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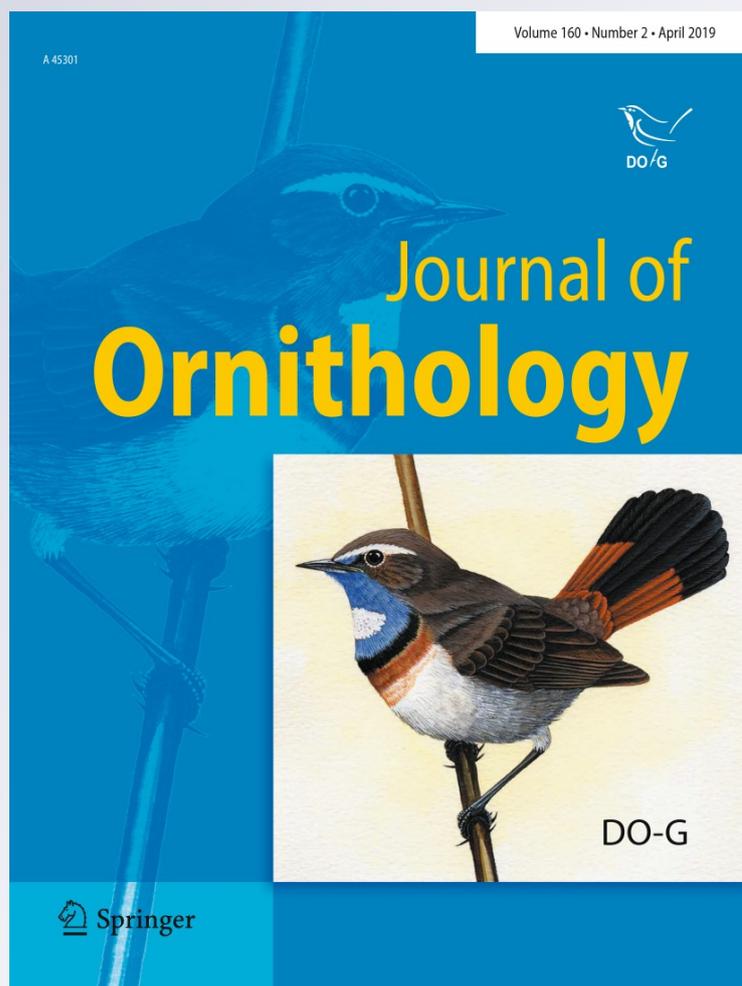
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No adverse effects on Lesser Spotted Eagle breeding in an area of high White-tailed Eagle density

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Abstract

Mesopredators frequently suffer lethal and/or non-lethal negative effects when breeding in sympatry with more powerful apex predators. The recent recovery of the White-tailed Eagle *Haliaeetus albicilla* (WTE) population throughout its range indicates the return of the largest predator of the raptor communities there. In this study, we assess the importance of habitat overlap and spatial distribution to the reproduction of the Lesser Spotted Eagle *Clanga pomarina* (LSE), a species that breeds sympatrically in areas of high WTE density near the Baltic Sea, but is three times smaller than the latter. Fewer water bodies surround the nesting sites of the LSE, and it uses agricultural areas and transitional habitats more frequently than the WTE. The same breeding territories are faithfully occupied by the LSE annually, irrespective of the distance between these and those of the WTE. We found that the breeding success of the LSE was not affected by the proximity or breeding output of the nearest pair of WTEs, nor was this affected by the number of WTE pairs present within a 3-km radius of nests. Our data suggest that the smaller LSE coexists with an abundant top predator without any obvious adverse effects on its population dynamics.

Keywords Interspecific interaction · Coexistence · Competition · Raptor · Top predator · Mesopredator

Zusammenfassung

In Gebieten mit hoher Seeadler-Dichte zu brüten, hat für Schreiadler keine Nachteile

Schwächeren Greifvögeln entstehen oft tödliche oder fast-tödliche Nachteile, wenn sie sympatrisch mit deutlich stärkeren Greifvögeln brüten. Die Erholung der Seeadlerpopulationen (*Haliaeetus albicilla*) in letzter Zeit bedeutete eine Rückkehr des größten aller Greifvögel. In dieser Studie untersuchten wir, wie wichtig Habitatüberlappung und räumliche Verteilung für den Fortpflanzungserfolg des nur ein Drittel so großen Schreiadlers (*Clanga pomarina*) sind, der sympatrisch mit Seeadlern in Gebieten nahe der Ostsee brütet, in denen die Seeadlerdichte besonders hoch ist. Im Vergleich zu den Seeadlern gab es um die Brutplätze der Schreiadler herum weniger Gewässer, und sie nutzten landwirtschaftlich genutzte Flächen und Übergangshabitate häufiger als die Seeadler. Unabhängig von ihrem Abstand zu den Seeadlern benutzten die Schreiadler jedes Jahr genau die gleichen Brutplätze. Der Fortpflanzungserfolg der Schreiadler war unbeeinträchtigt von der Entfernung zum nächstgelegenen Seeadlerpaar und dessen Bruterfolg wie auch von der Anzahl von Seeadlerpaaren innerhalb eines Umkreises von 3 km. Unsere Ergebnisse legen nahe, dass der kleinere Schreiadler ohne feststellbaren Nachteil für seine Populationsdynamik mit großen Greifvögeln koexistieren kann.

