Ann. Zool. Fennici 53: 165–174 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 20 April 2016

Spatio-temporal patterns of owl territories in fragmented forests are affected by a top predator (Ural owl)

Łukasz Kajtoch[1,*], Marcin Matysek[2] & Tomasz Figarski[1]

[1)] *Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Slawkowska 17, PL-31-016 Krakow, Poland (*corresponding author's e-mail: lukasz.kajtoch@gmail.com)*
[2)] *Institute of Nature Conservation, Polish Academy of Sciences, A. Mickiewicza 33, PL-31-120 Krakow, Poland*

Received 7 Dec. 2015, final version received 6 Apr. 2016, accepted 6 Apr. 2016

Kajtoch, Ł., Matysek, M. & Figarski, T. 2016: Spatio-temporal patterns of owl territories in fragmented forests are affected by a top predator (Ural owl). — *Ann. Zool. Fennici* 53: 165–174.

Competitive intraguild interactions can modify the spatial and temporal territory use of predators, e.g., this phenomenon was reported among species of owls (Strigidae). This study made use of owl guild present in fragmented forests in southern Poland to investigate how the occurrence of the dominant Ural owl affects the territory distribution of subordinate (in descending order): tawny owl, boreal owl and pygmy owl. Surveys carried out in 2014–2015 showed that the tawny owl decreases in density and the distances between its territories increase in sympatry with Ural owl. The tawny owl increases in abundance during the non-breeding season, in particular in sympatry with the Ural owl, where young tawny owls try to settle within territories of the Ural owl. The distribution of the boreal owl territories was found to be random with respect to the tawny owl, but territories were clustered in space with the Ural owl territories, which suggests that the boreal owl distribution tends to follow the availability of suitable nesting places rather than the avoidance of the tawny owl. The distribution of the pygmy owl territories was random with respect to the Ural owl, but clumped with respect to the tawny owl, as both species occupied fir-spruce stands avoided by the Ural owl. In summary, this study broadens the basic knowledge about spatio-temporal relations within the owl guild by showing that the occurrence of the dominant Ural owl is a substantial factor in shaping the distribution of owls in fragmented forests.

Introduction

Species that utilize similar resources in the environment are prone to interspecific competition, which is a phenomenon particularly noticeable in the guild of predators. Predators can compete for food and/or space in two main aspects: temporal (spans of activity) and spatial (habitat availability) (Cody 1974, Schoener 1974). In evolutionary-related and ecologically similar species, home ranges are usually spatially separated because of strong competitive interactions (Schoener 1982) and intraguild predation [killing and eating of potential competitors; Polis and Holt (1992)]. These phenomena should be particularly visible in heterogeneous habitats (e.g., fragmented forests), where the optimal localities are generally occupied by the dominant predator

(Fretwell 1972). Although there are many studies dealing with the spatial segregation of predators during the reproductive season (Lundberg 1980, Korpimäki 1986, Tschechkin 1997, Vrezec 2003), the data on competitors' coexistence apart from this crucial period of the year are lacking.

Competition and spatial segregation in particular among predators have been confirmed in many studies on diurnal raptors (e.g., goshawks *Accipiter gentilis* and common buzzards *Buteo buteo*, Kostrzewa 1991; eagles *Aquila* spp., Katzner *et al*. 2003), raptors and owls (e.g., eagle-owls *Bubo bubo* and peregrine falcons *Falco peregrinus*, Brambilla *et al*. 2010) and owls (e.g., eagle owls *Bubo bubo* and tawny owls; *Strix aluco*, Sergio *et al*. 2007; boreal owls *Aegolius funereus* and pygmy owls *Glaucidium passerinum*, Suhonen *et al*. 2007; tawny and Ural owls *Strix uralensis*, Lundberg 1980, Korpimäki 1986, Tschechkin 1997, Vrezec 2003).

Contrary to negative (aggressive) interactions, there are only a few studies showing neutral or positive interactions. Most 'protected' associates are found in Anseriformes, Charadriiformes and Passeriformes, which benefit from common breeding, while 'protective' associates come from Falconiformes, Accipitriformes and Strigiformes, whose presence shelter nests of some other birds (mainly gooses and passerines) (*see* review in Quinn & Ueta 2008). Within owl guilds 'protective' associates are a rare phenomenon and were reported, e.g., by Vrezec (2003) for boreal owls breeding within Ural owl territories to avoid the tawny owl proximity. Consequently, mutualistic or commensalic interactions could be underestimated in spatial ecology studies (Odum 1971, Begon *et al*. 1996, Forsman *et al*. 2002).

