

Interaction between the White-tailed Eagle and Common Buzzard estimated by diet analysis and brood defence behaviour

Aušra Kamarauskaitė, Deivis Dementavičius, Saulis Skuja, Mindaugas Dagys & Rimgaudas Treinys*

A. Kamarauskaitė, Vilnius University Life Sciences Centre, Saulėtekio av. 7, LT-10257 Vilnius, Lithuania

D. Dementavičius, Nature Research Centre, Akademijos str. 2, LT-08412 Vilnius, Lithuania

S. Skuja, Vilnius University Life Sciences Centre, Saulėtekio av. 7, LT-10257 Vilnius, Lithuania

M. Dagys, Nature Research Centre, Akademijos str. 2, LT-08412 Vilnius, Lithuania

R. Treinys, Nature Research Centre, Akademijos str. 2, LT-08412 Vilnius, Lithuania.

** Corresponding author's e-mail: rimga.t@gmail.com*

Received 4 March 2019, accepted 28 August 2019

Recent evidence suggests that the White-tailed Eagle (*Haliaeetus albicilla*) – the largest avian predator to have recently recovered in Europe – may prey on mesopredators and their broods. Mesopredators may respond to predators near their nests by exhibiting offspring defence behaviour. The present study involved White-tailed Eagle diet analysis, and we report on their predation on Common Buzzard (*Buteo buteo*) nestlings and the results of a field experiment conducted near the nests of Common Buzzards to test how they respond to the appearance of a top predator. The remains of nestling Common Buzzards were observed in 9% of successful nests, while evidence on the consumption of other raptor species was scarce. Additionally, our results indicate that habitat and pair/territory identity may explain the probability of predation on mesopredators, thus suggesting a spatially varying effect on smaller raptors. During the field experiment, Common Buzzards responded to a White-tailed Eagle dummy placed near nest sites during only half of the observed visits. Moreover, the response of Common Buzzards was not explained by their proximity to the breeding pairs of White-tailed Eagles. The probability of Common Buzzards alarm calls and attacks increased in the latest stage of the breeding season, although this was largely due to differences in defence behaviour between pairs, which suggests individual differences in aggressiveness towards predators. In summary, our data indicate that the White-tailed Eagle may prey upon the broods of Common Buzzard under certain environmental conditions, and that this source of prey could easily be accessed due to the weak brood defence behaviour by Common Buzzards.



1. Introduction

Superpredation is a form of predation in which a top predator kills and consumes another predator, independent of the degree of resource overlap and competitive interaction (Lourenço *et al.* 2014). This type of predation is widespread in avian predator communities with several-fold differences in body size between the predator and prey (Sergio & Hiraldo 2008). Top raptors predate on adults, nestlings, fledglings or dispersing young of another raptor species (see references in Sergio *et al.* 2003, Sergio & Hiraldo 2008, Lourenço *et al.* 2011). Superpredation is primarily caused by food acquisition since, just as any other prey, such behaviour would yield energetic gains (Polis *et al.* 1989).

Previous studies have established that the dietary breadth of an avian predator increases when the abundance of a preferred prey species declines (Whitfield *et al.* 2009 and references therein). When a predator population increases, new pairs settle in progressively poorer sites (Brown 1969), and predators may experience food limitation under this sequential habitat occupation process (Löhms 2001). Despite the specific reasons causing a decrease in principal prey species, a top predator may shift to exploit alternative prey under food stress conditions (Korpimäki *et al.* 1990, Reif *et al.* 2001). Alternative prey species may belong to a high trophic level (Hoy *et al.* 2017) or even to be competitors to the larger raptor (Morosinotto *et al.* 2017). Due to heterogeneity of the prey resources in the environment, spatial variation is expected.

The subordinate species may respond to a superpredator in different ways. It may avoid superpredator's neighbourhood when occupying territories (Sergio *et al.* 2003, Chakarov & Krüger 2010), skip habitats associated with the superpredator (Sergio *et al.* 2007, Björklund *et al.* 2016, Michel *et al.* 2016) or reduce vocalisations or movements (Zuberogoitia *et al.* 2008). However, a locally abundant territorial subordinate species may be limited in responding to increased superpredators through site or habitat changes (Mueller *et al.* 2016). Prey species may respond to predators by offspring defence behaviour including alarm calling, distraction displays, and attack responses (Rytönen & Soppela 1995). Moreover, in many altricial species, brood defence increases

with offspring age (Onnebrink & Curio 1991). Due to frequent encounters, individuals may learn about predator capabilities and would thus exhibit higher defence intensity than inexperienced birds (Rytönen & Soppela 1995). More aggressive responses towards a local increase in predators may be also due to the disappearance of less-aggressive individuals from that population (Mueller *et al.* 2016). Hence, it could be assumed that breeding individuals may respond differently during contact with predators in enemy-free areas compared to areas inhabited by that predator.