Introduction

Avian top predators can adversely affect smaller-sized sympatric birds of prey through lethal and/or non-lethal effects (Sergio and Hiraldo 2008). Apex predators may prey on subordinate raptors to obtain energetic gains (Mikkola 1976; Lourenço et al. 2014; Hoy et al. 2017). Subordinate predators may also suffer reproduction costs when nesting in the vicinity of dominant predators (Sergio et al. 2003, 2007;

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Chakarov and Krüger 2010; Gamauf et al. 2013). Furthermore, individuals of subordinate species may select habitats far from those of predators as an avoidance strategy (Sergio et al. 2003; Chakarov and Krüger 2010), or avoid using habitats associated with a high predation risk (Sergio et al. 2007; Björklund et al. 2016; Michel et al. 2016) by abandoning their territories, which may lead to a decrease in their local population density. Moreover, negative effects on subordinate raptors increase with dominant predator density due to the depletion of enemy-free space (Sergio et al. 2007). Overall, the non-lethal effects of an apex predator may have more adverse consequences for mesopredator populations than occasional predation (Mueller et al. 2016). In recent decades, some avian top predator populations have recovered and recolonised previously abandoned areas (Terraube and Bretagnolle 2018). Therefore, understanding the interactions between top predators and mesopredators is not only of scientific interest but is also important for conservation, particularly when both species are protected (Sergio and Hiraldo 2008).

Sergio and Hiraldo (2008) pointed out the need for research on as many different species as possible in order to understand the generality of top predator and mesopredator interaction phenomena. Numerous studies on birds of prey and/or owl species systems have addressed the top–bottom control of subordinate predators (Sergio et al. 2003, 2007; review in Sergio and Hiraldo 2008; Zuberogoitia et al. 2008; Chakarov and Krüger 2010; Lourenço et al. 2014; Björklund et al. 2016; Michel et al. 2016; Mueller et al. 2016; Morosinotto et al. 2017; Rebollo et al. 2017). However, only a limited number of studies on raptor systems include the powerful and diurnal White-tailed Eagle *Haliaeetus albicilla* (WTE), which has recently recovered throughout its range following the suppression of DDT throughout Europe (Helander and Stjernberg 2002).

Here, we study the internationally protected WTE (body mass ~ 3.1–6.9 kg) and the Lesser Spotted Eagle *Clanga pomarina* (LSE; body mass ~ 1.1–2.2 kg), which breed sympatrically in a region east of the Baltic Sea. Despite the fact that the WTE is approximately three times as big as the LSE, in a typical intraguild killer–victim raptor system (Sergio and Hiraldo 2008), no strong evidence exists regarding the killing and consumption of the LSE by the WTE. Across Europe, no LSE remains were found in the diet of the WTE (Helander 1983; Sulkava et al. 1997; Struwe-Juhl 2003; Sándor et al. 2015). However, these findings should be treated with caution, as the majority of comprehensive dietary reports were based on research in areas where the LSE does not breed. To our knowledge, non-lethal effects on the LSE, if any, have not been tested in regions where both eagle species are abundant breeders. Moreover, an overlap in the breeding habitats of WTE and LSE was previously found to be small on a regional scale (Treinys et al. 2011).

Hence, it is necessary to test the interactions between these two species at a fine landscape scale in an area where both species breed sympatrically.

The present study focuses on habitat overlap, territory occupancy, and importance of spatial distribution on the reproduction of the mesopredator, the LSE, in relation to the top predator, the WTE. We predicted that: (1) habitat segregation between the two eagle species is due, to some extent, to different prey and nest site requirements; (2) constant reoccupation of breeding territories by the LSE indicates that predation risk is of low importance to it; (3) there is no relationship between LSE reproduction and the proximity of WTE nests.

Methods

Data on WTE and LSE nest occupancy rates and breeding performance were collected in a ~ 520-km² coastal area of the Curonian Lagoon, western Lithuania (55°22'N, 21°22'E) between 2012 and 2017 (Fig. 1). During the fieldwork, we observed flying activity, feeding, territorial behaviour, food deliveries, and other behaviours using binoculars and spotting scopes from areas with a good view of forested areas between April and August. Based on the observations, we checked specific forest patches during the spring–summer or autumn–winter seasons, when the visibility of nests was high due to the absence of leaves. Field methods for subsequent nest site checks to assess the breeding output for each species have previously been described (Treinys et al. 2016, 2017). The study area covers ~ 0.8% of Lithuania, but contains ~ 15% of all WTE breeding pairs in the country, and thus comprises the highest density in the country. Over the study period, up to 23 pairs of WTE and 12 pairs of LSE nested in the area, thus this study area was suitable for the study of their interactions due to the high density of the larger species. DNA analyses have identified few hybridisation events between LSE and Greater Spotted Eagles *Clanga clanga* in this area over the past decade (Väli 2010, 2018). Considering the similar size, behaviour, and ecology of these two closely related spotted eagle species, and the usual identification of individuals as LSE during field observations, we treated all spotted eagle pairs as LSEs.

For habitat comparisons, we calculated habitat variables of 12 and 23 nest sites occupied by LSE and WTE, respectively, in 2017. We used a geographic information system (GIS) environment (ArcGIS 10.0 software; ESRI 2011) and the latest available CORINE Land Cover database for 2012 (CLC2012) as a habitat layer. The CLC2012 database for Lithuania is characterised by 30 out of 44 available classes of CLC nomenclature (third level) (Heymann et al. 1994). Buffer zones with a radius of 3 km were created around occupied nest sites to describe land cover within

