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ORIGINAL PAPER

Coexistence of protected avian predators: does a recovering population of White-tailed Eagle threaten to exclude other avian predators?

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Abstract The processes of competition and predation determine the degree to which species can coexist; the importance of competition in particular has been emphasized at high trophic levels. Competition exclusion will occur when habitat overlap between sympatric species is high. In this study, we investigated nesting habitat overlap between internationally protected diurnal tree-nesting avian predators of central Europe, namely, White-tailed Eagle (*Haliaeetus albicilla*), Lesser Spotted Eagle (*Aquila pomarina*), Black Stork (*Ciconia nigra*), and Osprey (*Pandion haliaetus*). We found significantly different nesting habitats among the study species and suggest that this could be a consequence of the resource-based segregation, but not a consequence of asymmetrical interspecific competition. The results also show that habitat of the recovering populations of White-tailed Eagle overlapped with the habitat used by the Lesser Spotted Eagle, Black Stork, and Osprey to varying extents with a niche overlap values being below the competition exclusion threshold. Nevertheless, we suggest that competition by White-tailed Eagle at a population level may limit Osprey, though not Lesser Spotted Eagle or Black Stork.

Keywords Habitat · Overlap · Avian predator · Coexistence · Conservation

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Introduction

Ecological differences among species that lead to niche partitioning and therefore coexistence can occur because (1) different species may specialize in distinct resources (classical resource partitioning); (2) different species may be limited by the same resources or natural enemies, but differ in terms of when they exploit the resource or respond to natural enemies (temporal niche partitioning); and (3) species could differ in terms of where they experience, and respond to, limiting factors (spatial niche partitioning; Amarasekare 2003). The processes of competition and predation determine the degree to which species can coexist (Martin 1988), with predation being considered to have at least a similar or even greater effect on animal communities than competition (Krüger 2002b; Suhonen et al. 2007). Although the role and relative importance of factors shaping species' interaction and communities has been the subject of hot controversy (Krüger 2002b), competition importance has been emphasized at high trophic levels (Hakkarainen et al. 2004).

Coexistence can be thought of as resulting from competing species exhibiting differences along four major niche axes: resources, natural enemies, space, and time (Amarasekare 2003). In the community of sympatric diurnal raptors, however, differences along the resources axis could play a most important role: food abundance along with the availability of suitable nest sites has been considered the most important resource in raptors (Newton 2003). Sympatric raptors usually consume different prey (Giovanni et al. 2007; Olsen et al. 2010), but intense competition for nest sites could occur among forest-dwelling raptors (Krüger 2002a), which typically prefer old growth forests at different spatial scales (Treinys and Mozgeris 2010 and references therein). Heavy stick nests of medium-size and large raptors can only be constructed in large trees (Kostrzewa 1996; Lõhmus 2006), and this demand greatly reduces the potential nesting habitat. Timber harvesting reduces the availability of suitable nesting structures for raptors in managed forests (Lõhmus 2003). Consequently, a lack of suitable forest patches could increase competition for available nest sites (Hakkarainen et al. 2004). During the last two decades, differences between nesting habitat of sympatric diurnal forest-dwelling raptors mostly analyzed the species system of Northern Goshawk *Accipiter gentilis*, Common Buzzard *Buteo buteo*, and Honey Buzzard *Pernis apivorus* (Kostrzewa 1996; Gamauf 2001; Krüger 2002a; Hakkarainen et al. 2004), but other species systems are covered as well (*Aquila chrysaetos*, *Aquila heliaca*, and *Haliaeetus albicilla* (Katzner et al. 2003); *Aquila clanga* and *Aquila pomarina* (Lõhmus and Väli 2005); and *Aegypius monachus*, *A. pomarina*, *Hieraaetus pennatus*, and *A. gentilis* (Poirazidis et al. 2007)). In this study, we attempted to cover a new set of species and investigated habitat overlap of sympatric differently sized internationally protected diurnal tree-nesting avian predators of central Europe: White-tailed Eagle *H. albicilla*, Lesser Spotted Eagle *A. pomarina*, Black Stork *Ciconia nigra*, and Osprey *Pandion haliaetus*. All these species are long lived, exhibit a high degree of site-fidelity, have large home-ranges, avoid vicinity of humans, prefer to nest in mature forests, and build large stick nests in old trees (Cramp and Simmons 1980; Helander and Stjernberg 2003; Janssen et al. 2004; Jiguet and Villarubias 2004; Lõhmus and Sellis 2003; Meyburg et al. 2001; Skuja and Budrys 1999; Struwe-Juhl 2000; Šablevičius 2001; Treinys et al. 2009).