The White-tailed Eagle (*Haliaeetus albicilla*) is the largest avian predator in the temperate and boreal latitudes of Europe, but evidence of their predation on avian mesopredators remains scarce (review in Sergio & Hiraldo 2008). Previous studies on White-tailed Eagle diet from different geographical areas have demonstrated that their principal prey includes fish and waterfowl, while providing only occasional evidence of predation on diurnal and nocturnal raptors (Helander 1983, Sulkava *et al.* 1997, Struwe-Juhl 2003, Whitfield *et al.* 2013, Sîndor *et al.* 2015, Nadjafzadeh *et al.* 2016).

However, since their populations continue to grow, the White-tailed Eagle has effectively expanded its range along the environmental gradient while increasing local densities, thereby resulting in the occupation of less suitable breeding territories (Ekblad *et al.* 2016, Treinys *et al.* 2016, Heuck *et al.* 2017). Due to the exploitation of a broader environmental gradient, White-tailed Eagle diet has also changed over several decades to correspond to prey availability (Sulkava *et al.* 1997, Ekblad *et al.* 2016). The Common Buzzard (*Buteo buteo*) is the most abundant among birds of prey in Europe (Mebs & Schmidt 2006). Nestlings of this species have recently been repeatedly observed as prey items in the nests of White-tailed Eagles breeding in Germany (Müller & Lauth 2006, Neumann & Schwarz 2017), which suggests that predation on the broods of this abundant mesopredator could also be expected elsewhere. In the present study, we focus on the interaction between these species assuming that they represent a predator–prey system.

First, by analysing prey material collected during White-tailed Eagle nestling ringing in coastal and inland habitats, we report on White-tailed Ea-

gle predation on Common Buzzard nestlings. Second, we performed a field experiment near the nests of Common Buzzard to test how they respond to the appearance of a top predator during different stages of the breeding period in an area inhabited by White-tailed Eagle as well as in an area where this raptor does not yet breed. The following predictions were made: a) As a prey item, the Common Buzzard will be more likely to occur in the nests of White-tailed Eagles breeding in inland habitats compared to coastal habitats (coastal habitats provide optimal feeding conditions due to the high availability of principal prey – fish and waterfowl – for the White-tailed Eagle); b) the defence behavior of the Common Buzzard to the presence of White-tailed Eagle near their nests will increase when the distance to the nearest nest of the predator decreases (aggressive behaviour in Common Buzzard towards its predator – the Eagle Owl (*Bubo bubo*) – increased when the latter species was present in high abundance throughout the landscape; Mueller *et al.* 2016); and c) the defence behavior of the Common Buzzard to White-tailed Eagle presence will be the strongest close to the fledging period (a frequently observed pattern among altricial species; Onnebrink & Curio 1991).

2. Material and methods

2.1. Data collection and analysis of the White-tailed Eagle diet

The search for new – and monitoring of known – occupied White-tailed Eagle nesting territories was conducted in Lithuania (65,200 km², central coordinate 55°100'N, 23°39'E; Fig. 1) using procedures previously described in detail (Dementavičius 2007, Treinys *et al.* 2016, Dementavičius *et al.* 2019). The range of the White-tailed Eagle in Lithuania was estimated based on information regarding the breeding territories collected between 1995 and 2015. The White-tailed Eagle range for 1995–2005 and its expansion between 2006 and 2015 are presented in Fig. 1. The Range Tool for Article 12 (Birds Directive) and Article 17 (Habitat Directive), available at the European Topic Centre on Biological Diversity (Mac Sharry 2012), was employed. The pan-European