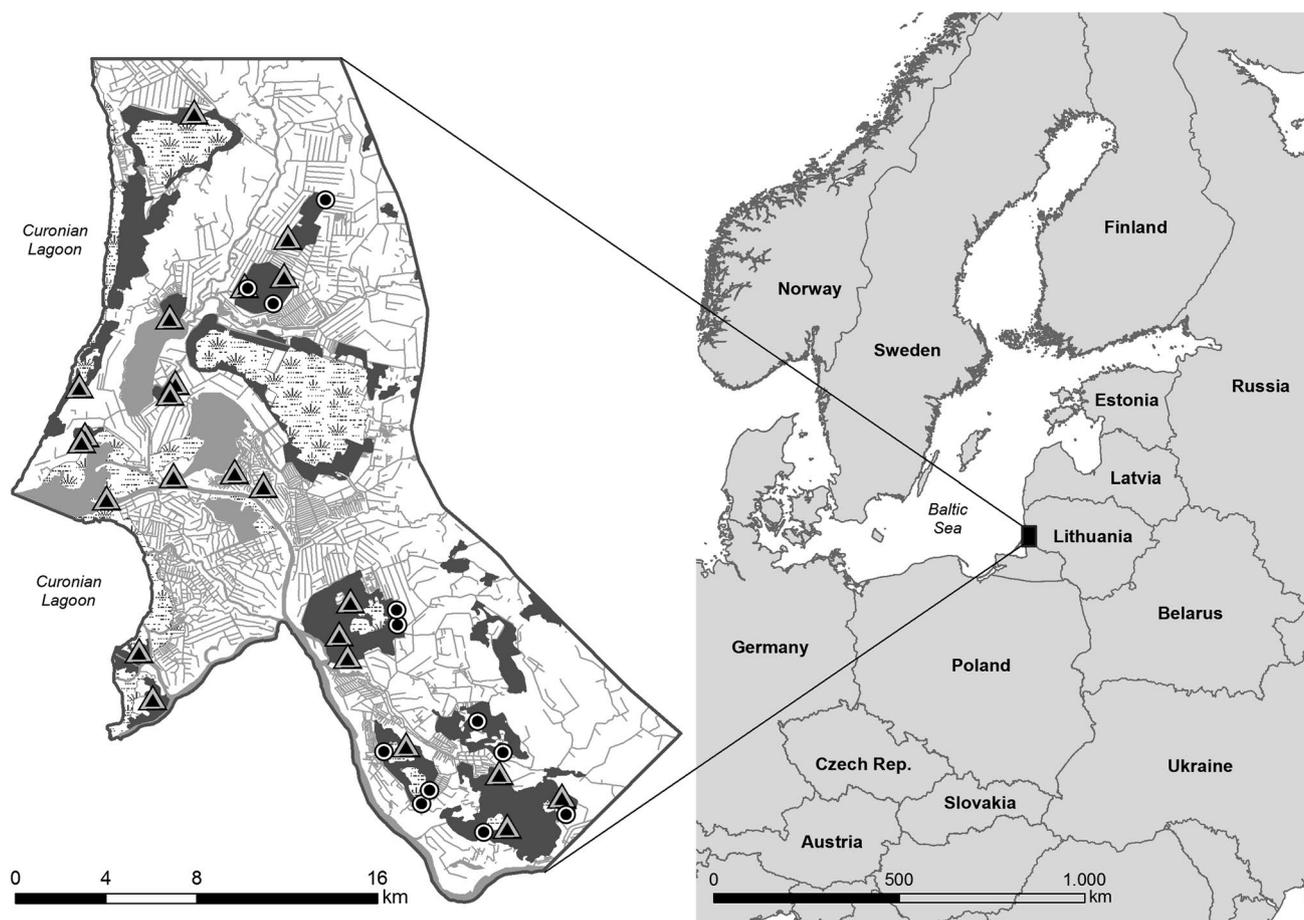


Fig. 1 Location of the study area and distribution of Lesser Spotted Eagle (LSE; circles; $n=12$) and White-tailed Eagle (WTE; triangles; $n=23$) nest sites

the surrounding environment [the same approach was used for the comparison of habitat approximating the previous home-range scale of these species (Treinys et al. 2011)]. The proportion of agricultural areas (CLC classes 211, 242), meadows (CLC class 231), shrublands (CLC classes 243, 324), deciduous forests (CLC class 311), mixed-coniferous forests (CLC classes 312 and 313 were amalgamated as they represent usually non-flooded forests), wetlands (CLC classes 411, 412), and water bodies (CLC classes 511, 512, 521) were calculated within each buffer zone. To reduce collinearity, we retained six variables that were not strongly intercorrelated ($r < 0.6$) for further analysis: the proportion of agricultural areas, meadows, shrublands, water bodies, deciduous forests, and mixed-coniferous forests (procedure described by Treinys et al. 2016). Generalised linear models were used to compare the habitat composition of observed eagle nest sites. Species was a binary response variable (0, LSE nest site; 1, WTE nest site), and all possible combinations of the aforementioned six habitat variables were included as fixed variables. A binomial error structure and a logit link function were used in these models.

To describe the competitive environment of the LSE, we used: (1) the distance to the nearest nest occupied by WTE; (2) the number of nest sites occupied by WTE pairs within a radius of 3 km; and (3) the breeding success of WTEs in the nearest nest (0 = failure, 1 = at least one fledgling raised). The principle was that more food is required when the nearest WTE pair has a brood, which makes both adults increasingly tied to the nest, thereby potentially resulting in an increased number of encounters with neighbouring LSEs.

We estimated the effect of these explanatory variables and their combinations on the reproduction of the LSE through generalised linear mixed models. In these models, the breeding performance of the LSE during the 2012–2017 period ($n=56$) (0 = failure, 1 = success; this species usually raises one nestling) was the dependent variable with binomial error structure and logit link function, and the LSE pair identity and year were included as independent random factors. Since the distance to the nearest nest occupied by WTE and the number of WTE nest sites within a radius of 3 km were related ($r_s = -0.7$, $n=56$), we included these variables in the models as interacting fixed effects, without the additive

effect of each. For an overview of the model structures, see Table 1.