The owl guild provides an excellent model system for studying interspecific competition (Zuberogoitia *et al*. 2005). In the mountainous forests of east-central Europe, the owl guild consists of up to six species. However, one of them, the eagle owl, is restricted mainly to higher elevations and another, the long-eared owl *Asio otus*, is a species of forest edges and midfield woods. Consequently, the four owl species forming the forest guild in submontane areas (e.g., foothills) are: the tawny owl, the Ural owl, the boreal owl and the pygmy owl (Mikkola 1987, Hagemeijer & Blair 1997). Recent studies on the co-distribution and habitat displacement of owls have shown that all of these four species in certain conditions could segregate in respect to space and breeding habitats. Data from Scandinavia and Belarus indicate keen interspecific competition between the *Strix* owls (Lundberg 1980, Korpimäki 1986, Tschechkin 1997). In the continuous montane forests of the Dinaric Alps, the tawny, Ural and boreal owls occupy different altitudes: the tawny owl is restricted to lower localities, the boreal owl to the highest ones, and the Ural owl is the most widespread (Vrezec 2003, Vrezec & Tome 2004a, 2004b). Moreover, Vrezec and Tome (2004a, 2004b) provided evidence for boreal owl's affinity to Ural owl localities and explained that it is a result of boreal owl avoidance of tawny owl territories, as this species is known to hunt smaller owls. It is known that the pygmy owl and the boreal owl compete for food (Suhonen *et al*. 2007) and boreal owls could kill pygmy owls (Mikkola 1976), but apart from reports of pygmy owls killed by Ural owls and tawny owls (Mikkola 1976) there have been no studies dealing with the interaction between the pygmy owl and the *Strix* species. It is known that aggressive interactions have been reported between the Ural (dominant) and tawny (subordinate) owls (Mikkola 1976, Vrh & Vrezec 2006). Recently, Kajtoch *et al*. (2015) described the distribution of the tawny owl with respect to the presence of the Ural owl in the fragmented forests of the Carpathian Foothills. They showed that, during the breeding season, the tawny owl in sympatry with the Ural owl is forced to occupy peripheral and smaller woods of younger age and dense tree canopies far from the wood patches that are optimal for the Ural owl (mainly old beech or pine woods). Similar breeding territory displacement has also been recently reported for the submontane area in Romania (Bolboacă *et al*. 2013).

We took advantage of recent studies on owl populations in submontane hilly areas in the Carpathians and their surroundings (Kajtoch 2006, Turzański 2009a, Bylicka 2011, Bylicka *et al*. 2010, Pitucha & Wojton 2012, Matysek *et al*. 2015). Using these studies as a foundation, we executed a special survey to check if the distribution of tawny owl territories differs between the breeding (spring) and non-breeding (autumn)

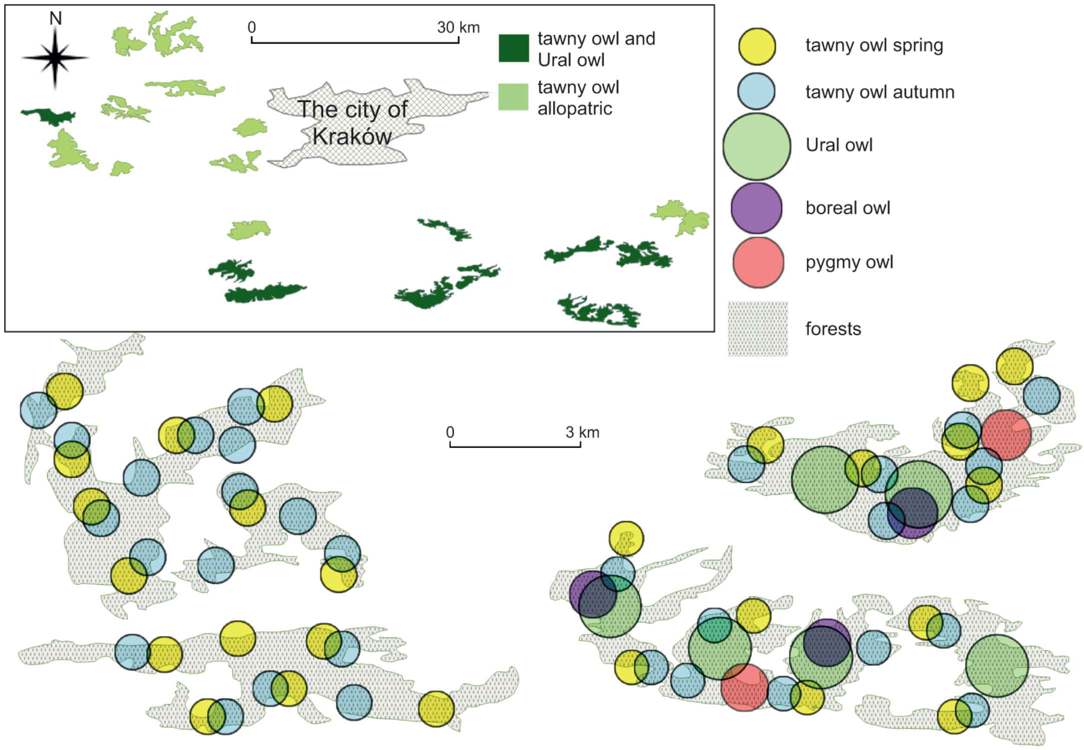

Fig. 1. Simplified landscape of the forest complexes where owls were surveyed, and examples of distribution owl territories in selected forests. Sizes of circles correspond to average areas occupied by owl species according to Sonerud *et al.* (1986), Strøm and Sonerud (2001), Bylicka *et al.* (2010), and Cios and Grzywaczewski (2013).

periods. We hypothesized that, in allopatric populations, the density of the tawny owl should be constant over the year, whereas in sympatry with the Ural owl, the subordinate species should decrease in abundance and increase the distances between its own territories from autumn to spring. The second aim was to verify the hypothesis created by Vrezec and Tome (2004a, 2004b) that the boreal owl prefers to breed in the vicinity of the Ural owl as a result of tawny owl avoidance (the boreal owl is 'protective' associated with the Ural owl). Thirdly, we hypothesized that the pygmy owl avoids the Ural owl due to the overlapping periods of their hunting activities.