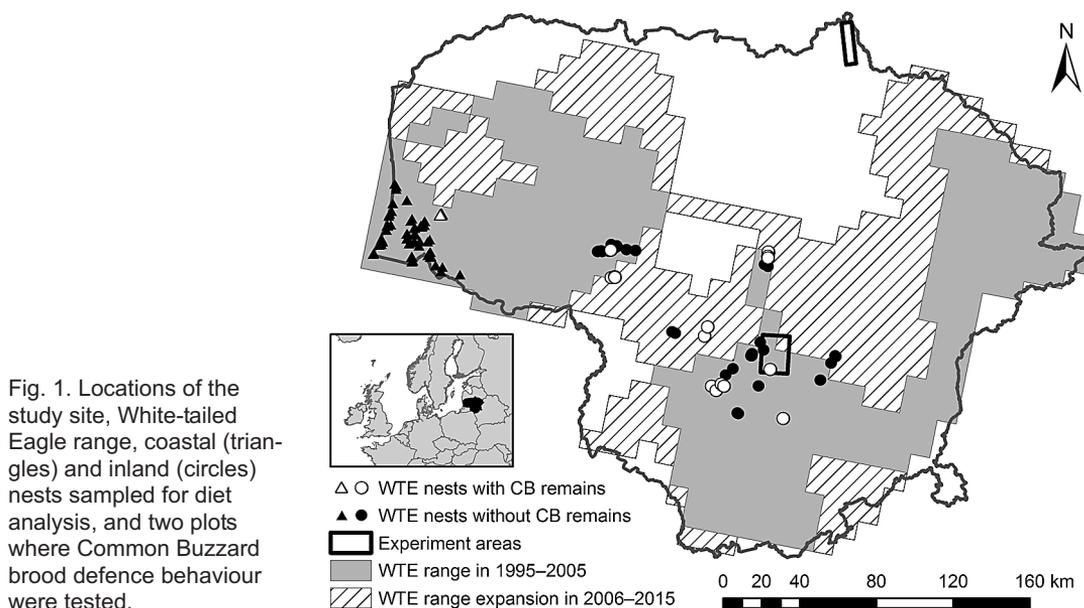
ETRS89 LAEA5210 grid with 10-km resolution was used, and a gap distance of five grid cells was set for range modelling (for details: Treinys *et al.* 2016).

Prey and their remains in White-tailed Eagle nests were collected in coastal and inland areas (Fig. 1) once per season when the ringing of nestlings was performed during May–June between 2001 and 2016. Altogether, we observed 249 successful breeding attempts of 53 White-tailed Eagle pairs, which constitutes ca. 33% of the Lithuanian population. Prey and their remains were identified to the lowest identifiable taxonomic level. Fresh, whole, or otherwise easily identified prey items were identified in the field. The remaining items, such as body parts, bones, feathers, fur, skulls, etc., were collected and later identified using reference animal collections in the T. Ivanauskas Zoological Museum (Kaunas, Lithuania).

The “minimum approach” was applied when counting the number of prey items from the remains (i.e., if two different parts of the same species were found, they were recorded as belonging to only one individual). In total, 1,705 prey items belonging to the Aves, Mammalia, and Pisces classes were identified. We estimated the effect of habitat (i.e., coastal or inland; see Fig. 1) on the occurrence of Common Buzzard as a prey item in successful nests (0 = absent, 1 = at least one individual of Common Buzzard found) using a generalised linear mixed model (GLMM) with binomial error structure and logit link function. White-tailed Eagle pair identity was included as a random factor. We compared Akaike Information Criterion corrected for a small sample size (*AICc*) and the weight of that model to the reduced model, which included only random factor but no fixed effects.

2.2. Field experiment and behavioural analysis

An experiment to test the behavioural responses of nesting Common Buzzards towards White-tailed Eagles was performed during summer (May–June) of 2018 in two plots located in Central and Northern Lithuania (Fig. 1). The first plot was selected in a forest located near a large water reservoir, where the first breeding pair of White-tailed Eagles was found in 1995 (Malinauskas 1998),



and after which the number of pairs around that area increased, as revealed by monitoring (D. Dementavičius, unpubl.). The nearest neighbour distance between Common Buzzard and White-tailed Eagle nests in this plot ranged from 0.8 km to 14.1 km. The second plot was located in a large forest near the northern border of the country. Despite extensive raptor studies since the 2000s, no breeding pairs of White-tailed Eagle have been found at this site or close to it until 2018 (S. Skuja, R. Treinys, unpubl.). The nearest neighbouring White-tailed Eagle pair on the Lithuanian side was ca. 32 km away in a south-easterly direction (D. Dementavičius, unpubl.) and ca. 21 km away in a north-easterly direction in Latvia (J. Kuze, pers. comm.). The nearest neighbour distance between Common Buzzard and White-tailed Eagle in this area ranged from 21 km to 34.9 km.