The White-tailed Eagle (body mass, ~3.1–6.9 kg) is largely a resident raptor species occupying territories most of the year (Dementavičius and Treinys 2009). Populations in the countries around the Baltic Sea decreased rapidly in the 1960s and 1970s, but wide-range protective measures yielded positive results, and the population of the species increased substantially between 1970 and 1990 (Helander and Stjernberg 2003; Stjernberg et al. 2005). Following a continued population increase across Europe during 1990–2000, the European breeding population currently comprises 5,000–6,600 pairs (BirdLife International 2004). The first breeding pairs in Lithuania were found in 1987, and latest figures suggest the breeding population to be ~90 pairs (Dementavičius 2007). White-tailed Eagles prey mainly on fish and waterfowl (Cramp and Simmons 1980), but is known to kill other raptors (Dementavičius 2004; Helander 1983; Mikkola 1983). The Lesser Spotted Eagle is a migratory species with a body mass of ~1.1–2.2 kg (Cramp and Simmons 1980). Its European population (14,000–19,000 pairs) is declining (BirdLife International 2004), as is the Lithuanian population (Treinys et al. 2007), which comprises 1,931–2,869 pairs (Mischenko et al. in press). It preys mainly upon small mammals, although certain species of amphibians are also common in its diet (Meyburg et al. 2001). The Black Stork is a migratory species with a body mass of ~2.4–3.2 kg (Janssen et al. 2004). Between 7,800 and 12,000 pairs breed in Europe (BirdLife International 2004), where the recent trends are geographically distinct: range expansion and population increases dominate in the west, while declines are reported in the east (Janssen et al. 2004). The Lithuanian population has declined and currently comprises 650–950 pairs (Treinys et al. 2008). It feeds on fish and amphibians (del Hoyo et al. 1992). The Osprey is a migratory ichthyophagous species with a body mass of ~1.1–2.1 kg (Cramp and Simmons 1980). Most European populations were either stable or increasing between 1990 and 2000, and the European population is now believed to have reached 7,600–11,000 breeding pairs (BirdLife International 2004). In Lithuania, the population has increased over the last two decades to ~50 pairs (Šablevičius 2001).

Carrete et al. (2005) suggested that when habitat overlap is slight, interspecific competition seems to be a secondary factor in the population decline of a subdominant raptor species. The population increase of the largest species in an avian predator community may present a special conservation dilemma when the dominant and the subdominant species are of conservation concern (Sergio and Hiraldo 2008). In that case, knowledge on habitat overlap could be a useful tool in conservation decision-making processes. The four species selected for our study are all of conservation concern and share similar resources. One of these species, the dominant competitor, has seen its population undergo rapid recovery in recent years. Consequently, in this study, we first analyzed the four species coexistence and then focused on habitat overlap between White-tailed Eagles and the other three species. We hypothesized that the habitat of the recovering populations of White-tailed Eagles will extensively overlap with habitats of other avian predators.

Methods

Data collection

The study was carried out over the period 1997–2008 in Lithuania (65,200 km^2, 55°10′N, 23°39′E). We searched for occupied territories and nest trees for the four bird species in various parts of the country (Fig. 1) using methods described in detail elsewhere (Dementavičius 2007; Treinys et al. 2008). The nest search efforts for each species were not intentionally concentrated around nest sites of whatever other species or within potential habitat of particular species to avoid bias in habitat preference. A nest was considered to be occupied if it contained eggs or nestlings (or their remains) or if it had been repaired by a non-breeding pair or single bird in the spring. Only the most recently occupied nest within a distinct territory of a pair was accepted for analysis retaining the principle "one pair—one nest." Links between particular pairs and nests were reliably established due to the following: (1) conspecific densities of the studied species were low, (2) the species show great loyalty to nesting territories over many years, (3) we routinely monitored known territories and searched for occupied nests in different years, and (4) alternative nests of the same pair were usually situated close to nests previously used. In a few cases where the nest–pair relationship was complicated, the nearest neighbor distance, i.e., the shortest known distance between two successful nests of the species, was used to resolve the issue. Nevertheless, we cannot rule out exceptional cases in each species that a pair or one of the mates settled in a new nest a large distance from the previously used nest.