The information-theoretical approach for model selection and multi-model inference procedure were applied (Burnham and Anderson 2002). Akaike's information criterion, with a correction for small sample size (AICc), was used to select the best models from model sets. The models were ranked by $\Delta AICc = AICc_i - AICc_{min}$ (where $AICc_{min}$ is the best model in a model subset). Model weight was estimated through the normalised Akaike weights, $\exp(-0.5 \times \Delta AICc) / \sum_{r=1}^R \exp(-0.5 \times \Delta AICc_r)$. A threshold of $\Delta AICc \leq 2$ was used to separate models supported by the data from poorly supported models. Due to model selection uncertainty in the case of habitat comparison, we applied an averaging procedure to a subset of models supported by the data (i.e. $\Delta AICc \leq 2$) to obtain estimates of the relative importance of habitat variables. The packages lme4 (Bates et al. 2013) and MuMIn (Bartoń 2013) in the statistical environment R were used for these calculations (R version 2.15.2; R Core Team 2014).

Results

Habitat composition varied around the nest sites of the two eagle species (Fig. 2). Three models were supported by the data (i.e. $\Delta AICc \leq 2$), indicating differences in habitat composition within a 3-km radius around nest sites occupied by each eagle species. The highest-ranked model ($\Delta AICc = 0.00$, weight = 0.55) included proportions of agricultural areas, meadows, and shrublands, while the second-ranked model ($\Delta AICc = 1.72$, weight = 0.23) included only the proportion of water bodies, while the third supported model ($\Delta AICc = 1.85$, weight = 0.22) included proportions of agricultural areas,

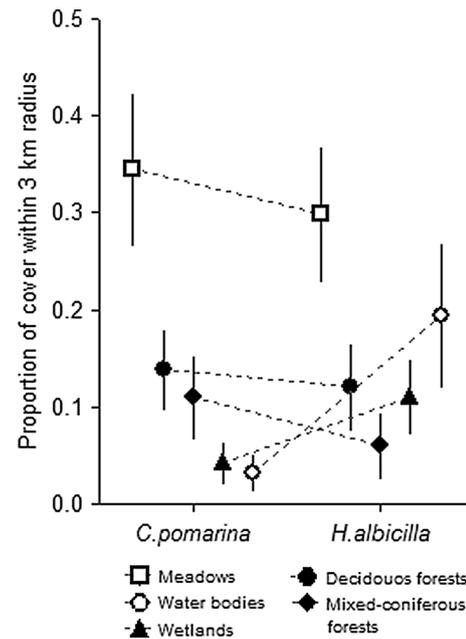


Fig. 2 Distribution of habitat variables within a 3-km radius of LSE (*Clanga pomarina*; $n=12$) and WTE (*Haliaeetus albicilla*; $n=23$) nest sites (mean \pm SE)

meadows, shrublands, and deciduous forest. The best model had a 42% coefficient of determination in explaining differences in the composition of nest site surroundings between the two sympatric eagle species. The averaging of these three models ($\Delta AICc \leq 2$) suggested that the abundance of agricultural areas, meadows, and shrublands were over three times more influential in segregating habitat composition around nest sites occupied by LSE and WTE compared to the two remaining explanatory variables (i.e. water bodies and deciduous forests).

Table 1 Models used to test the relationship between the reproductive output of the Lesser Spotted Eagle (LSE) and explanatory variables describing a competitive environment

Model	Explanatory variables				$R^2m\%$	$R^2c\%$	$\Delta AICc$	Weight
	Ha succ	NND	Ha 3 km	NND \times Ha 3 km				
Null					0.0	51.2	0.00	0.36
No. 1	+				3.4	57.7	1.10	0.21
No. 2			-		2.6	50.5	1.62	0.16
No. 3				-	1.6	52.9	1.90	0.14
No. 4	+		-		8.1	52.9	1.97	0.13
No. 5		+					2.19	
No. 6	+			-			2.44	
No. 7	+	+					3.47	

Ha succ Breeding success of White-tailed Eagle (WTE), *NND* nearest neighbour distance between WTE- and LSE-occupied nests, *Ha 3 km* number of nests occupied by WTE pairs within a 3-km radius of LSE nests, *NND \times Ha 3 km* interaction variable, R^2m marginal coefficient of determination, R^2c conditional coefficient of determination, *AICc* Akaike's information criterion with correction for small sample size, *Weight* AICc model weights calculated for models where $\Delta AICc \leq 2$

The results indicated that agricultural areas, meadows, shrublands, and deciduous forests—but not water bodies—were more abundant within a radius of 3 km around the nest sites of LSEs compared to nest sites occupied by WTEs.

LSEs faithfully occupied their territories annually (Table 2). Moreover, an additional two new territories were established in 2014 and 2017. Between one and three occupied WTE nests were present within a 3-km radius of the nests of LSEs ($n = 12$ in 2017), averaging 1.8 pairs \pm 0.9 SD. The shortest distance between LSE and WTE nest sites, when simultaneous successful reproduction of both species was observed, was only 0.14 km. The mean distance between LSE nests and the nearest nests occupied by WTEs in 2017 was 1.6 km \pm 0.8 SD ($n = 12$).

Five models were included in the subset of the models supported by the data (i.e. $\Delta AICc \leq 2$) when the relationship between the reproductive output of the LSE and explanatory variables was modelled; similar weights indicated model selection uncertainty (Table 1). The best model included only random variables, while the remaining supported models included the breeding success of WTEs, the number of WTE pairs in a 3-km radius, and the interaction between the number of WTE pairs in a 3-km radius and the distance to the nearest WTE nest as fixed variables. These results suggested that LSEs tended to reproduce successfully when fewer WTE pairs nested within a 3-km radius, and the nearest pair had a brood. However, these models had 1.7–2.8 times less support compared to the best model, which included only random variables. Furthermore, low coefficients of determination for weaker models that included fixed effect components suggested a low influence of the presence and reproduction of neighbouring WTEs in explaining the breeding success of the LSE.