In April 2018, we checked previously known Common Buzzard nests for occupancy and selected a total of 28 nest sites for a treatment (i.e., 14 occupied nest sites in each study plot). Common Buzzard nests were known from former studies conducted in these plots (Central Lithuania plot: Mammen & Stubbe 2002; North Lithuania plot: Kamarauskaitė *et al.* 2019). The raptor nest searches were conducted during the leafless period (October–March), and later checked for occupancy from April to June. Nests were searched also observing territorial and feeding behaviour of

Common Buzzards during the breeding period.

During the experiment, a White-tailed Eagle dummy was mounted on a tripod at a height of 1 m above the ground and left exposed in the most visible place in the vicinity of an occupied nest (mean distance from the nest of 45 m). A speaker was used to play calls of the male White-tailed Eagle under the tripod, and the dummy was hidden when transported to each point. The dummy was exposed for 30 min, with the calls being played for the first 15 min of each treatment. During the treatment, an observer dressed in camouflaged clothing was hidden in a place that provided an optimal overview of the space surrounding the dummy. During the 30 min treatment, the following Common Buzzard behaviours were registered: 1) the time of the first alarm call; 2) the number of alarm calls; and 3) the number of attacks towards the dummy (mainly mock attacks were performed; attacks with physical contact were observed only a few times, in which case the treatment was stopped to avoid injuries to the birds). The number of responding adults was also registered. Each nest site was visited three times between 18 May and 22 June. The same nests were visited at different times of day between 8 am and 9 pm. All visits and observations were performed by the same person. After the breeding season, all nests were checked for breeding success. Most treatment pairs raised broods successfully, though we removed visits to

pairs which failed prior to analysis or when an approximate brood failure date was known (only visits after brood failures were excluded). One visit was removed because the dummy was exposed too far from a nest (190 m).

The relationship between behavioural responses and explanatory variables was tested using GLMMs. Two binary response variables were used for modelling: 1) response by alarm calls (0 – absence of alarm calls or only a single call registered during a 30 min treatment, 1 – multiple alarm calls); and 2) response by attack (0 – no mock or real attack observed, 1 – mock or real attack(s) performed towards the dummy). The four explanatory variables and all of their possible combinations were included in the models: distance to the nearest White-tailed Eagle nest occupied in 2018, breeding stage, time of day, and the distance from the dummy to the nest. The mean Common Buzzard brood hatch date in Lithuania is 14 May and the mean fledging date is 27 June (Drobėlis 2004); thus, breeding stages were classified as: early (visits made between 18 and 21 May), middle (between 1 and 7 June), and late (between 19 and 22 June). Time of day was divided into morning (treatment performed between 8 am and 10 am), midday (performed between 10 am 5 pm), and evening (performed between 5 pm and 9 pm). The pair identity of the Common Buzzard was included as a random term in all models fitted with binomial error structure and logit link function.

The relative importance of each model was estimated through ranking the models by Eq. 1, where $AICc_{\min}$ is the best model in the model subset.

$$\Delta AICc = AICc_i - AICc_{\min} \quad (1)$$

Model weight was estimated through the normalized Akaike weights, Eq. 2.

$$\frac{\exp(-0.5 \times \Delta AICc)}{\sum_{r=1}^R \exp(-0.5 \times \Delta AICc_r)} \quad (2)$$

To separate good models from less supported models, the threshold $\Delta AICc \leq 2$ was used. The packages “lme4” (Bates *et al.* 2015), “MuMIn” (Bartoń 2019), “sjmisc” (Lüdecke 2018), “sjPlot” (Lüdecke 2019a), “sjlabelled” (Lüdecke 2019b) and “ggplot2” (Wickham 2016) were used in the

statistical environment R version 3.6.0 (R Core Team 2019). We reported marginal and conditional R^2 estimated by a “theoretical” method applied for binomial family models.