Habitat measurement

The location of nests, together with the corresponding description of habitat at three spatial scales (the macrohabitat, the nest tree location, and the nest stand), were stored in a GIS database. The macrohabitat was defined as a circular plot of 3 km radius around the nest tree. Studied species have very large home-ranges of various, frequently non-circular configurations (Bai et al. 2009; Jiguet and Villarubias 2004; Meyburg et al. 2007; Scheller et al. 2001; Struwe-Juhl 2000; authors observations); thus, we subjectively selected a 3-km radius around nest trees of all studied species to represent the most important characteristics of the nesting habitats at the landscape scale. The same 3-km radius was used by other authors to represent the landscape scale of Black Stork (Lõhmus et al. 2005) and Lesser Spotted Eagle nesting sites (Langgemach et al. 2001). In spite of the circular plots being a simplification of real home-ranges or territories, this approach is still applicable in studies dealing with habitat preferences (e.g., Lõhmus et al. 2005) and habitat segregation of species differing in home-ranges (e.g., Krüger 2002a). The CORINE land cover database (Vaitkuvienė and Dagys 2008) was used to describe the macrohabitat within each nesting area. The total share of the following land cover types were calculated for each macrohabitat: (1) artificial surfaces (CORINE land cover code 1), (2) arable land (code 211), (3) extensively used agricultural areas (codes 231, 242, and 243), (4) deciduous forest (code 311), (5) coniferous forest (code 312), (6) mixed forest (313), (7) wetlands (411, 412), and (8) water bodies (code 5). Additionally, the total length of all (9) hydrographic objects (i.e., rivers and drainage channels) and (10) roads with pavement was summed for each territory using a base map at a scale of 1:50,000 (database LTDBK50000V). To describe the location of a nest tree in the landscape, the distance (in meters) to the nearest of the following landscape features was estimated using a base map at a scale of 1:50,000 (database LTDBK50000V): (11) field (agricultural area >10 ha in size, omitting small openings in forest), (12) water body, (13) stream (river or dyke), (14) road with pavement, (15) bog, or (16) human (farmstead or settlement). Using the State Forest Cadastre Data Base from the State Forest Survey Service, for each nest stand, (17) the age and mix of tree species was described: share of (18) pine, (19) spruce, (20) broad-leaved tree species (oak, ash etc.), (21) birch, (22) black alder, (23) aspen, and (24) softwood (grey alder, *Salix* sp.etc.).

Statistical analysis

Proportions were arcsine-square-root transformed and distances log-transformed prior to analysis. To reduce collinearity, we used a method of variable reduction commonly employed in habitat selection studies (Sergio et al. 2006 and references therein); consisting in that, when we found pairs of explanatory variables strongly correlated (r>0.5), we considered them as estimates of one underlying factor, and only one of the two (the most important by the study organism) was retained for analysis (Bosakowski et al. 1992; Sergio et al. 2006; Poirazidis et al. 2007). For final set of variables, see Appendix.

