

May Sympatric Lesser Spotted Eagles and Black Storks Compete for Nesting Sites in Spatially Varying Environments?

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Abstract

Disclosing of biotic interactions between sympatric species is important from both theoretical and practical perspectives, especially when the species are of conservation concern. In ecologically similar species, environmental heterogeneity may change the intensity of their competitive interactions due to varying species responses along the environmental gradients. In this study, we analysed the overlap in nesting sites between the internationally protected, mature forest-dwelling Lesser Spotted Eagle *Clanga pomarina* and the Black Stork *Ciconia nigra*. The importance of landscape heterogeneity for habitat segregation between these species was also assessed. The nesting sites of 123 pairs of Lesser Spotted Eagles and 78 pairs of Black Storks, located across different landscapes of the Central, Central-Eastern and Eastern Lithuanian ecoregions were described. A series of discriminant analyses were performed to explore regional patterns of habitat differentiation between the species. Habitat differentiation between the species was estimated by niche overlap values (range 0-1, with a value 0.6 suggested to be the threshold between coexistence and competition), which were 0.5, 0.63 and 0.55 for the Central, Central-Eastern and Eastern ecoregions, respectively. Different habitat factors and/or their combinations explained the habitat differentiation between the species in each ecoregion. Although our data shows the coexistence of the Lesser Spotted Eagle and the Black Stork, in certain regions these mature forest-dwelling predators may use too similar habitats and compete for prime sites under specific landscape structures and short supply of suitable patches. Therefore, we propose the necessity of the importance of a regional estimation on biotic interactions when developing conservation programmes and allocating conservation actions within the target region.

Keywords: *Clanga pomarina*, *Ciconia nigra*, coexistence, competition, habitat, spatial variation

Introduction

Limited resources and overlap in resource use are necessary conditions underlying interspecific competition between sympatric species (Dhondt 2012). Large and medium-sized, forest-dwelling birds as raptors and Black Stork usually prefer mature stands for nesting (Penteriani 2002, Bielański 2006, Treinys and Mozgeris 2006, Treinys et al. 2016), as heavy twig nests can only be constructed in large trees (Kostrzewa 1996, Löhmus 2006). Krüger (2002) suggested that intense competition tends to occur among some forest-dwelling raptors for nesting sites. Furthermore, timber harvesting in managed forests usually reduces the availability of such suitable nesting structures for these birds (e.g. Löhmus 2003). Thus, ow-

ing to the association of tree nesting large and medium-sized birds with mature forest stands, together with the reduced availability of suitable habitat due to timber harvesting, competition for available nesting sites among these tree-nesting bird species is intensified (Hakkarainen et al. 2004). However, spatial heterogeneity in the competitive environment provides additional axes over which sympatric species can differ, thereby broadening opportunities for coexistence (Amarasekare 2003). Supporting this idea, habitat preferences of forest-dwelling bird species can vary regionally, as has been demonstrated in the case of the Lesser Spotted Eagle in the northern part of the distribution range (Väli et al. 2004).

A variety of conservation measures have been suggested to enhance nesting habitats for large and medium-