Discussion

Over the 6-year duration of this study, we observed nesting events of WTEs and LSEs in a compact coastal area, where the former species was twice as abundant as the latter. The nest sites of these two species differed mostly in abundance of agricultural areas, meadows, and shrublands around them. The same breeding territories were faithfully occupied by the LSEs annually, and none of them were abandoned. The breeding success of the LSE was not explained by the proximity and breeding output of the nearest pair of the WTE, or the number of pairs of the larger species in the breeding territory of the smaller one. In summary, our data suggest that smaller eagle species can coexist with locally abundant larger predators without any obvious adverse effects on the population dynamics of the former.

Habitats surrounding the nest sites overlapped to some extent, though there were fewer water bodies and more agricultural areas, meadows, transitional habitats, and deciduous forests surrounding LSE nests compared to those of the WTE. Subordinate species tend to avoid or be displaced from suitable habitat shared with a dominant predator as a common resource (Sergio et al. 2007; Kajtoch et al. 2015; Michel et al. 2016), or avoid habitats preferred by the dominant species (Björklund et al. 2016) in order to minimise predation risk. Could it be that the under-selection of water bodies by the LSE acts as a mechanism to minimise interference predation risk from the more powerful predator? Indeed, water bodies are the prime hunting habitats of the WTEs for their principal prey—fish and waterfowl (Helander and Stjernberg 2002; Nadjafzadeh et al. 2016). However, LSEs usually hunt in forests, agricultural areas, and especially prefer meadows (Scheller et al. 2001), i.e. habitats containing their key prey species: voles, other small mammals, and amphibians (Treinys and Dementavičius 2004; Zub et al. 2010).

Table 2 Territory occupation (*Occ.*) by LSE pairs between 2012 and 2017 in the study area

Territory	2012	2013	2014	2015	2016	2017
Sakuciu_V	Occ.	Occ.	Occ.	Occ.	Occ.	Occ.
Sakuciu_PR	Occ.	Occ.	Occ.	Occ.	Occ.	Occ.
Zalgiriu_hibridas	Occ.	Occ.	Occ.	Occ.	Occ.	Occ.
Zalgiriu_berzas	Occ.	Occ.	Occ.	Occ.	Occ.	Occ.
Medziokles_P	Occ.	Occ.	Occ.	Occ.	Occ.	Occ.
Medziokles_PR	Occ.	Occ.	Occ.	Occ.	Occ.	Occ.
Medziokles_V	Empty	Empty	Occ.	Occ.	Occ.	Occ.
Kulynu_PR	Occ.	Occ.	Occ.	Occ.	Occ.	Occ.
Kulynu_S	Unknown	Occ.	Occ.	Occ.	Occ.	Occ.
Leitgiriu_SR	Occ.	Occ.	Occ.	Occ.	Occ.	Occ.
Bertzū_PV	Occ.	Occ.	Occ.	Occ.	Occ.	Occ.
Bundulu_S	Empty	Empty	Empty	Empty	Empty	Occ.

Considering the prey and typical hunting habitats of the LSE, we propose that the fewer water bodies and more cultivated agricultural areas surrounding their nest sites are a result of resource-induced preferences, and are not due to habitat-mediated avoidance of encounters with the larger species.

We did not find evidence of the LSE selecting nest sites to avoid the WTE, since all controlled nest sites were reoccupied year after year, irrespective of interspecific distances. The subordinate species may minimise the adverse effects on its reproduction of breeding close to the predator through spatial avoidance decisions made at an early stage of the breeding season (Björklund et al. 2016). Adult LSEs typically arrive at breeding sites used in previous years (Väli and Bergmanis 2017) during April (Meyburg et al. 2007; Väli 2018), when WTEs are either incubating or have already hatched their broods [for data on pairs near the Baltic Sea, see Helander (1985); Mečionis and Jusys (1994)]. It is unlikely that, upon arrival at traditional nest sites, LSEs would overlook established WTE pairs and underestimate the predation risk from them. Furthermore, the breeding performance of the LSE was not explained by the distance to nests occupied by WTEs or the number of WTE nests within a 3-km radius of their own nests.

Subordinate predators typically suffer reproduction costs when nesting in the vicinity of dominant predators (Sergio et al. 2003, 2007; Chakarov and Krüger 2010; Gamauf et al. 2013). Hence, reproductive costs may be a selective force for the avoidance of dominant species through a distance-sensitive strategy. For example, Black Kite *Milvus migrans* spatially avoided the Eagle Owl *Bubo bubo* (Sergio et al. 2003), and the Tawny Owl *Strix aluco* avoided the Eagle Owl in a moderate density predator environment (Sergio et al. 2007). Moreover, Honey Buzzard *Pernis apivorus* (Gamauf et al. 2013) and Sparrowhawk *Accipiter nisus* (Rebollo et al. 2017) avoided the Northern Goshawk *Accipiter gentilis*. Also, Northern Goshawks abandoned their territories when the abundance of Eagle Owls increased in the same area (Chakarov and Krüger 2010). In the present study, the majority (75%) of observed LSE nesting attempts were within 2.3 km of occupied WTE nests, and one or two pairs of the larger eagle usually nested within a 3-km radius of the smaller eagle. The average distance of WTE feeding flights during the breeding period is 3.8 km from the nest (Struwe-Juhl 2000); the range is ca. 2.5–15 km from the nests (references in Heuck et al. 2017). Hence, it is most likely that the LSE territories were located within the home ranges of the larger eagle species; nonetheless, their population dynamics were unaffected by top–bottom control. Therefore, we ask: which factors may favour the coexistence of these two eagle species within the coastal area in question? We propose four mutually non-exclusive reasons for the species' coexistence observed in our study system.