Material and methods

The study was conducted in a submontane hilly landscape in southern Poland (in the vicinity of the city of Krakow). The details about the composition of the landscape and habitat availability can be found in Bylicka *et al.* (2010), Kajtoch *et al.* (2015) and Matysek *et. al.* (2015). The study design was prepared in two steps following the particular aims of this research. For the purpose of studying the differences in tawny owl occurrence with respect to the season and Ural owl presence, all available 22 forest complexes with an area of more than 3.5 km^2 were selected (3.5–11.2 km^2; *see* Fig. 1). Those were the forests which could shelter at least several territories of owls, including the Ural owl, which is known to occupy only forests with an area greater than 1 km^2, and have the highest probability of occurring in forests with an area of 4 km^2 (Bylicka *et al.* 2010). In all of those forests, bird inventory was carried out using broadcasting owls hooting and listening to the birds from survey points located roughly uniformly across the forests (in nodes located approx. 1 km apart forming a network which covered the whole area of the examined forests). Surveys were performed during the peak period of the owl post/pre-breeding and breeding activities (in September–October 2014 and from mid-February to April 2015, and partially repeated in the autumn of 2015), according to the methodology of owl detection (e.g. Redpath 1995). In spring, owl voices were broadcasted in the following sequence: pygmy owl — boreal owl — tawny owl — Ural owl, divided by two to three minutes of listening. The pygmy owl was also searched for during additional surveys executed during dusk and dawn. In autumn, only tawny owl voices were broadcasted. All records of owls were marked with the GPS. Special emphasis was put on recording simultaneously-hooting birds (Galeotti & Pavan 1993, Galeotti 1998). In late spring, special emphasis was also put on the localization of calling juveniles (which confirms breeding status and allows for the determination of the centre of territory). In autumn, only the centres of areas where particular individuals responded more actively and repeatedly could be determined.

For the description of spatial relations among the owl species in the examined area, two basic metrics were calculated. First, crude densities of the owl species were calculated for each of the surveyed forests, and then the density values for the tawny owl obtained for "allopatric" (only the tawny owl present) and "sympatric" (the tawny and Ural owls) territories were compared using the Wilcoxon *t*-test (when the same complexes were compared between spring and autumn) or the Mann-Whitney *U*-test (when forests with allo- and sympatric *Strix* owls were compared). Second, distances to the nearest neighbouring territory (to the certain or estimated centre of breeding territory in breeding season and to the location where the most active and repeated bird voices were recorded in non-breeding season) were measured. These distances were calculated conspecifically for the tawny owl separately for spring and autumn for two groups: "allopatric" and "sympatric". The distances were calculated heterospecifically between: tawny owl and Ural owl, tawny owl and boreal owl, Ural owl and boreal owl, tawny owl and pygmy owl as well as Ural owl and pygmy owl during the breeding period. Distances between the boreal owl and the pygmy owl were not considered due to the very low number of forests containing both species. Next, distances among owl territories in different ways of clustering were compared using the Mann-Whitney *U*-test. Moreover, distribution patterns were calculated according to the nearest neighbour distance method with the use of the standard normal deviate (Krebs 1989). The expected distance (D_E), standard error (SE), Average Nearest Neighbour ratio (ANN), *Z*-score and *p* values were calculated according to Mitchell (2005). An ANN ratio equal to 1 indicates random distribution, ANN > 1 indicates uniform (dispersed) distribution and ANN < 1 indicates clumped (clustered) distribution. As uniform distribution maximises nearest neighbour distances, this implies negative interactions between species separated in space (Odum 1971). In contrast, a clumped distribution indicates some possible positive interactions and a random distribution indicates no interactions. Finally, Generalized Linear Models were built to evaluate the impact of two factors which could affect tawny owl densities and distances: (i) season (breeding *vs.* non-breeding) and (ii) Ural owl density. The significance of these models was evaluated using the Wald statistics in Statistica 11 (StatSoft Inc.).

Results

Density data

Fifteen Ural owl territories were detected in 10 out of 22 forests, and those territories were constant during the duration of the study. During the breeding season (spring), tawny owls were recorded in all of the examined forests with 43 territories being sympatric and 47 territories being allopatric with respect to Ural owl presence in the forest. Also, in non-breeding season (autumn), tawny owls were found in all forests with Ural owls (52 territories) and all forests without Ural owls (51 territories). The distribution of autumn territories of the tawny owl in 2014 was nearly the same in some forests as that in 2015. The densities of the tawny owl in sympatry with the Ural owl was significantly lower in spring than in autumn (Wilcoxon *t*-test: $t = 1.00$, $p = 0.028$), but such differences were not significant in allopatry ($t = 18.00$, $p = 0.594$) (Table 1 and Fig. 2). There were also no differences when comparing autumn densities of the tawny owl in allopatry and sympatry (Mann-Whitney U-test: $U = 57.0$, $p = 0.869$) but in spring these differences were nearly signifcant ($U = 31.00$, $p = 0.060$) (Table 1 and Fig. 2).

Six territories of the boreal owl were found in five forests and also six territories of the pygmy owl were recorded in six forests, and all those territories were in the forests also occupied by the Ural owl.