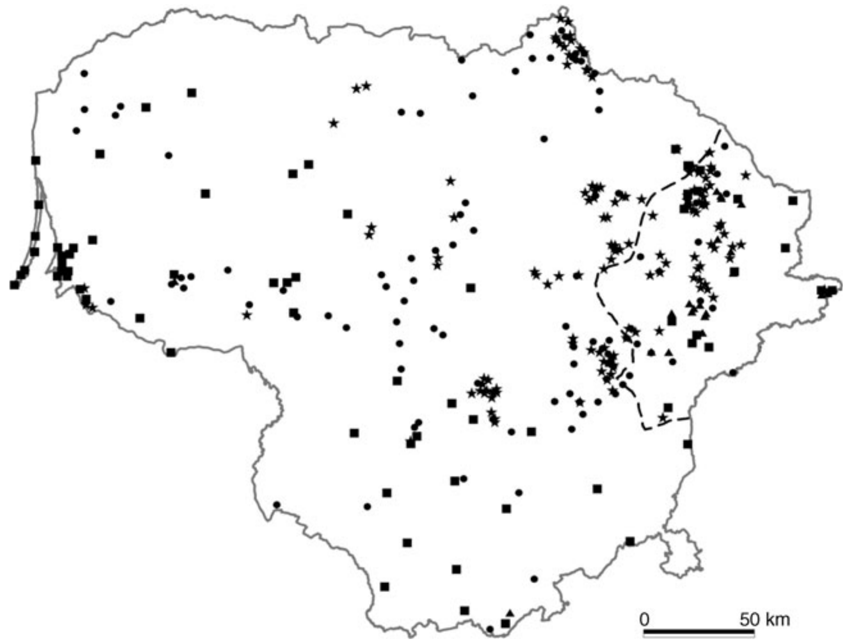

Fig. 1 Distribution of the White-tailed Eagle (*squares*), Lesser Spotted Eagle (*asterisks*), Black Stork (*dots*), and Osprey (*triangles*) nests. *Black broken line* represents boundaries of eastern Lithuania eco-region

We performed stepwise discriminant analyses to explore the pattern of habitat differentiation among the four species at country level. We then focused on the relationship between three pairs of species, each pair including White-tailed Eagle. This is particularly important as the expanding population of this dominant competitor in the tree-nesting large avian predator community could pose a conservation dilemma through competition exclusion mechanism. To analyze the coexistence pattern in greater depth, we used a series of a stepwise discriminant function analyses to test overall habitat overlap of the three pairs of species (White-tailed Eagle vs. Lesser Spotted Eagle, White-tailed Eagle vs. Black Stork, and White-tailed Eagle vs. Osprey) and then calculated a niche overlap value, following Krüger (2002a):

$$\mathrm{NO} = e^{\left[\frac{-d^2}{2\left(s_1^2+s_2^2\right)}\right]}$$

where NO is the niche overlap value, d is the distance between the species means of a discriminant function, and s_1^2 and s_2^2 are the respective variances for species 1 and 2. An overlap value above 0.6 has been proposed to indicate that two species should not coexist (competition exclusion principle); at values below, they can coexist. In general, the higher the overlap value between two species, the less likely is long-term population coexistence (Krüger 2002a, b).

Spatial heterogeneity in the competitive environment provides additional axes over which species can differ, thus broadening opportunities for coexistence (Amarasekare 2003). To avoid erroneous conclusions due to use of countrywide data, we repeated analyses as described above with a subset of 99 nests (15 of White-tailed Eagle, 45 of Lesser Spotted Eagle, 19 of Black Stork, and 20 of Osprey) found in the eastern Lithuania eco-region (classification according to Kuliešis and Kasperavičius 1999; Fig. 1). Landscape of this eco-region (7,710 km^2) consists of 16% coniferous forest, 14% mixed forest, 7% deciduous dominated forest, 51% agricultural land, 6% water bodies, 1% bogs, 3% semi-natural areas, and 2% artificial surfaces. Calculations were performed with Statistica 6.0.

Results

Altogether, we described the habitat of 133 pairs of Lesser Spotted Eagle, 104 pairs of Black Stork, 69 pairs of White-tailed Eagle, and 23 pairs of Osprey, covering ca. 5–7%, 11–16%, 77%, and 46% of the species' national populations, respectively. Three discriminant functions were constructed with seven variables chosen as significant discriminators (Table 1) with an overall highly significant model ($F_{42,926}$=10.871, p<0.0001; Fig. 2). These variables classified 69.3% of nests correctly. The first function (the most important variable—water share within 3 km) accounted for 65% of the total variance observed and clearly separated Lesser Spotted Eagle and Black Stork (little water in the macrohabitat) from White-tailed Eagle and Osprey (macrohabitats rich in water). The second function (the most important variable—distance to the nearest field) accounted for 25% of the total variance observed and separated Lesser Spotted and White-tailed Eagle from Black Stork and Osprey, the former two nearer the field, the latter deeper in the forest. The third function (the most important variable—distance to the nearest bog)

Table 1 Stepwise discriminant analyses of the White-tailed Eagle (HA), Lesser Spotted Eagle (AQ), Black Stork (CN), and Osprey (PH) nests at country (n=329) and eastern Lithuania eco-region (n=99) scales