3. Results

3.1. The Common Buzzard as prey in the White-tailed Eagle diet

In prey remains collected for 16 years in successful White-tailed Eagle nests, a total of 31 individuals of three raptor species were identified. The raptors accounted for 1.8% of all prey items identified ($n = 1705$) or 5.7% of total avian prey items ($n = 546$). Raptors found in prey remains included 29 Common Buzzard nestlings, one adult Common Kestrel (*Falco tinnunculus*), and one fledgling Tawny Owl (*Strix aluco*). Common Buzzard nestlings were present as prey in 9.2% of the White-tailed Eagle nests sampled for prey items ($n = 249$) or in the nests of 17% of sampled White-tailed Eagle pairs ($n = 53$) (Fig. 1). Overall, 19 White-tailed Eagle nests contained the remains of one predated Common Buzzard individual, two nests contained two predated buzzard individuals, and two nests contained three predated buzzard individuals. Common Buzzards were less frequently observed as a prey item in White-tailed Eagle nests located in the coastal area (3.6% of nests with Common Buzzard prey, $n = 139$) compared to nests in inland areas (16.4%, $n = 110$).

The model containing habitat type as a fixed effect received much greater support (weight = 0.81) compared to the model including only a random effect (i.e., pair identity; $\Delta AICc = 2.85$, weight = 0.19) in explaining the occurrence of Common Buzzard prey in White-tailed Eagle nests. According to this model, the occurrence probability of Common Buzzard in the diet of White-tailed Eagles was significantly higher in nests of the pairs breeding in inland compared to coastal habitats ($2.96 \pm 1.36 SE$, $P < 0.03$). Furthermore, the results also indicate that the probability of a White-tailed Eagle preying on a Common Buzzard was strongly associated with the pair identity factor (marginal and conditional $R^2 = 16\%$ and 75% , respectively). Common Buzzard prey items in the coastal area were found in the nest of

one pair of White-tailed Eagle that nested the greatest distance from major water bodies and large rivers (Fig. 1).

3.2. Common Buzzard response to the White-tailed Eagle dummy and playback calls

The final field experiment sample consisted of 73 visits to 25 pairs that had broods during the visits. The most commonly observed type of behavioural response by the Common Buzzard was alarm calling, which was registered during 49% of the visits. When behavioural response was observed during these visits, 50% of the first Common Buzzard alarm calls were registered within five minutes, while 75% were registered within 12 min from the beginning of call playback. One or two adult Common Buzzards were involved in alarm calls at a similar frequency (52% and 48%, respectively, $n = 36$). The Common Buzzard usually alarmed intensively with many calls (mean number of calls per visit = 166 ± 148 *SD*, range 3–586, $n = 36$). An over three-fold difference in the mean number of alarm calls during visits was observed when behavioural responses were performed by one (78 ± 69 *SD*, $n = 19$) compared to two adult individuals (264 ± 153 *SD*, $n = 17$).

Common Buzzards also reacted to the White-tailed Eagle dummy by performing attacks during 22% of visits ($n = 73$). All attacks were performed only during visits when Common Buzzards responded to alarm calls. The number of attacks performed by Common Buzzards during these 30-min visits ranged from 1 to 17, with a mean of 5.8 ± 4.5 *SD* ($n = 16$). Again, more attacks were registered when both adults participated in a response to the dummy (6.4 ± 4.9 *SD*, $n = 11$) compared to visits when attacks were performed by only one bird (4.4 ± 3.6 *SD*, $n = 5$).

Common Buzzard responses to eagle predator by alarm calling varied temporally. Modelling the relationship between visits with/without alarm calls and four explanatory variables resulted in two models being supported by the data (i.e., $\Delta AICc \leq 2$). The best supported model included only breeding period as a fixed effect. According to estimates of the highest ranked model, Common

Buzzard response probability to the White-tailed Eagle dummy by alarm calls was similar between the early and the middle stage (0.76 ± 0.78 *SE*, $P = 0.33$) but was greater during the late breeding stage compared to the early one (2.55 ± 0.96 *SE*, $P < 0.01$). The marginal coefficient of determination for this fixed effect is 14.5%. Second, a similarly well-supported model (i.e., $\Delta AICc = 0.49$) included two fixed effects – breeding period and time of day.

In addition to the breeding period effect, the results of the second ranked model tended to support the decreased response of Common Buzzards by alarm calls in the evening compared to the morning hours (-2.96 ± 1.69 *SE*, $P = 0.08$), but not between morning and midday hours (-0.83 ± 1.03 *SE*, $P = 0.42$) (for response variation, see Fig. 2). The marginal coefficient of determination for that model with two fixed effects was 22%. Pair identity was included in these two models as a random effect and received solid support, as indicated by the conditional marginal effects (58% and 65% for the first and second models, respectively). These values indicate that the individual traits of pairs are more important in explaining the response of Common Buzzards to the top avian predator dummy compared to breeding stage and time of day.