Distance data

Average distances among tawny owl territories in sympatry with the Ural owl were 1.2 times greater during spring than in autumn (Mann-Whitney U-test: $U = 729.5$, $p = 0.023$) and 1.1 times greater in allopatry ($U = 996.0$, $p = 0.059$) (Table 1 and Fig. 2). Breeding distances of the tawny owl were 1.5 times greater in sympatry than in allopatry ($U = 467.5$, $p < 0.001$), and non-breeding distances were 1.4 times greater in sympatry than in allopatry ($U = 523.0$, $p < 0.001$) (Table 1 and Fig. 2). Distances among the tawny owl and the nearest Ural owl territories were on average nearly the same in spring and autumn ($U = 1256.5$, $p = 0.614$) (Table 1 and Fig. 2).

Boreal owl territories were on average 4.6 times closer to Ural owl territories than to tawny owl territories ($U = 2.00$, $p = 0.013$) (Table 1 and Fig. 2). In contrast, pygmy owl territories were 2.3 times further from Ural owl than from tawny owl territories ($U = 5.00$, $p = 0.044$) (Table 1 and Fig. 2).

The ANN ratios indicate that tawny owl territories were distributed uniformly, regardless of the season and presence of the Ural owl (Table 2). Also, the distances of tawny owl territories from the nearest Ural owl territories confirmed their uniform distribution, whereas Ural owl territories were distributed randomly with respect to tawny owl territories. The boreal owl showed clumped distribution with respect to the Ural owl, but random distribution with respect to the tawny owl (the pygmy owl showed a pattern opposite to that of the boreal owl) (Table 2).

GLMs revealed that neither "season" nor "Ural owl density" significantly affected the tawny owl density (respectively: Wald = 1.2, $p = 0.273$ and Wald = 0, $p = 0.838$), whereas both these factors significantly contributed to the diversity of tawny owl distances (respectively: Wald = 14.3, $p < 0.001$ and Wald = 4.1, $p = 0.044$).

Table 1. Basic statistics of owls densities and distances among territories in examined forests. TO = tawny owl, UO = Ural owl, BO = boreal owl, PO = pygmy owl.

	Mean	Min	Max	SD
Density (territory per 1 km^2)				
Spring TO (sympatric with UO)	0.60	0.43	1.0	0.181
Autumn TO (sympatric with UO)	0.75	0.43	1.5	0.328
Spring TO (allopatric)	0.71	0.45	1.04	0.169
Autumn TO (allopatric)	0.76	0.25	1.43	0.320
UO	0.10	0	0.33	0.118
BO	0.03	0	0.22	0.064
PO	0.03	0	0.20	0.058
Distances (m)				
Spring TO-TO (sympatric with UO)	1512.7	700	3000	511.0
Autumn TO-TO (sympatric with UO)	1300.0	700	2500	427.4
Spring TO-TO (allopatric)	1011.8	100	1800	383.0
Autumn TO-TO (allopatric)	936.0	300	2500	411.0
Spring TO-UO	1395.7	100	3300	712.2
Autumn TO-UO	1337.5	400	3100	668.3
BO-UO	258.3	100	600	180.0
BO-TO	816.7	400	1200	331.2
PO-UO	1516.7	700	2200	725.0
PO-TO	666.7	300	1100	338.6