Feeding habit of WTE and high abundance of its main prey

The most important trigger for both lethal and non-lethal effects among predators in communities is active food acquisition (frequently related to food stress situations) (Lourenço et al. 2014). Fish, waterfowl and sea birds are the principal prey items of the WTE, while different sized raptors have scarcely, if at all, been observed in WTE diet samples (Helander 1983; Sulkava et al. 1997; Struwe-Juhl 2003; Whitfield et al. 2013; Sándor et al. 2015; Ekblad et al. 2016; Nadjafzadeh et al. 2016). The hunting of aquatic prey, adopted through their life history, may be the single most important reason that individual adult raptors living in terrestrial habitats are not perceived as prey by the WTE. Furthermore, in an extensive review on intraguild predators in raptor assemblages (Sergio and Hiraldo 2008) the predators most frequently preying on other raptors were mainly associated with terrestrial (Eagle Owl, Golden Eagle, Northern Goshawk etc.) and not with aquatic habitats (i.e. no evidence for Osprey *Pandion haliaetus*, kites *Milvus* sp., WTE etc.). Food stress situations, however, may drive predation on subordinate predator species (Hoy et al. 2017) since—just as for any other prey—this would yield energetic gains that would translate into individual fitness (Polis et al. 1989). Abundant shallow eutrophic water bodies, riparian flooded meadows, and a dense hydrographical network in the study area provided plentiful fish prey and migrating, staging and breeding waterfowl prey, which are likely key reasons for the high density of WTEs in the area, and an indication of the absence of food limitation.

Absence of overlap in resources used by the two species

The competitor-removal hypothesis suggests the elimination of a competitor to free up resources (Sergio and Hiraldo 2008; Lourenço et al. 2014). WTE and LSE hunt different prey items in different habitats (Scheller et al. 2001; Treinys and Dementavičius 2004; Helander and Stjernberg 2002; Nadjafzadeh et al. 2016). In Lithuania, LSEs nest most frequently in spruce (52%), oak (16%), and birch (15%), while WTEs most frequently nest in pine (54%), aspen (16%), and black alder (16%). Furthermore, WTE nests are located in tree canopies with an average height of 22 m from the ground (Treinys et al. 2012), while LSEs nest at an average height of 15 m (Treinys 2015). Since the diet and nesting habitats of these species differ greatly, we observed minimal shared resources between the species that would have stimulated competitive interactions. In addition, the different habitat preferences of the LSE and the WTE may function, at least to some extent, as a component of spatial segregation in our study area.

Temporal segregation in breeding phenology

The later breeding phenology of subordinate predators may promote their coexistence with a dominant raptor (Rebollo et al. 2017). Nestlings of the LSE primarily hatch in the first half of June, when WTE nestlings are already close to fledging or have already fledged. The parents of some altricial bird species adjust food delivery to the growth rate of their nestlings. As such, prey delivery peaks during the second part and again declines at the end of the nestling period [e.g. Golden Eagle *Aquila chrysaetos* (Collopy 1984); Eurasian Kestrel *Falco tinnunculus* (Steen et al. 2012)]. Hence, the LSE nestling period may be outside the highest food demand period for the WTE. We previously observed nestlings of the Common Buzzard as a prey item in the nests of WTEs (Dementavičius 2004; Dementavičius, unpublished data on prey remains from Lithuania) as did Müller and Lauth (2006) and Neumann and Schwarz (2017) elsewhere. Contrary to the LSE, the nestling rearing stages of the WTE and Common Buzzard overlap greatly in Lithuania (Drobelis 2004), likely favouring the robbing of buzzard nests by WTE for easily obtained prey.

Effective anti-predator behaviour

Kareksela et al. (2013) suggested that an individual giving an alarm call could benefit from alerting a predator that it had been detected. Most diurnal raptors attempt to drive larger predators from their nests with broods (Bloom et al. 2006). Moreover, individuals of mesopredator species may become more aggressive from learning to cope with intruders when the local density of a top predator increases (Mueller et al. 2016). LSEs typically respond to WTEs that intrude near nests with broods through alarm calls, attacking them with their talons, or similar types of mobbing behaviour. The same types of behavioural response have not been observed toward conspecifics or similar-sized raptors such as kites, buzzards, and harriers (Dementavičius and Treinys, unpublished), which suggests that the WTE is considered a threat to broods by the LSE. It is not clear whether behavioural responses alone of the LSE are sufficient to cope with the abundant WTEs in our study sites, though anti-predator behaviour could be an important part of the mechanism behind the long-term coexistence of these two eagle species.

Conclusion

In summary, our research resulted in some important findings from which we can make some suggestions. First, empirical observations of encounter behaviour between the heterospecifics, LSE and WTE, the superficial similarity of these species' systems to those of raptor systems with well-known forms of interaction, and the fine-scale sympatric

distribution of these species, could lead, if left untested, to the erroneous interpretation of results as asymmetrical interference competition or intraguild predation. Without investigating interactions between target species, extrapolation from superficial parallels between these and similar species may be harmful when making important decisions for conservation and management. Secondly, it remains unclear if the relationship observed in this study between the LSE and the WTE could also be expected under different landscape conditions. Sergio et al. (2007) observed that a negative effect on subordinate species increased with the density of a dominant predator. However, if the density of dominant predators decreases in response to limited food supply (Newton 2003), then the opposite pattern could be also expected. Poor availability of the main prey item for a top predator creates food limitation, which may lead to a shift towards alternative prey [alternative prey hypothesis (Korpimäki et al. 1990)], some of which may belong to a higher trophic level, as demonstrated by Hoy et al. (2017). Hence, future studies on changes in apex and mesopredator interactions along an environmental gradient may greatly contribute to our understanding of competition or intraguild predation processes at high trophic levels.

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Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

References

- Bartoń K (2013) MuMin: multi-model inference. R package version 1.9.13. CRAN. <http://CRAN.Rproject.org/package=MuMin>
- Bates D, Maechler M, Bolker B (2013) lme4: linear-mixed effects models using Eigen and Eigen. Retrieved from: <http://CRAN.R-project.org/package=lme4> (R package version 0.999999-2)
- Björklund H, Santangeli A, Blanchet FG, Huitu O, Lehtoranta H, Lindén H, Valkama J, Laaksonen T (2016) Intraguild predation and competition impacts on a subordinate predator. *Oecologia* 181:257–269
- Bloom PH, Clark WS, Kidd JW (2006) Capture techniques. In: Bird DM, Bildstein KL (eds) Raptor research and management techniques. Hancock House, Blaine, pp 193–219
- Burnham K, Anderson D (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Chakarov N, Krüger O (2010) Mesopredator release by an emergent superpredator: a natural experiment of predation in a three level guild. *PLoS One* 5(12):e15229
- Collopy MW (1984) Parental care and feeding ecology of Golden Eagle nestlings. *Auk* 101:753–760

- Dementavičius D (2004) Common Buzzard (*Buteo buteo*) and White-tailed Eagle (*Haliaeetus albicilla*): breeding parasitism or atypical feeding behaviour? *Acta Zool Lituan* 14:76–79
- Drobelis E (2004) Lietuvos miškų plėšrieji paukščiai [Birds of prey of Lithuania forests]. Aplinkos ministerija, Vilnius
- Ekblad CMS, Sulkava S, Stjernberg TG, Laaksonen TK (2016) Landscape-scale gradients and temporal changes in the prey species of the White-tailed Eagle (*Haliaeetus albicilla*). *Ann Zool Fenn* 53:228–240
- ESRI (2011) ArcGIS desktop: release 10. Environmental Systems Research Institute, Redlands
- Gamauf A, Tebb G, Nemeth E (2013) Honey Buzzard *Pernis apivorus* nest-site selection in relation to habitat and the distribution of Goshawks *Accipiter gentilis*. *Ibis* 155:258–270
- Helander B (1983) Reproduction of the White-tailed Sea Eagle *Haliaeetus albicilla* (L.) in Sweden, in relation to food and residue levels of organochlorine and mercury compounds in the eggs. Ph.D. thesis, Department of Zoology, University of Stockholm, Stockholm
- Helander B (1985) Reproduction of the White-tailed Sea Eagle *Haliaeetus albicilla* in Sweden. *Holarct Ecol* 8:211–227
- Helander B, Stjernberg T (2002) Action plan for the conservation of White-tailed Sea Eagle (*Haliaeetus albicilla*). BirdLife International, Strasbourg
- Heuck C, Herrmann C, Schabo DG, Brandl R, Albrecht J (2017) Density-dependent effects on reproductive performance in a recovering population of White-tailed Eagles *Haliaeetus albicilla*. *Ibis* 159:297–310
- Heymann Y, Steenmans C, Croissille G, Bossard M (1994) CORINE land cover. Technical guide. Office for Official Publications of the European Communities, Luxembourg
- Hoy SR, Petty SJ, Millon A, Whitfield DP, Marquiss M, Anderson DIK, Davison M, Lambin X (2017) Density-dependent increase in superpredation linked to food limitation in a recovering population of Northern Goshawks *Accipiter gentilis*. *J Avian Biol* 48:1205–1215
- Kajtoch Ł, Żmihorski M, Wieczorek P (2015) Habitat displacement effect between two competing owl species in fragmented forests. *Popul Ecol* 57:517–527
- Kareksela S, Härmä O, Lindstedt C, Siitari H, Suhonen J (2013) Effect of Willow Tit *Poecile montanus* alarm calls on attack rates by Pygmy Owls *Glaucidium passerinum*. *Ibis* 155:407–412
- Korpimäki E, Huhtala K, Sulkava S (1990) Does the year-to-year variation in the diet of Eagle and Ural Owls support the alternative prey hypothesis? *Oikos* 58:47–54
- Lourenço R, Penteriani V, Rabaça JE, Korpimäki E (2014) Lethal interactions among vertebrate top predators: a review of concepts, assumptions and terminology. *Biol Rev* 89:270–283
- Mečionis R, Jusys V (1994) The White-tailed Eagle (*Haliaeetus albicilla*) at Kuršių lagoon. *Acta Ornithol Lituan*. 9–10:138–142
- Meyburg B-U, Meyburg C, Matthes J, Matthes H (2007) Heimzug, verspätete Frühjahrsankunft, vorübergehender Partnerwechsel und Bruterfolg beim Schreiadler *Aquila pomarina*. *Vogelwelt* 128:21–31
- Michel VT, Jiménez-Franco MV, Naef-Daenzer B, Grübler MU (2016) Intraguild predator drives forest edge avoidance of a mesopredator. *Ecosphere* 7(3):e01229
- Mikkola H (1976) Owls killing and killed by other owls and raptors in Europe. *Br Birds* 69:144–154
- Morosinotto C, Villers A, Thomson RL, Varjonen R, Korpimäki E (2017) Competitors and predators alter settlement patterns and reproductive success of an intraguild prey. *Ecol Monogr* 87:4–20
- Mueller AK, Chakarov N, Hesecker H, Krüger O (2016) Intraguild predation leads to cascading effects on habitat choice, behaviour and reproductive performance. *J Anim Ecol* 85:774–784
- Müller M, Lauth T (2006) Aufzucht eines jungen Mäusebussards *Buteo buteo* in einer Brut des Seeadlers *Haliaeetus albicilla* endet nicht erfolgreich. *Orn Rundbrief Meckl-Vorp* 45:399–401
- Nadjafzadeh M, Hofer H, Krone O (2016) Sit-and-wait for large prey: foraging strategy and prey choice of White-tailed Eagles. *J Ornithol* 157:165–178
- Neumann J, Schwarz J (2017) Seeadlerpaar mit besonderer Vorliebe für junge Mäusebussarde. Teil 3. Großvogelschutz im Wald 28–30
- Newton I (2003) The role of natural factors in the limitation of birds of prey numbers: a brief review of the evidence. In: Thompson DBA, Redpath SM, Fielding AH, Marquiss M, Galbraith CA (eds) *Birds of prey in a changing environment*. Stationery Office, Edinburgh, pp 5–24
- Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu Rev Ecol Syst* 20:297–330
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rebollo S, Martínez-Hestekamp S, García-Salgado G, Pérez-Camacho L, Fernández-Pereira JM, Jenness J (2017) Spatial relationships and mechanisms of coexistence between dominant and subordinate top predators. *J Avian Biol* 48:1226–1237
- Sándor A, Alexe V, Marinov M, Dorosencu A, Domşa C, Kiss BJ (2015) Nest-site selection, breeding success, and diet of White-tailed Eagles (*Haliaeetus albicilla*) in the Danube Delta, Romania. *Turk J Zool* 39:300–307
- Scheller W, Bergmanis U, Meyburg BU, Furkert B, Knack A, Roper S (2001) Raum-Zeit-Verhalten des Schreiadlers (*Aquila pomarina*). *Acta Ornithoecol* 4:75–236
- Sergio F, Hiraldo F (2008) Intraguild predation in raptor assemblages: a review. *Ibis* 150(Suppl. 1):132–145
- Sergio F, Marchesi L, Pedrini P (2003) Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. *J Anim Ecol* 72:232–245
- Sergio F, Marchesi L, Pedrini P, Penteriani V (2007) Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? *Anim Behav* 74:1607–1616
- Steen R, Sonerud G, Slagsvold T (2012) Parents adjust feeding effort in relation to nestling age in the Eurasian Kestrel (*Falco tinnunculus*). *J Ornithol* 153:1087–1099
- Struwe-Juhl B (2000) Funkgestützte Synchronbeobachtung—eine geeignete Methode zur Bestimmung der Aktionsräume von Großvogelarten (Ciconiidae, Haliaeetus) in der Brutzeit. *Popul Ecol Rap- tor Owl* 4:101–110
- Struwe-Juhl B (2003) Why do White-tailed Eagles prefer coots? In: Helander B, Marquiss M, Bowerman B (eds) *Sea Eagle 2000:317–325*. Swedish Society for Nature Conservation, Stockholm, Sweden
- Sulkava S, Tornberg R, Koivusaari J (1997) Diet of the White-tailed Eagle *Haliaeetus albicilla* in Finland. *Ornis Fenn* 74:65–78
- Terraube J, Bretagnolle V (2018) Top-down limitation of mesopredators by avian top predators: a call for research on cascading effects at the community and ecosystem scale. *Ibis* 160:693–702
- Treyns R (2015) Species action plan for the Lesser Spotted Eagle. Accepted by the Ministry of Environment of the Republic of Lithuania, 27 February 2015, by order no. D1-185
- Treyns R, Dementavičius D (2004) Productivity and diet of Lesser Spotted Eagle (*Aquila pomarina*) in Lithuania. *Acta Zool Lituan* 14:83–87
- Treyns R, Dementavičius D, Mozgeris G, Skuja S, Rumbutis S, Stončius D (2011) Coexistence of protected avian predators: does a recovering population of White-tailed Eagle threaten to exclude other avian predators? *Eur J Wildl Res* 57:1165–1174
- Treyns R, Dementavičius D, Rumbutis S, Sorokaite J, Brazaitis G (2012) Species action plan for the White-tailed Eagle. Accepted