Variable	Wilks' λ	F	P
Country scale (F (3, 312))			
Water share within 3 km	0.416	37.937	<0.00001
Nearest distance to the field	0.354	16.977	<0.00001
Nearest distance to the bog	0.328	8.042	0.00004
Birch share in the nest stand	0.325	6.844	0.0002
Hardwood share in the nest stand	0.319	4.744	0.003
Spruce share in the nest stand	0.317	4.355	0.005
Black alder share in the nest stand	0.317	4.172	0.006
Eco-region scale (F (3, 88))			
Birch share in the nest stand	0.361	8.259	0.00007
Water share within 3 km	0.347	6.788	0.0004
Nearest distance to the field	0.335	5.553	0.002
Nearest distance to the bog	0.310	2.960	0.04

accounted for 10% of the total variance and ranked Black Stork, White-tailed Eagle, Lesser Spotted Eagle, and Osprey in descending order in terms of distance from bog (where Black Stork is the furthest, Osprey the closest).

Using the eastern Lithuania eco-region data subset, another three discriminant functions were constructed (but only two of these were significant) with four variables chosen as significant discriminators (Table 1) with an overall highly significant model ($F_{24,255}$=5.835, p< 0.0001). These variables classified 76.8% of nests correctly. All four variables (i.e., water share within 3 km, the distance to the nearest field, distance to the nearest bog, and share of birch trees in nest stand) were chosen as significant discriminators in the countrywide scale analysis too.

White-tailed Eagle vs. Lesser Spotted Eagle Five variables were chosen as significant discriminators with an overall highly significant model ($F_{14,187}$=14.237, p<0.0001). These variables classified 87.6% of nests correctly (Table 2). White-tailed Eagles selected nests in areas with a higher abundance of water bodies and coniferous forests, further from humans, in older stands with a lower proportion of hardwood trees compared to Lesser Spotted Eagle. The niche overlap value between the two eagles was 0.07 and

Fig. 2 *Scatter plots* of two discriminant functions. *Dotted*, *dash-dot-dash*, *solid*, and *broken ellipses* are the 95% confidence limits for Lesser Spotted Eagle (AQ), Black Stork (CN), White-tailed Eagle (HA), and Osprey (PH), respectively

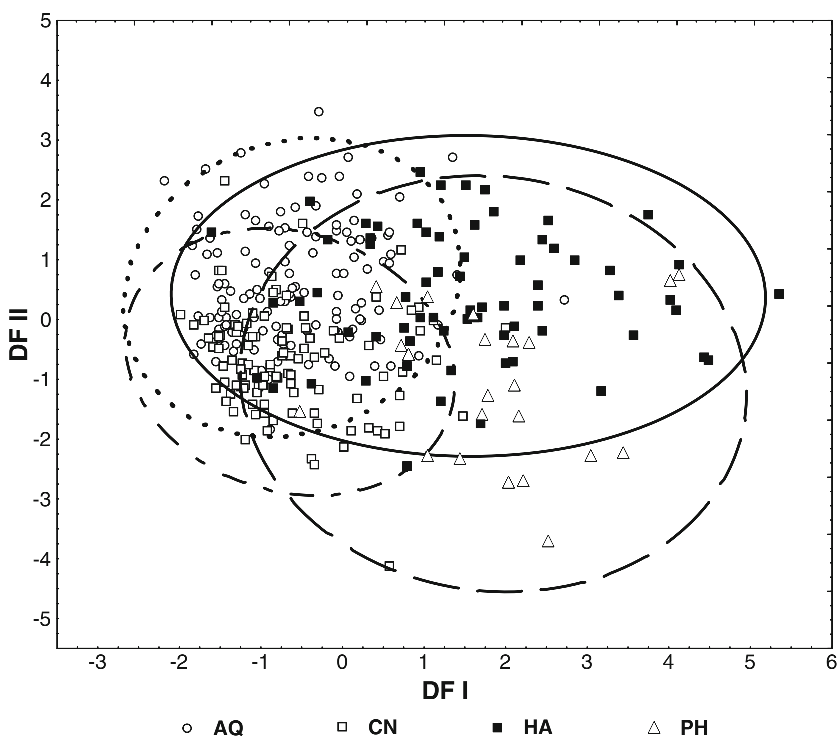

Table 2 Niche overlap values and classification matrix of the White-tailed Eagle (HA) and Lesser Spotted Eagle (AQ), White-tailed Eagle (HA) and Black Stork (CN), and White-tailed Eagle (HA) and Osprey (PH) nests at country and eastern Lithuania eco-region scales

Real species	*n*	Predicted species		% Correct	Total % correct	Niche overlap value
Country scale						
		AQ	HA			
AQ	133	128	5	96.2	87.6	0.07
HA	69	20	49	71.0		
		CN	HA			
CN	104	96	8	92.3	87.2	0.34
HA	69	14	55	79.7		
		PH	HA			
PH	23	11	12	47.8	84.8	0.57
HA	69	2	67	97.1		
Eco-region scale						
		AQ	HA			
AQ	45	43	2	95.6	90.0	0.33
HA	15	4	11	73.3		
		CN	HA			
CN	19	17	2	89.5	88.2	0.36
HA	15	2	13	86.7		
		PH	HA			
PH	20	18	2	90.0	82.9	0.50
HA	15	4	11	73.3		

shows nearly perfect habitat differentiation. A separate discriminant analysis performed by including these eagle nests from the eastern Lithuania eco-region again resulted significant model ($F_{6,53}$=7.511, p<0.0001). Three significant variables classified 90% of nests correctly as either White-tailed or Lesser Spotted Eagle (Table 2). Out of these three variables, one variable (water share within 3 km) was chosen as a significant discriminator in the countrywide sale discriminant function, and two new significant variables emerged (nearest distances to the field and to the bog). White-tailed Eagle selected nests with a greater distance between the nest and the nearest field and with a smaller distance from the nest to the nearest bog. The calculated niche overlap value of 0.33 between these two eagles was much higher than the corresponding one in the country scale data. Nevertheless, this value was 1.8 times less than the critical threshold (0.6; Krüger 2002b).

White-tailed Eagle vs. Black Stork Six variables were chosen as significant discriminators with an overall highly significant model ($F_{9,163}$=25.464, p<0.0001). These variables classified 87.3% of nests correctly (Table 2). Black Storks selected nests in areas with fewer water bodies and coniferous forests, nested further away from fields, and in nest stands with a higher share of birch and hardwood trees and lower share of black alder trees compared to White-tailed Eagle. The niche overlap value between eagle and stork was 0.34 and shows marked habitat difference. A separate discriminant analysis performed using nests from the eastern Lithuania eco-region resulted significant model ($F_{5,28}$=6.665, p<0.0003) with the three significant variables. These three variables classified 88.2% of nests correctly as either White-tailed Eagle or Black Stork (Table 2). All three variables (water share within 3 km, share of birch trees in nest stand, and share of hardwood trees in nest stand) had entered the countrywide scale discriminant function. The calculated niche overlap value of 0.36 between eagle and stork in eastern Lithuania eco-region was only slightly higher than the corresponding one in the full data set.

White-tailed Eagle vs. Osprey Three variables were chosen as significant discriminators with an overall highly significant model ($F_{6,85}$=7.49, p<0.0001). These variables classified 84.8% of nests correctly (Table 2). Ospreys nested in landscape patches with higher proportion of mixed forests, selected nests closer to bogs, and further away from fields compared to White-tailed Eagle. The niche overlap value between White-tailed Eagle and Osprey was 0.57, i.e., close to the critical threshold (0.6; Krüger 2002b) and indicates that there is potential for competition for nesting habitat between the two species. Again, a discriminant analysis by using the data subset from eastern Lithuania eco-region resulted significant model ($F_{6,28}$= 4.216, p<0.004) with the three significant variables. These three variables classified 82.9% of nests correctly as either White-tailed Eagle or Osprey (Table 2). Out of these three variables, two variables (mixed forest share within 3 km and distance to the nearest field) had entered the countrywide scale discriminant function, and one was new (share of softwood in nest stand). Osprey in the eastern Lithuania eco-region nested in stands with a higher proportion of softwood trees. The calculated niche overlap value of 0.50 between these two eagles was even lower than the corresponding one of the country scale data.