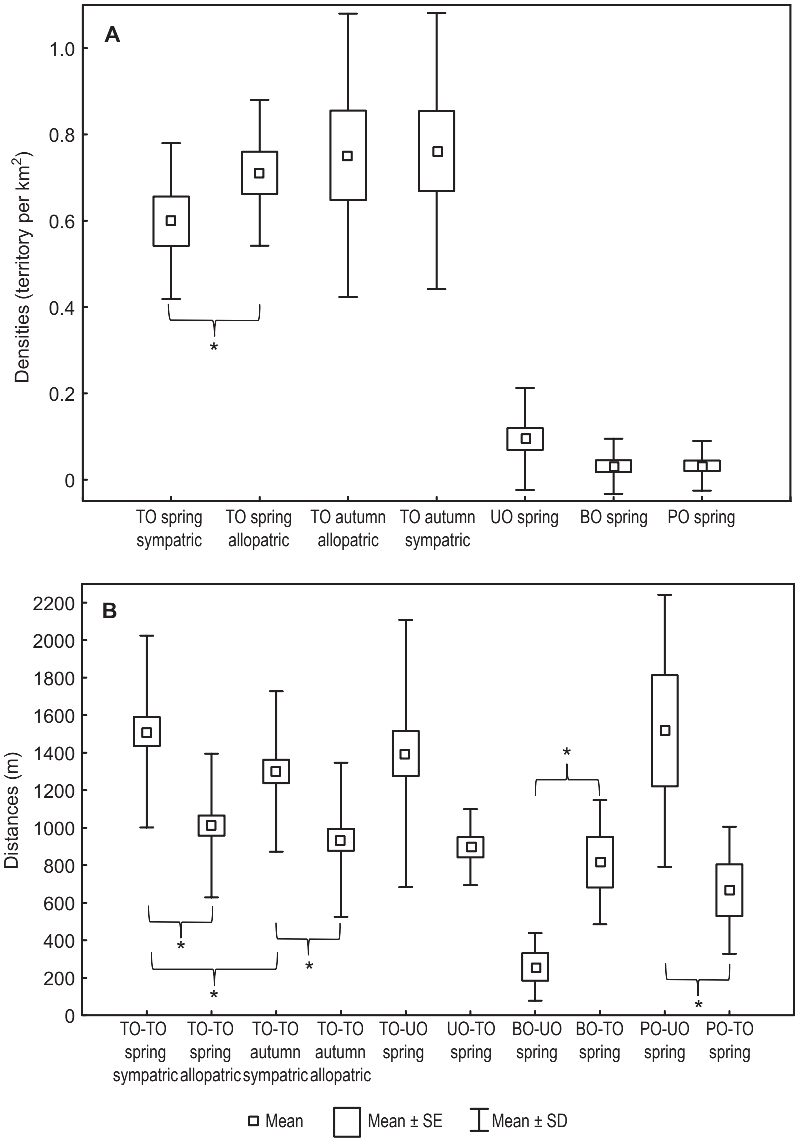

Fig. 2. Box-plots visualizing differences in (**A**) densities and (**B**) distances calculated for owl territories in the examined area (TO = tawny owl, UO = Ural owl, BO = boreal owl, PO = pygmy owl). Asterisks (*) indicate significant ($p < 0.05$) or nearly-significant ($p = 0.05$) differences.

Discussion

The survey presented here broadens the knowledge of tawny owl and Ural owl competitive relations with respect to the seasons, an aspect which has not been investigated so far. Using the example of the owl guild from the fragmented forests of southern Poland, it can be confirmed that tawny owls avoid areas occupied by a stronger and more aggressive congener (Ural owl) and this avoidance behaviour leads to a decrease in the tawny owl densities in forests co-occupied by the Ural owl as compared with forests without the latter. However, this effect was rather weak, probably due to the relatively low densities of the Ural owl in fragmented forests (Kajtoch 2006, Matysek *et al*. 2015). Consequently, distances among tawny owl territories are significantly greater in sympatry with the Ural owl than in allopatry. It is interesting that the average distances among tawny owl territories in sympatry are similar to the heterospecific distances between the tawny owl and the neighbouring Ural owl. This observation could be explained as a uniform distribution of the tawny owl with respect to the Ural owl, which should decrease the risk of direct aggressive interactions. This fits with the findings of a previous study on the same population (Kajtoch *et al*. 2015), which showed that the tawny owl is forced by a stronger congener to avoid most suitable forests within breeding territories of a stronger competitor. Within Ural owl territories, there are usually no tawny owl individuals and the same situation has been reported concerning other sympatric populations in Scandinavia, the Moldavian Plateau and the Dinaric Alps (Lundberg 1980, Korpimäki 1986, Vrezec 2003, 2004a, 2004b, Bolboacă *et al*. 2013). However, the question of whether the tawny owl totally avoids Ural owl territories or tries to settle but is consistently chased or killed by the Ural owl, or whether some tawny owl individuals are present in Ural owl territories but avoid hooting to decrease risk has not been resolved. This issue needs further research with the use of bird tracking techniques.

The observations made in this study show that the tawny owl generally increases abundance during the non-breeding season. This is a simple consequence of the presence of young (first-year) birds which look for their breeding sites in forests. It is interesting that relatively more non-breeding birds appear in forests also occupied by Ural owls (increase of approx. 24%) than in Ural-owl-free forests (increase of approx. 9%). It is probable that in allopatric subpopulations of the tawny owl there are simply no available areas where young birds can attempt to establish their territories as all or most suitable forest patches are already occupied by conspecific settled pairs. The situation is different in sympatric forests as some areas are tawny-owl-free due to the presence of Ural owl territories. The Ural owl is territorial annually; however, it is probably less aggressive outside the breeding season (first author's, unpubl. data). This probably gives some tawny owls the opportunity to settle in 'seemingly free' forest patches, but such territories are apparently temporal and vanish before the following spring when Ural owls aggressively defend the borders of the breeding territories. This phenomenon also needs confirmation and verification for other populations from other areas and other environmental conditions.

Another issue raised in this paper was the verification of whether the findings of Vrezec and Tome (2004a) from the Dinaric Alps on boreal owl's 'protective' association with the Ural owl due to the avoidance of the tawny owl apply to owl populations in the Carpathian Foothills. The gathered data indeed confirmed that boreal owl territories clustered in space with Ural owl territories. However, due to a low number of examples, these results should be interpreted

Table 2. Mean con- and heterospecific nearest-neighbour distances (in km) between tawny owl (TO), Ural owl (UO), boreal owl (BO) and pygmy owl (PO). D_O and D_E = observed and expected distances, respectively; ANN = average nearest-neighbour ratio; Z = standard normal deviate. Distribution: random when ANN = 1, uniform (dispersed) when ANN > 1, and clumped (clustered) when ANN < 1.