sized tree-nesting birds, including setting aside stands of forest from timber harvesting, installing of nesting platforms (Newton 2003, Saurola 1997), or leaving mature trees during final cutting in order to boost the availability of potential nest trees in future stands (Lõhmus 2006). However, in order to facilitate and efficiently allocate conservation strategies, it is necessary to better understand coexistence among sympatric species, and the influence of spatial variation on these biotic interactions. Despite extensive research on competitive interactions in different communities of large and medium-sized raptors (Bosakowski et al. 1992, Krüger 2002, Katzner et al. 2003, Hakkarainen et al. 2004, Treinys et al. 2011, Gamauf et al. 2013), the coexistence of sympatric, internationally protected Lesser Spotted Eagle *Clanga pomarina* and the Black Stork *Ciconia nigra*, which are distributed in the forests of Central Europe (Cramp and Simmons 1980, Janssen et al. 2004), has not yet been analysed. Despite Black Stork systematically is not a bird of prey, breeding ecology is identical to diurnal raptors at least in temperate forests. Black Stork and Lesser Spotted Eagle breed in the same forests, exhibit a high degree of site fidelity, avoid the vicinity of humans, prefer to nest in mature stands, build and nest in a large stick nests on old trees (Cramp and Simmons 1980, Janssen et al. 2004, Lõhmus and Sellis 2003, Meyburg et al. 2001, Skuja and Budrys 1999, Treinys et al. 2009, Treinys and Mozgeris 2010, Treinys et al. 2016). Moreover, idea that nesting habitat of these species overlap promoted by empirical observations that pairs of both species may occupy even the same nests, hence the same nesting sites but in different years (Skuja and Budrys 1999). Both species are sensitive to forestry operations because of loss of existing (in case if not protected) either suitable nesting habitats during clearings (Meyburg et al. 2001, Treinys and Mozgeris 2006, Strazds 2011). Because of extensive sympatric distribution in temperate forests, seemingly similar nesting sites, observed occupation of the same nests and the limited availability of nesting habitats, exploitative competition between these two species may be assumed. To address this knowledge gap, in this study we analyse the overlap in nest-site characteristics of the Lesser Spotted Eagle and Black Stork, and its regional variation. We expect that competition between species occurs if nesting sites overlap extensively (i.e. there is a niche overlap value higher than 0.6; for details see Krüger 2002). We also investigate whether spatial heterogeneity is an important source of variation for interspecific interaction, based on the following criteria: 1) the niche overlap values differ considerably among landscape types, and 2) different environmental variables contribute to the segregation of nesting sites of eagles and storks in different landscape types.

Materials and Methods

We searched for territories and nest-trees occupied by the Black Stork and Lesser Spotted Eagle in the Eastern-Central part of the Lithuania (Figure 1) during the period of 2000-2008, applying the methods described by Treinys and Mozgeris (2006) and Treinys et al. (2008). Data on nesting sites were collected in a similar manner, over the same period for both species. Given that these birds are long-living, reoccupying the same sites year after year, temporal changes in habitat preference were not likely to bias our findings. 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 a single bird in the spring. In cases where a pair used several nests during the study period, only the most recently occupied nest within the individual territory of the pair was included in the analysis. Altogether, we described the nesting sites of 123 pairs of Lesser Spotted Eagles and 78 pairs of Black Storks. All nests were attributed to one of the three ecoregions (in this study termed as Central, Central-Eastern and Eastern) with borders taken from the master plan of the territory of the Republic of Lithuania (Valstybės Žinios 2002) (see Figure 1). High-productivity mixed deciduous-spruce forests dominate in the Central ecoregion, high-productivity mixed spruce-deciduous forests – in the Central-Eastern ecoregion and medium-productivity mixed pine-spruce forests – in the Eastern ecoregion, respectively.

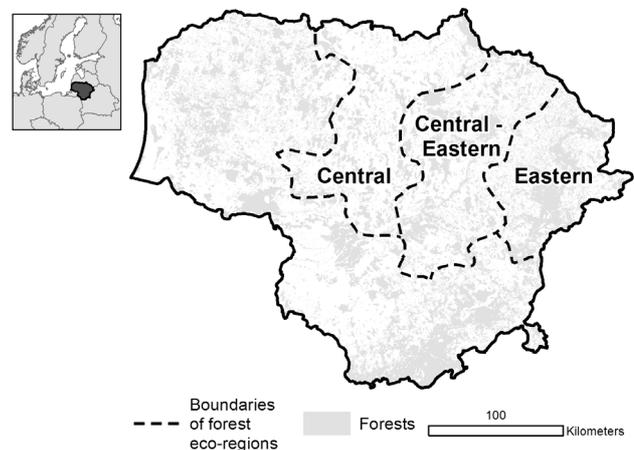


Figure 1. Study location and borders of the ecoregions

To describe the location of a nest-tree in the landscape, the distance (in meters) was estimated to the nearest of the following landscape features: field (agricultural area > 10 ha in size, omitting small openings in forest), stream (river or dyke), road with pavement, water body and human inhabitation (farmstead or settlement), using a base map at a scale of 1:50000 (database

LTDBK50000V – this database was chosen as the data source best corresponding to the years of data collection). Distances were then square root transformed for further analysis. For each nest stand (mean size 3.8 ha), the age, site moisture score (1, 2, 3, 4 and 5, increasing in moisture), relative stocking level (based on basal area of the stand) and share of volume proportions of pine, spruce, broad-leaved tree species (oak, ash, etc.), birch, black alder and aspen were taken from the State Forest Cadastre Data Base, available from the State Forest Service, and referring to the year of bird nests searches.