Common Buzzard attacks towards the White-tailed Eagle dummy were also time dependent. Modelling the relationship between visits with/without an attack observed and four explanatory variables resulted in only one model being supported by the data. This model included the same two fixed effects as previously, namely breeding period and time of day. The results of this model indicate a tendency towards increased dummy attack probability with advancing breeding period (early breeding stage vs. middle breeding stage 7.60 ± 4.62 *SE*, $P < 0.1$; early breeding stage vs. late breeding stage 11.44 ± 5.50 *SE*, $P < 0.04$) and time of day (morning hours vs. midday hours 14.89 ± 7.76 *SE*, $P = 0.06$; morning hours vs. evening hours 19.31 ± 10.13 *SE*, $P = 0.06$) (Fig. 2). However, both of these fixed effects were less relevant in explaining the response of Common Buzzard by attacks compared with pair identity, as judged from the marginal (10%) and conditional coefficient of determination (99%).

4. Discussion

Analysis of the data on White-tailed Eagle diet during the 16 observed breeding seasons revealed that the remains of nestling Common Buzzards were found in 9% of the successful nests of 17% of the pairs studied but made up less than 2% of all prey items identified. Notably, evidence on the consumption of other raptor species was scarce. Furthermore, our results suggest that habitat (as a proxy indicator of prey availability) may explain the probability of predation on species belonging to high trophic levels.

During the field experiment, Common Buzzards responded to the White-tailed Eagle dummy near nest sites during only half of the conducted visits. Contrary to our expectations, the proximity to White-tailed Eagle nests did not explain the behavioural response of the Common Buzzard. As expected, the response probability of the Common Buzzard only increased in the latest stage of the breeding season; however, the most plausible predictor of the response was pair identity, which suggests individual differences in brood defence behaviour. In summary, our data indicate that White-tailed Eagles may prey upon broods of the Common Buzzard under certain environmental conditions (but not on adult individuals), and that this source of prey could be relatively easy to access due to the weak brood defence behaviour of the Common Buzzard.

Raptors constituted ca. 2% of prey items identified in our sample, and at least one individual raptor was found in 9% of visited nests. These findings confirm that the White-tailed Eagle preys upon mesopredators during the nestling period. On the other hand, Lewis *et al.* (2004) demonstrated that 10 raptor prey items delivered to Northern Goshawk (*Accipiter gentilis*) nests under video-recording were absent in the prey remains, which suggests that our study could potentially underestimate the preying on Common Buzzard nestlings. This suggestion is also supported by repeated observations of Common Buzzard nestlings as prey items using trail cameras in nests of White-tailed Eagle in Germany (Neumann & Schwarz 2017). In the diet samples of previous studies from other European regions, raptors were found either occasionally or were completely absent (Helander 1983, Sulkava *et al.* 1997, Struwe-

Juhl 2003, Whitfield *et al.* 2013, Sjøndor *et al.* 2015). The average contribution of diurnal raptors in the diet of the most well-known superpredators, such as the Golden Eagle (*Aquila chrysaetos*), Northern Goshawk, and Eagle Owl in terrestrial ecosystems in Europe ranges from 0.7% to 1.2% by number, and from 0.3% to 2.0% by biomass (Lourenço *et al.* 2011) – though this figure may even reach 6% by number in the diet (Northern Goshawk; Hoy *et al.* 2017). In this context, we suggest that the White-tailed Eagle can be classified as a superpredator; however, the evidence stems almost entirely from Common Buzzard nestlings in our study.

We suggest four complementary reasons to explain the nearly single-species predation on the Common Buzzard in our region: 1) the effect of habitat/territory quality of the White-tailed Eagle; 2) the abundance of the Common Buzzard; 3) strong overlap in breeding seasons and activity rhythms of the White-tailed Eagle and Common Buzzard; and 4) weak brood defence by the Common Buzzard.