Comparison	D_O	D_E	SE	ANN	Z	p	Distribution
Conspecific							
TO spring sympatric	1.49	0.65	0.05	2.30	16.69	< 0.0001	uniform
TO spring allopatric	1.01	0.58	0.04	1.75	10.21	< 0.0001	uniform
TO autumn sympatric	1.32	0.64	0.05	2.08	14.14	< 0.0001	uniform
TO autumn allopatric	0.94	0.58	0.04	1.60	8.12	< 0.0001	uniform
Heterospecific							
UO-TO spring	0.90	1.16	0.16	0.77	–1.63	0.1035	random
TO-UO spring	1.40	0.74	0.07	1.88	9.98	< 0.0001	uniform
TO-UO autumn	1.34	0.70	0.06	1.92	11.08	< 0.0001	uniform
BO-UO	0.19	1.39	0.32	0.13	–3.70	0.0002	clumped
BO-TO	0.88	1.39	0.32	0.63	–1.58	0.1140	random
PO-UO	1.52	1.51	0.32	1.00	0.02	0.9862	random
PO-TO	0.67	1.51	0.32	0.44	–2.62	0.0088	clumped

with caution. On the other hand, although the distance between the boreal owl and the nearest tawny owl was greater than to the nearest Ural owl, the distribution of boreal owl territories was random with respect to the tawny owl. This suggests that the tawny owl presence is not a crucial factor which could prevent the boreal owl from breeding. However, in such conditions the close proximity to the Ural owl provides protection for the boreal owl, so the distance to the tawny owl might be of secondary importance. Explanations for this pattern should be sought in suitable habitats available in the examined area. Unfortunately, we did not have accurate enough data on the habitat preferences of boreal owls to make detailed analyses, but it is known that this owl chooses older beech–fir or pine-wood patches with tree hollows for breeding (Vrezec 2003). The same woods are also preferred by the Ural owl (Bylicka *et al.* 2010, Kajtoch *et al.* 2015). Consequently, the boreal owl could prefer to breed in the vicinity of the Ural owl due to the availability of suitable nesting places, but not necessarily as a result of tawny owl avoidance behaviour. Moreover, the Ural owl, just like the tawny owl, is known to decrease the reproductive success of the boreal owl due to increased predation risk (Hakkarainen & Korpimäki 1996). Apparently, in the fragmented woods of the Carpathian Foothills, relations among the tawny owl, Ural owl and boreal owl do not correspond directly to the patterns reported for this owl guild from the Dinaric Alps investigated by Vrezec and Tome (2004a).

Finally, the hypothesis that the pygmy owl avoids the Ural owl seems to be supported by our results. Again, however, the low number of samples makes final confirmation difficult. The distances between pygmy owl and Ural owl territories were significantly greater than between pygmy owl and the nearest tawny owl territories. Simultaneously, the distribution of pygmy owl territories was estimated to be random with respect to the Ural owl, but clumped with respect to the tawny owl. This suggests that some other factors could contribute to this pattern of owl distribution. Possibly, predation of the Ural owl on the pygmy owl is only occasional and has a lower importance for pygmy owl's territory choice. The clumped distribution of the pygmy owl with respect to the tawny owl could be related to the effect of the Ural owl forcing the tawny owl to breed in non-optimal woods (e.g., Wiącek *et al.* 2010). Kajtoch *et al.* (2015) recently showed that the tawny owl in sympatry with the Ural owl also breeds in fir–spruce woods, which are avoided in allopatry, and these coniferous woods are optimal habitats for the pygmy owl (Strøm & Sonerud 2001).

Examined relations among the studied owl species do not rule out possible effects of other factors such as distribution and abundance of prey and other predators. It was shown that carnivore communities are structured and co-existing species switch their habitat preferences and/or temporal activity (e.g., Torreta *et al.* 2015, Gompper *et al.* 2016). Unfortunately, neither this study nor other data allow for estimation if prey availability limits in some way the distribution of the studied owl species. The data from the Atlas of Mammalian Distribution in Poland (http://www.iop.krakow.pl/ssaki/) suggest that there are no differences in the presence of most important rodent prey (such as voles *Microtus* spp. and *Myodes glareolus*, mice *Apodemus* spp. and shrews *Sorex* spp.) across the whole study area, but these data are too general to make any detailed conclusions. The same concerns carnivores (e.g., martens *Martes martes* and *M. foina*). In contrast, there are available data on the occurrence of diurnal raptors across the study area (Turzański 2009b, Kajtoch 2009). The most abundant diurnal raptor was found to be the common buzzard *Buteo buteo*, but this species does not tend to interact with the studies examined (except that it is the occasional prey of the Ural owl; Mikkola 1976). Among other raptors, the northern goshawk *Accipiter gentilis* was reported to hunt on all studied owl species, but its nestlings could also be prey of the Ural owl (Mikkola 1976). The author's observations suggest that most Ural owl territories overlap with territories of goshawks. This is related to two factors: (i) Ural owls often utilize nests abandoned by goshawks, and (ii) both species prefer similar types of older woods with sparse canopy due to their hunting behaviour. This spatial relation could raise the question of whether distribution of subordinate owl species is restricted only by the Ural owl presence or also by the co-occurrence of goshawks. This hypothesis should be investigated in future research.

In summary, this study broadens the basic knowledge about spatio-temporal relations within the owl guild by showing that the occurrence of the dominant Ural owl is a significant factor in shaping the distribution of owls in fragmented forests. The presented data show that intraguild competition among predators is complex, hierarchical and connected with many factors, among which co-occurrence of dominant species could be the most important but not exclusive. Moreover, this research discusses seasonal changes in predators' (owls') distribution in relation to presence of dominant species (here Ural owl). This last aspect is innovatory, as majority of the studies on competition among predators were carried out during the breeding period only. The information gathered in here could also be important for the conservation of owl species. As the the Ural owl, the boreal owl and the pygmy owl are all protected under the Birds Directive, plans for the protection of their populations and the management of their habitats should be based on detailed knowledge of species ecology and behaviour.