Discussion

The most important results of our study are (1) the nesting habitat of the four tree-nesting avian predatory species differed; (2) the habitat of White-tailed Eagle overlapped with the habitat used by the Lesser Spotted Eagle, Black Stork, and Osprey to varying degrees with niche overlap values being below competition exclusion thresholds; and (3) habitat difference between the studied species was rather weakly influenced by the spatial scale.

The observed differences in habitat among the studied species could be a consequence of resource-based segregation but not a consequence of asymmetrical interspecific competition. To support this, we provide two pieces of evidence:

1. At country and eco-region scale, the studied species differed along macrohabitat, nest placement in the landscape, and nest stand variables. Moreover, the difference is also prominent at the scale of nest tree: most White-tailed Eagle and Osprey nests were built in pine, but at different frequencies: 54% and 88%, respectively (Drobelis 2004; Dementavičius, unpublished data). Most Lesser Spotted Eagle nests were built in spruce (48%; Treinys and Mozgeris 2006), while most Black Stork were in oak (76%; Treinys et al. 2008). The smallest overlap between Northern Goshawk, Common Buzzard, and Honey Buzzard habitat was found at the macrohabitat scale and greatest at nest tree scale (Gamauf 2001). This pattern could be explained by different prey (for diet, see Cramp and Simmons 1980) and by morphological similarities in these medium-sized forest dwelling raptors (for details, see Kostrzewa 1996). The species in the current study differ considerably in morphology and prey selected. Osprey and White-tailed Eagle prey on similar fish species (e.g., Drobelis 2004; Tuvi and Väli 2007), whereas Black Stork, though it also preys mainly on fish (Treinys et al. 2009), takes fish of different species (mainly *Rutilus rutilus* and *Alburnus alburnus*; authors data). Amphibians constitute a significant part of both Lesser Spotted Eagle and Black Stork diet (Treinys and Dementavičius 2004; Treinys et al. 2009). The diet similarities of two species groups (i.e., White-tailed Eagle–Osprey and Lesser Spotted Eagle–Black Stork) correspond to the nesting habitat overlap too (see Fig. 2).
2. It is thought that habitat selection and segregation in raptor communities could be shaped by interspecific competition avoidance mechanism (Kostrzewa 1996; Krüger 2002a). Though solitary pairs probably bred, White-tailed Eagle was essentially absent as a breeding species in Lithuania for almost 50 years (Dementavičius 2007), a situation contrary to that of Lesser Spotted Eagle, Black Stork, and Osprey. The present distribution of White-tailed Eagle across the country has a clumped pattern with the lowest densities occurring in northern and central Lithuania (Dementavičius 2007), regions that also hold the highest densities of Lesser Spotted Eagle and Black Stork (Kurlavičius 2006). The core population of Osprey is located in eastern Lithuania, the distribution pattern unchanged from the period prior to the recovery of White-tailed Eagle (Drobelis 2004; authors data). Katzner et al. (2003) found that interspecific competition for nesting habitat and territories appear to be unlikely determinants of the distribution and abundance of tree-nesting eagle species in Kazakhstan (*A. chrysaetos*, *A. heliaca*, and *H. albicilla*).

A recovering population of White-tailed Eagle may threaten to limit Ospreys at a population level (i.e., the dominant competitor reduces the density of the subdominant species; Busche et al. 2004), but not Lesser Spotted Eagles or Black Storks. Nesting habitat segregation between White-tailed Eagle and the three smaller predatory species (Lesser Spotted Eagle, Black Stork, and Osprey) was supported by empirical field data: during 12 years of study in the checked territories (n=329), we observed only two cases where White-tailed Eagle and Lesser Spotted Eagle occupied the same individual nest in different years and only two cases where White-tailed Eagle and Osprey nested in the same nests in different years. No nests were observed where White-tailed Eagle and Black Stork nested in a single nest in subsequent years. Extensive habitat overlap between Northern Goshawk, Common Buzzard, and Honey Buzzard was often accompanied by the use of the same nesting patches/nest trees, resulting in the exclusion of weaker competitors (Hakkarainen et al. 2004). The coexistence opportunity between White-tailed Eagle and Osprey was most dubious. The calculated niche overlap value between the species was 0.50 and 0.57 depending on the spatial scale, indicating potential for competition. Moreover, reversed correct classification of nests at two spatial scales (Table 2) led us to suppose that a further increase in the population of the dominant species could limit Osprey by displacement from nesting sites within eastern Lithuania and simultaneously suppress the possibility for the smaller species to disperse outside its historical species range in the country. Another study found niche overlap between Northern Goshawk and Common Buzzard (Krüger 2002a) at very similar levels as we found in the cases of White-tailed Eagle and Osprey. Despite Goshawk and Buzzard nesting in different habitats, the niche overlap was rather high, 0.504