We performed a series of stepwise discriminant analyses to explore the pattern of habitat differentiation between species nesting in the three ecoregions (see Krüger 2002, Treinys et al. 2011). The niche overlap values for each ecoregion were calculated based on Krüger (2002):

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

where *NO* is the niche overlap value; *d* is the distance between the species means of a discriminant function; *s*₁ and *s*₂ are the respective variances of discriminant scores for species 1 and 2. An overlap value above 0.6 was proposed as a threshold to indicate that two species should not coexist (competition exclusion principle), while all values below 0.6 indicated their coexistence. In general, the higher the overlap value between two species, the less likely that long-term population coexistence will occur (Krüger 2002). Discriminant analyses were also used to show the within-species habitat variation occurring across the ecoregions and to compare the nesting sites of two species in the three ecoregions simultaneously.

Results

Nesting sites of both the Black Stork (*F*_{16,136} = 4.5, *p* < 0.0001; Figure 2) and the Lesser Spotted Eagle (*F*_{16,226} = 4.7, *p* < 0.0001; Figure 3) varied across the three ecoregions studied. The Black Stork nesting sites differed significantly across the ecoregions in terms of their distance to the nearest water body, stream and in relative stocking level of the stand first layer (Table 1). The Lesser Spotted Eagle nesting sites differed significantly in the three ecoregions by the distance to nearest water body and by the share of spruce and hardwood in the first stand layer (Table 1).

The nesting sites of analysed avian predators in the three ecoregions differed significantly (*F*_{55,859} = 5.87, *p* < 0.0001) resulting in the spatial variation of habitat overlap (Figure 4). The pair-wise comparison of habitats of two species within each ecoregion provided deeper insight. The constructed discriminant function for the nesting sites in the Eastern Lithuania ecoregion included seven variables, four of which were significant discrimi-

Table 1. Summary of results from discriminant function analyses of Lesser Spotted Eagle and Black Stork nesting sites. Reported are P values of variables, which were included in the final models. Statistical significance is indicated in bold

Variable	Species in 3 ecoregions		Eagle vs. Stork in ecoregion		
	Eagle	Stork	Eastern	Central-Eastern	Central
Distance to: field	< 0.0001	0.29		< 0.0001	0.0001
road	0.12	0.14	0.03	0.15	
human inhabitation					0.32
water body		0.003			
stream		0.0002	0.004	0.03	
Proportion of:					
pine	0.11	0.18			
spruce	0.01	0.21	0.18	0.28	
birch			0.01	0.15	0.046
broad-leaved	0.001		0.28		0.01
black alder	0.12	0.26	0.03		
aspen					0.11
Relative stocking level	0.07	0.003			
Stand age	0.13			0.25	
Site moisture			0.09		

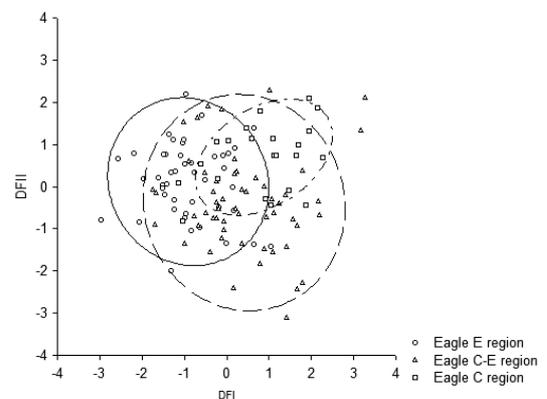


Figure 2. Scatter plots of two discriminant functions (DFI and DFII), separating nesting sites of Lesser Spotted Eagle in three ecoregions. Solid, broken and dash-dot-dash ellipses are the 95% confidence limits for nesting sites in Eastern, Central-Eastern and Central ecoregions, respectively