- by the Ministry of Environment of the Republic of Lithuania, 1 February 2012, by order no. D1-106
- Treinys R, Dementavičius D, Rumbutis S, Švažas S, Butkauskas D, Sruoga A, Dagys M (2016) Settlement, habitat preference, reproduction, and genetic diversity in recovering the White-tailed Eagle *Haliaeetus albicilla* population. *J Ornithol* 157:311–323
- Treinys R, Väli Ü, Berganis U (2017) Strong territoriality and weak density-dependent reproduction in Lesser Spotted Eagles *Clanga pomarina*. *Ibis* 159:343–351
- Väli Ü, Dombrovski V, Treinys R, Bergmanis U, Daróczy SJ, Dravecky M, Ivanovski V, Lontkowski J, Maciorowski G, Meyburg BU, Mizera T, Zeitz R, Ellegren H (2010) Widespread hybridization between the Greater Spotted Eagle *Aquila clanga* and the Lesser Spotted Eagle *Aquila pomarina* (Aves: Accipitriformes) in Europe. *Biol J Lin Soc* 100:725–736
- Väli Ü, Bergmanis U (2017) Apparent survival rates of adult Lesser Spotted Eagles *Clanga pomarina* estimated by GPS-tracking, colour rings and wing-tags. *Bird Study* 64:104–107
- Väli Ü (2018) Timing of breeding events of the Lesser Spotted Eagle *Clanga pomarina* as revealed by remote cameras and GPS-tracking. *Ardea*. <https://doi.org/10.5253/arde.v106i1.a>
- Whitfield DP, Marquiss M, Reid R, Grant J, Tingay R, Evans RJ (2013) Breeding season diets of sympatric White-tailed Eagles and Golden Eagles in Scotland: no evidence for competitive effects. *Bird Study* 60:67–76
- Zub K, Pugacewicz E, Jędrzejewska B, Jędrzejewski W (2010) Factors affecting habitat selection by breeding Lesser Spotted Eagles *Aquila pomarina* in northeastern Poland. *Acta Ornithol* 45:105–114
- Zuberogoitia I, Martínez JE, Zabala J, Martínez JA, Azkona A, Castillo I, Hidalgo S (2008) Social interactions between two owl species sometimes associated with intraguild predation. *Ardea* 96:109–113

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