or 0.566 depending on the approach, meaning coexistence was close to the critical competition threshold, thus resulting in reduced reproductive output and displacement of the subdominant species, i.e., Common Buzzard, to suboptimal nest sites (Krüger 2002a, b). Carrete et al. (2005) stated that (1) when habitat overlap is slight, interspecific competition is of secondary importance in the decline of subdominant eagle species, and (2) many abandoned territories of subdominant Bonelli's Eagle *Hieraaetus fasciatus* have later been occupied by a superior competitor, Golden Eagle *A. chrysaetos*, suggesting that these territories may correspond to suitable overlap habitat.

Conservation decisions concerning the coexistence of sympatric species should be made with caution when they are applied at a spatial scale different to the derived habitat overlap model. Shifting from the countrywide to the region-wide scale resulted in lower number of variables influencing the difference between the habitats of the four species; nevertheless, a significant difference was retained. These findings are in line with the general pattern that spatial heterogeneity in the competitive environment provides additional axes over which species can differ (Amarasekare 2003), but indeed, at a larger spatial scale, the opportunity for species coexistence is not necessarily broadened. Furthermore, detail analyses of habitat overlap between White-tailed Eagle and its sympatric species show that coexistence opportunity by increasing spatial scale is species dependent and is not necessarily unidirectional. Switching to the countrywide spatial scale resulted in 4.7-fold decrease in niche overlap values between White-tailed Eagle and Lesser Spotted Eagle, whereas the value remained almost unchanged between White-tailed Eagle and Black Stork and even increased between White-tailed Eagle and Osprey.

The current expansion of the White-tailed Eagle in Lithuania is not a threat for the Lesser Spotted Eagles and Black Storks, but may be a threat limiting the expansion of Ospreys. Habitat use of birds, however, could change over space (Väli et al. 2004) or time (Marchesi et al. 2002) and reshape the coexistence pattern within raptor communities. We suppose that at certain periods or in particular areas, studied species could become more dependent on similar habitats than shown in this study.

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Appendix

Means and standard deviations of prime untransformed macrohabitat, nest tree location, and nest stand variables around nest trees of Lesser Spotted Eagle (n=133), Black Stork (n=104), White-tailed Eagle (n=69), and Osprey (n=23) used for analyses

Variable	Lesser Spotted Eagle	Black Stork	Sea Eagle	Osprey
Share in macrohabitat of				
Build-up areas	0.012±0.017	0.009±0.013	0.015±0.028	0.002±0.006
Coniferous forests	0.086±0.131	0.091±0.147	0.19±189	0.32±0.237
Mixed forests	0.172±0.108	0.19±0.119	0.147±0.107	0.248±0.133
Water bodies	0.024±0.038	0.01±0.025	0.161±0.159	0.092±0.106
Nearest distance (meters) to				
Field	219±190	635±554	947±1,666	1,400±1,118
Human	673±338	900±560	1,142±726	1,339±1,246
Stream	333±323	544±513	1,530±3,201	1,297±975
Road with pavement	1,566±953	1,782±1,078	1,641±1,033	2,775±2,081
Bog	5,314±4,756	6,359±5,369	4,359±4,626	1,661±1,910
Share in stand of				
Spruce	0.28±0.28	0.21±0.25	0.19±0.24	0.20±0.27
Hardwood	0.17±0.27	0.19±0.26	0.04±0.13	0.03±0.13
Birch	0.20±0.23	0.24±0.25	0.17±0.22	0.11±0.20
Black alder	0.10±0.20	0.12±0.22	0.14±0.29	0.05±0.15
Aspen	0.08±0.12	0.11±0.15	0.07±0.17	0.01±0.03
Softwood	0.06±0.18	0.05±0.13	0.03±0.13	0.01±0.06
Stand age (year)	85±26	86±28	92±34	90±56

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