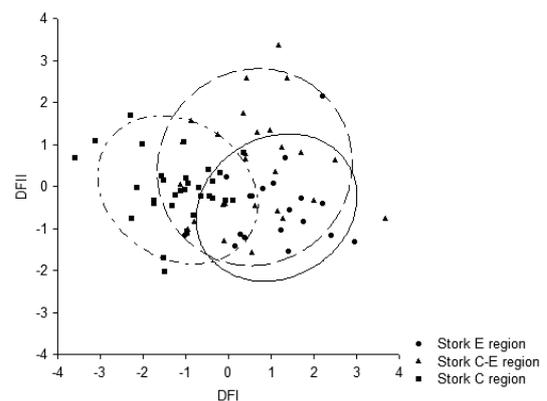


Figure 3. Scatter plots of two discriminant functions (DFI and DFII), separating nesting sites of Black Storks in three ecoregions. Solid, broken and dash-dot-dash ellipses are the 95% confidence limits for nesting sites in Eastern, Central-Eastern and Central ecoregions, respectively

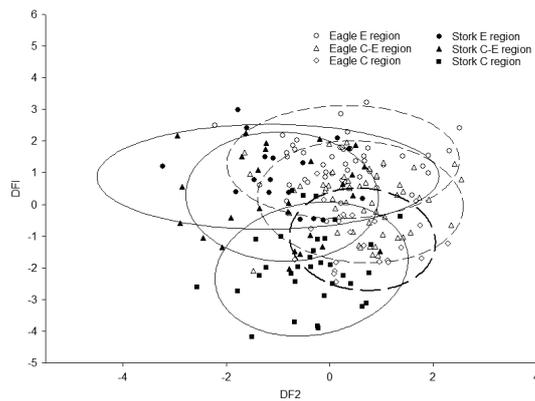


Figure 4. Scatter plots of two discriminant functions (DFI and DFII), separating six groups of nesting sites (i.e. two species × three ecoregions). Solid and broken ellipses are the 95% confidence limits for Black Stork and Lesser Spotted Eagle nesting sites, respectively

nators with a generally highly significant model (Table 1, $F_{7,57} = 6.1, p < 0.0001$). Of the nests assessed, 83% were correctly classified; however, a somewhat lower percentage for correct classification was achieved for Black Stork nests (58%) (Table 2). In this region, the Lesser Spotted Eagles selected nesting sites closer to streams and roads when compared to the Black Storks. The eagles' nests were located in stands with a lower proportion of birch and black alder compared to stork nests. The calculated niche overlap value was 0.55, i.e., slightly lower than the critical threshold value 0.6.

Table 2. Classification matrix of Lesser Spotted Eagle and Black Stork nesting sites in the three ecoregions of Lithuania

	n	Predicted species			Total	
		Eagle	Stork	Correct		
Eastern ecoregion	Eagle	46	43	3	93%	83%
	Stork	19	8	11	58%	
	Central - Eastern ecoregion			3	95%	
Central ecoregion	Eagle	55	52	3	95%	83%
	Stork	27	11	16	59%	
Central ecoregion	Eagle	22	17	5	77%	81%
	Stork	32	5	27	84%	

The constructed discriminant function for nesting sites in the Central-Eastern Lithuania ecoregion included six (of which only two were significant) variables, resulting in highly significant model (Table 1, $F_{6,75} = 6.9, p < 0.0001$). Using these variables, 83% of nests were classified correctly (Table 2). Again, the correct classification was much higher for the Lesser Spotted Eagle nests. Lesser Spotted Eagles selected nesting sites closer to fields and streams, compared to the Black Storks. The calculated niche overlap value was 0.63, i.e. above the critical threshold value.

Five variables were included in the constructed discriminant function for the nesting sites of bird species in the Central Lithuania ecoregion (Table 1, $F_{5,48} = 6.4, p < 0.0001$). Three variables were significant discriminators.

Of nests assessed, 81% were correctly classified (Table 2), with minor differences between the two species. The Lesser Spotted Eagles selected their nesting sites closer to fields than the Black Storks. Lesser Spotted Eagles nests were built in stands with a higher share of birch and lower proportion of hardwood compared to the Black Storks. The calculated niche overlap value was 0.5, which is lower than for the Eastern and Central Lithuania ecoregions, as well as being lower than the critical threshold.

Discussion and Conclusions

This work is an extension of our previous study, where we tested the coexistence potential and landscape preferences of protected avian species (Black Stork, Lesser Spotted Eagle and Osprey) with the top predator, the White-tailed Eagle (Treinys et al. 2011). In this study we analysed two bird species that are relatively symmetrical in terms of competition ability and seeking a deeper insight into spatial variation of interaction between species. The main findings of our study are that 1) nesting sites of the Lesser Spotted Eagle and Black Stork vary across different landscapes, even within relatively small region (a part of Lithuania); and 2) the coexistence/competition potential between species is mediated by environmental heterogeneity. Furthermore, our data suggests that the location of the nesting sites within a landscape is a better discriminator than the characteristics of nest stand itself. Our data indicate the coexistence of the Black Stork and the Lesser Spotted Eagle. However, in certain regions, these mature forest-dwelling avian predators tend to use similar habitats and, therefore, may compete for suitable patches under certain landscape structures and in short supply of prime habitats.

The necessary conditions for the existence of interspecific competition between species are the limited resources and the overlap in resources use (Dhondt 2012). Our results indicate rather extensive nesting habitat overdispersion between the Black Stork and the Lesser Spotted Eagle, despite these species being taxonomically distant, relying on different main prey sources and having different feeding habitats (Cramp and Simmons 1980, Janssen et al. 2004). Moreover, the Lesser Spotted Eagle is considered to be a forest edge species (Bergmanis 2004) while the Black Stork has been classified as a forest interior species (Löhmus et al. 2005). The highest niche overdispersion (*NO* value is 0.63) was recorded in the Central-Eastern Lithuania ecoregion, indicating competition potential between these species for suitable nesting patches. In this region, nesting sites of both species only differed significantly in terms of the nest location in respect to the field and stream. Moreover, in the Eastern ecoregion (*NO* value is 0.55) distance to the field was

even not entered in the final set of variables included in discriminant function. These findings suggest that the traditional assumption of species distribution as regards to the forest edge may be an oversimplification of habitat segregation between these birds under certain landscape conditions. Furthermore, our results on niche overlap values (i.e. 0.5 – 0.63) are rather similar to the findings of Krüger (2002) (i.e. 0.5 – 0.57) despite different set of habitat variables used. This author analysed the overlap in nesting habitat between a goshawk and buzzard, species abundantly nesting in temperate European forests. Interestingly, Bosakowski et al. (1992) studying habitat overlap between two hawks (*Accipiter* spp.) in the United States also found similar niche overdispersion (i.e. 0.54). In the Eastern Lithuania ecoregion, the habitat overlap between the wetland-associated and fish-eating avian predators, the White-tailed Eagle and the Osprey, was even smaller (*NO* value is 0.5; Treinys et al. 2011) compared to the findings of the current study in the same ecoregion for the Black Stork and the Lesser Spotted Eagle (*NO* value is 0.55). Hakkarainen et al. (2004) found evidence of competition for the prime nesting sites in sympatric diurnal raptors in Fennoscandia forests, but Katzner et al. (2003) suggested coexistence among forest-dwelling eagle species in Central Asia. In summary, we suggest that there is high potential for competition between sympatric species in any avian predator community, at least at a landscape scale, which should be taken into consideration in cases of species of conservation concern.

As expected, the habitat segregation between the two forest dwellers varied across the analysed landscape types, with various variables resulting in these differences. Amarasekare (2003) suggested covariance between environment and competition when species differ in their responses to a spatially varying environment. Although variation in *NO* values (maximum by 0.13) and in variables separating the Black Stork and Lesser Spotted Eagle nesting sites in different ecoregions was not extensive, our findings could be considered as important both theoretically and practically. As the moderate habitat overlap was evident, even a small change in *NO* value for different landscapes may alter the understanding on interaction between these species.

According to our findings, it is likely that the Black Stork and the Lesser Spotted Eagle coexist but close to competition threshold. However, in certain landscape types, the potential for competition is also evident due to the similarity of nesting sites, which are of key importance for these site-tenacious, long-lived birds. Thus, our results support the importance of regional assessment of biotic interactions when developing conservation programmes and planning the location of conservation action within specific regions. We caution that no

single feature should be assumed to be the most important for segregation between habitats of two species, without tests in respect of different landscape types. Finally, considering that the Black Stork and the Lesser Spotted Eagle are site-tenacious species, reusing the same nesting sites for many years and maintaining relatively stable local densities between years, we encourage the investment in wide scale searches for occupied nesting sites and the protection of these stands from clear felling and disturbance during breeding season, as proposed by Mozgeris et al. (2015). We believe that this approach will mitigate the loss of mature stands as well as maintaining / stabilising biotic interactions (*cf.* Hakkarainen et al. 2004) between these two mature, forest-dwelling avian predators.

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