We have determined that the probability of raptor prey is significantly higher in the nests of White-tailed Eagle pairs breeding in inland compared to coastal areas. Moreover, pair/territory identity was an even more important predictor. These results are congruent with the findings of recent studies, which indicated that the superpredation phenomenon is spatially structured and varies among communities (Lourenço *et al.* 2011) and even within the same population along an environmental gradient (Hoy *et al.* 2017). The White-tailed Eagle adjusts its diet according to prey availability in the environment (Sulkava *et al.* 1997, Ekblad *et al.* 2016). Therefore, two complementary reasons may be linked to the observed spatial difference in raptor prey detection: a high abundance of fish and waterfowl prey in the coastal habitat and differences in Common Buzzard abundance in coastal and inland habitats (the mean Common Buzzard density in Lithuanian coastal forests was 11.5 pairs per 100 km² of forest, but density in inland forests ranged over a large gradient from 2.5 to 82 pairs; Drobek 2004). An increase of mesopredators in the diet of superpredators was related to a decrease in main prey abundance (Serrano 2000, Lourenço *et al.* 2011, Hoy *et al.* 2017) complemented by a higher

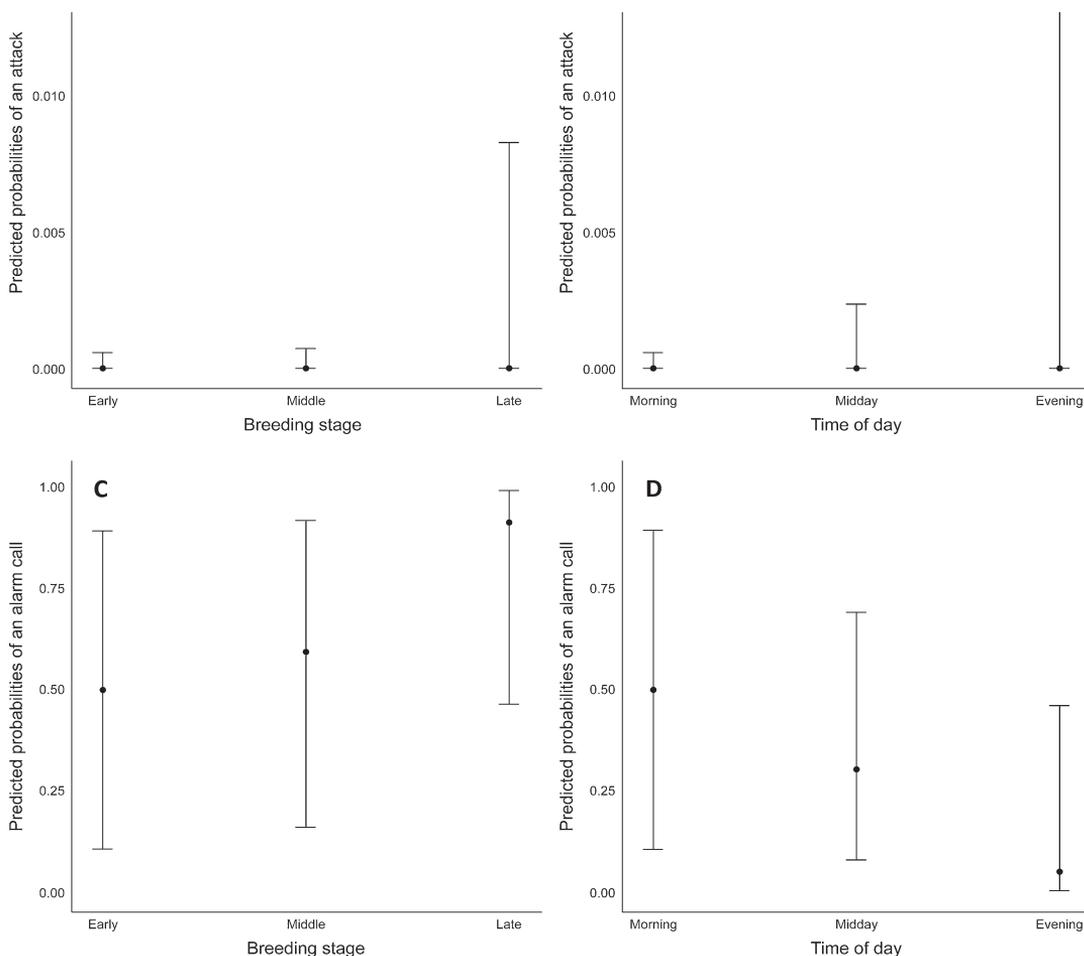


Fig. 2. