,373	1,038	14.03	< 0.001

distribution of the two species. The distances between Tawny and Ural Owls were twice as great as distances between Tawny Owls (Table 3), showing an avoidance pattern of Tawny Owl against Ural Owl. The joint population of these two species had a uniform distribution (Table 3), indicating negative interactions, in spite of the fact that Tawny Owl alone showed a strongly clumped distribution. We conclude that our second prediction was also correct – Tawny Owl occupies only refugial areas located at the bottom of the hill that were left empty by Ural Owl.

The most specialized in its habitat selection was Tengmalm's Owl, with the smallest niche breadth. It inhabited high elevations in a narrow altitude zone (see also Vrezec 2003), but otherwise, as shown by discriminant analysis (Fig. 2) and squared Mahalanobis distances, its habitat selection was very similar to the Ural's. Thus, clumps of Tengmalm's Owl were distributed within Ural Owl territories and their joint distribution pattern indicates that there were no particular interactions between them. Also heterospecific nearest neighbour distances were similar to conspecific ones (Table 3). The coexistence was possible due to the separation in other levels of niche, e.g. time of activity, nest-site type or some fine distinctions in food niche, such as predation on different size classes of small mammal prey.

In other parts of Europe also, apart from Northern Europe, Tengmalm's Owl occupies predominantly high elevations with montane or subalpine climate (e.g. Pedrini 1982, Dejaifve *et al.* 1990, Prodon *et al.* 1990, Dvorak *et al.* 1993, Glutz von Blotzheim & Bauer 1994). It is generally accepted that this is due to the presence of Tawny Owl, an important predator of Tengmalm's Owl in Europe (Mikkola 1983, Locker & Flügge 1998, König *et al.* 1999, Augst 2000). Our results support those findings. The species differ widely in habitat selection (squared Mahalanobis distances), and although both showed properties of clumped distribution, their distribution was significantly uniform when the populations were joint together, indicating strong negative interactions. Heterospecific nearest neighbour distances were two or even three times as great as conspecific (Table 3). Thus, the third prediction was also correct. Tengmalm's Owl occupies areas free of Tawny Owl, but manages to coexist with Ural Owl.

The remaining question is whether positive interactions can exist among predatory species of the same guild. By means of competitive exclusion, Ural Owl creates areas free of the Tawny Owl, which in turn, can be occupied by Tengmalm's Owl. Tengmalm's Owl would clearly benefit from the presence of the Ural Owl, without any effect on the latter. Positive interactions have been described between other birds before, as a heterospecific attraction (e.g. Slagsvold 1980, Monkkonen *et al.* 1996, Elmberg *et al.* 1997, Thomson *et al.* 2003) or as a type of commensalism (e.g. Miller & Nero 1983, Sherry & Holmes 1985), but not among predatory birds of the same guild. Data on altitudinal distribution of the Tengmalm's Owl in areas without Ural Owl support this hypothesis. In neighbouring areas with only Tawny Owl present, Tengmalm's Owl's range is shifted to altitudes over 900 m asl (e.g. Pedrini 1982, Dvorak *et al.* 1993, Sackl & Sammwald 1997, Božič & Vrezec 2000). But even if this positive interaction turns out to be correct, it does not fit the properties of an attraction mechanism, although it corresponds well to the predator protection pattern (Thomson *et al.* 2003). We suspect that Tengmalm's Owls are not attracted by the presence of Ural Owls, but by the space free of Tawny Owls. Evidence for our assumption was supplied by Hakkarainen and Korpimäki (1996) who showed a negative influence of Ural Owl on Tengmalm's Owl's reproductive success and breeding density, due to increased predation risk. More studies are needed for this specific type of commensalism between raptors, and should help us to understand better the structure and diversity of predator guilds and associations at the top of the food chain in every ecosystem.

Acknowledgements. For earlier discussions we would like to thank to Prof. Dr. Boris Kryštufek. Milijan Šiško and Tomaž Mihelič helped us in preparing the figure. Dr. Mateja Germ checked the earlier draft of the manuscript. The referees Drs Jukka Forsman and Patrik Byholm made valuable suggestions for improving the paper. We are grateful to the Slovenian Forest Service (Zavod za gozdove Slovenije, OE Ljubljana), for valuable data on the forest of Mt. Krim, especially to Mr. Sašo Skledar, Mr. Andrej Jeklar and Mr. Boštjan Jurjevčič. Dr. Roger H. Pain made a linguistic correction of the paper. The research was partly founded by the Ministry of Education, Science and Sport of Slovenia in the program of financing the postgraduate education of junior researchers.

Pöllölajien elinympäristönvalinta ja alueellinen esiintyminen

Artikkelin kirjoittajat tutkivat erikokoisten pöllölajien: viirupöllön, lehtopöllön ja helmipöllön elinympäristönvalintaa ja reviirien sijaintia Sloveniassa vuosina 1998–2003. Pöllöjen reviirien sijainti määritettiin vuosittain ääniatrappien avulla 41 tutkimuspisteestä. Samoilta pisteiltä tehtiin ympäristökuvaukset. Lisäksi alueen yleistä ympäristörakennetta selvitettiin 52 lisäpisteeltä. Viirupöllö tavattiin kaikkiaan 15 tutkimuspisteellä (36,6), lehtopöllö 17 (41,5) ja helmipöllö 13 (31,7) tutkimuspisteellä. Viirupöllö havaittiin dominantiksi pöllölajiksi, joka esiintyi valtaosalla lajin optimaalista habitaattia eli toiminnallista ekolokeroa. Lehtopöllöllä oli tutkituista lajeista laajin ekolokero. Lehtopöllö esiintyi pääasiassa sellaisilla alueilla, joilla ei tavattu viirupöllöjä. Nämä alueet olivat alavia maita, joilla ihmistoiminta oletettavasti esti viirupöllöjen asettumisen alueelle. Tutkituista pöllölajeista helmipöllö oli kaikkein erikoistunein elinympäristönvalinnassaan. Helmipöllön reviirit sijaitsivat korkeilla alueilla. Samoilla alueilla tavattiin myös viirupöllöjä, mutta tutkijat eivät havainneet helmipöllöjen ja viirupöllöjen välillä negatiivista vuorovaikutusta. Sen sijaan helmipöllön ja lehtopöllön välillä havaittiin negatiivisia vuorovaikutuksia ja lajit esiintyivätkin erilaisissa elinympäristöissä ja eri alueilla. Tutkijat esittävät, että helmipöllö hyötyy viirupöllön olemassaolosta, koska viirupöllön esiintymisen myötä alueelle syntyy lehtopöllöistä vapaita alueita helmipöllön käyttöön. Artikkelissa tuodaan esille asetelma, jossa petolintujen välillä havaitaan positiivisia vuorovaikutussuhteita.

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