Acknowledgements

We are grateful to Jakub Pełka and Anna M. Ociepa for providing information about some owl territories and to the anonymous reviewer for helpful comments and suggestions, which allowed the improvement of our paper. This work was supported by grant 9007/IP1/2014/72 (Iuventus Plus) from the Polish Ministry of Science and Higher Education (to Łukasz Kajtoch).

References

Begon, M., Harper, J. L. & Townsend, C. R. 1996: *Ecology: Individuals, populations and communities*. — Blackwell Science, Oxford.

Bolboacă, L. E., Baltag, E. S., Pocora, V. & Ion, C. 2013: Habitat selectivity of sympatric tawny owl (*Strix aluco*) and Ural owl (*Strix uralensis*) in hill forests from north-eastern Romania. — *Analele Științifice ale Universității „Alexandru Ioan Cuza" din Iași, s. Biologie animală* 59: 69–76.

Brambilla, M., Bassi, E., Ceci, C. & Rubolini, D. 2010: Environmental factors affecting patterns of distribution and co-occurrence of two competing raptor species. — *Ibis* 152: 310–322.

Bylicka, M. 2011: Sowy terenów leśnych zachodniej części Pogórza Przemyskiego [Owls in forests of the western part of the Przemyskie Foothills]. — *Chrońmy Przyrodę Ojczystą* 67: 415-425. [In Polish with English summary].

Bylicka, M., Kajtoch, Ł. & Figarski, T. 2010: Habitat and landscape characteristics affecting the occurrence of Ural Owl *Strix uralensis* in agroforestry mosaic. — *Acta Ornithologica* 45: 33–42.

Cios, S. & Grzywaczewski, G. 2013: Importance of selected factors influencing the size of tawny owl *Strix aluco* territories in the forests of Lublin region. — *Sylwan* 157: 348–357.

Cody, M. L. 1974: *Competition and the structure of bird communities*. — Princeton University Press, Princeton.

Forsman, J. T., Seppänen, T. & Mönkkönen, M. 2002: Positive fitness consequences of interspecific interaction with a potential competitor. — *Proceedings of the Royal Society of London B* 269: 1619–1623.

Fretwell, S. D. 1972: *Populations in a seasonal environment. — Princeton University Press,* Princeton.

Galeotti, P. 1998: Correlates of hoot rate and structure in male tawny owls *Strix aluco*: implications for male rivalry and female choice. — *Journal of Avian Biology* 29: 25–32.

Galeotti, P. & Pavan, G. 1993: Differential responses of territorial tawny owls *Strix aluco* to the hooting of neighbourds and strangers. — *Ibis* 135: 300–304.

Gompper, M. E., Lesmeister, D. B., Ray, J. C., Malcolm, J. R. & Kays, R. 2016: Differential habitat use or intraguild interactions: what structures a carnivore community? — *PLoS ONE* 11(1): e0146055, doi:10.1371/journal.pone.0146055.

Hagemeijer, E. J. M. & Blair, M. J. 1997: *The EBCC atlas of European breeding birds: their distribution and abundance*. — T. & A. D. Poyser, London.

Hakkarainen, H. & Korpimäki, E. 1996: Competitive and predatory interactions among raptors: an observational and experimental study. — *Ecology* 77: 1134–1142.

Kajtoch, Ł. 2006: Sowy *Strigidae* Pogórza Wielicko-Wiśnickiego i Beskidu Wyspowego [Owls *Strigidae* of Wieliczka-Wiśnicz Foothills and Beskid Wyspowy Mts]. — *Notatki Ornitologiczne* 47: 252–259. [In Polish with English summary].

Kajtoch, Ł. 2009: Szponiaste Falconiformes Podgórza Bocheńskiego, Pogórza Wielicko-Wiśnickiego oraz Beskidu Wyspowego [Raptors Falconiformes of Bocheński and Wielicko-Wiśnicki Foothills and Beskid Wyspowy Mts.]. — *Kulon* 14: 81–90. [In Polish with English summary].

Kajtoch, Ł., Żmihorski, M. & Wieczorek, P. 2015: Habitat displacement effect between two competing owl species in fragmented forests. — *Population Ecology* 57: 517–527.

Katzner, T. E., Bragin, E. A., Knick, S. T. & Smith, A. T. 2003: Coexistence in a multispecies assemblage of eagles in Central Asia. — *Condor* 105: 538–551.

Korpimäki, E. 1986: *Niche* relationships and life-history tactics of three sympatric Strix owl species in Finland. — *Ornis Scandinavica* 17: 126–132.

Kostrzewa, A. 1991: Interspecific interference competition in three European raptor species. — *Ethology Ecology and Evolution* 3: 127–143.

Krebs, Ch. J. 1989: *Ecological methodology*. — Harper & Row, New York.

Lundberg, A. 1980: Why are the Ural owl *Strix uralensis* and the tawny owl *Strix aluco* parapatric in Scandinavia. — *Ornis Scandinavica* 11: 116–120.

Matysek, M., Figarski, T., Wieczorek, P., Wyka, J., Kajtoch, Ł. 2015: Współwystępowanie puszczyków *Strix aluco* i puszczyków uralskich *S. uralensis* w pofragmentowanych lasach centralnej Małopolski [Co-existence of Tawny Owls *Strix aluco* and Ural Owls *S. uralensis* in fragmented forests in central Małopolska Province]. — *Ornis Polonica* 56: 287–297. [In polish whit English summary].

Mikkola, H. 1976: Owls killing and killed by other owls and raptors in Europe. — *British Birds* 69: 144–154.

Mikkola, H. 1987: *Owls of Europe*. — T. & A. D. Poyser, London.

Mitchell, A. 2005: *The ESRI guide to GIS analysis*, vol. 2. — ESRI Press, Redlands.

Odum, E. P. 1971: *Fundamentals of ecology*. — W. B. Saunders & Co., Philadelphia PA.

Pitucha, G. & Wojton, A. 2012: Liczebność i rozmieszczenie sów *Strigiformes* w lasach Pogórza Strzyżowskiego [Numbers and distribution of owls *Strigiformes* in the forests of the Strzyżów Foothills]. *Ornis Polonica* 53: 293–308. [In Polish with English summary].

Polis, G. A. & Holt R. D. 1992: Intraguild predation: The dynamics of complex trophic interactions. — *Trends in Ecology & Evolution* 7: 151–154.

Quinn, J. L. & Ueta, M. 2008: Protective nesting associations in birds. — *Ibis* 150: 146–167.

Redpath, S. M. 1995: Impact of habitat fragmentation on activity and hunting behavior in the tawny owl, *Strix aluco*. — *Behavioral Ecology* 6: 410–415.

Schoener, T. W. 1974: Resource partitioning in ecological communities. — *Science* 185: 27-39.

Schoener, T. W. 1982: The controversy over interspecific competition. — *American Scientist* 70: 586–595.

Sergio, F., Marchesi, L., Pedrini, P. & Penteriani, V. 2007: Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? — *Animal Behavior* 74: 1607–1616.

Sonerud, G. A., Solheim, R. & Jacobsen, B. V. 1986: Home range use and habitat selection during hunting in a male Tengmalm's owl *Aegolius funereus*. — *Fauna Norvegica C* 9: 100–106.

Strøm, H. & Sonerud, G. A. 2001: Home range and habitat selection in the pygmy owl *Glaucidium passerinum*. — *Ornis Fennica* 79: 1–13.

Suhonen, J., Halonen, M., Mappes T. & Korpimäki, E. 2007: Interspecific competition limits larders of pygmy owls *Glaucidium passerinum*. — *Journal of Avian Biology* 38: 630–634.

Torretta, E., Serafini, M., Puopolo, F., Schenone, L. 2015: Spatial and temporal adjustments allowing the coexistence among carnivores in Liguria (N-W Italy). — *Acta Ethologica*, doi:10.1007/s10211-015-0231-y.

Tschechkin, A. K. 1997: *Comparative food niche analysis of Strix owls in Belarus*. — In: Duncan, J. R., Johnson, D. H. & Nicholls, T. H. (eds.), *Biology and Conservation of Owls of the Northern Hemisphere: 2nd International symposium*: 456–460. Gen. Tech. Rep. NC-190, St. Paul, MN, U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station.

Turzański, M. 2009a: Sowy *Strigiformes* Ojcowskiego Parku Narodowego i jego otuliny [Owls *Strigiformes* of the Ojców National Park and its surroundings]. — *Parki Narodowe i Rezerwaty Przyrody* 28: 75–90. [In Polish with English summary].

Turzański, M. 2009b: Liczebność i efekty lęgów ptaków szponiastych Falconiformes oraz kruka *Corvus corax* na Wyżynie Krakowskiej w roku 2008 [Numbers and breeding effects of raptors Falconiformes and the Raven *Corvus corax* in the Wyżyna Krakowska upland [S Poland] in 2008]. — *Notatki Ornitologiczne* 50: 298–304. [In Polish with English summary].

Wiącek, J., Polak, M. & Grzywaczewski G. 2010: The role of forest age, habitat quality, food resources and weather conditions for tawny owl *Strix aluco* populations. — *Polish Journal of Environmental Studies* 19: 1039–1043.

Vrezec, A. 2003: Breeding density and altitudinal distribution of the Ural, Tawny, and Boreal Owls in North Dinaric Alps (Central Slovenia). *Journal Raptor Research* 37: 55–62.

Vrezec, A. & Tome, D. 2004a: Altitudinal segregation between Ural owl *Strix uralensis* and tawny owl Owl *Strix aluco*: evidence for competitive exclusion in raptorial birds. — *Bird Study* 51: 264-269.

Vrezec, A. & Tome, D. 2004b: Habitat selection and patterns of distribution in a hierarchic forest owl guild. — *Ornis Fennica* 81: 109–118.

Vrh, P. & Vrezec, A. 2006: Interspecific territorial vocal activity of the ural owl (*Strix uralensis*) towards tawny owl (*Strix aluco*), sympatric owl competitor: a playback experiment. — *Razprave IV razreda SAZU* 47: 99–105.

Zuberogoitia, I., Martínez, J. A., Zabala, J. & Martínez, J. E. 2005: Interspecific aggression and nest-site competition in a European owl community. — *Journal Raptor Research* 39: 156–159.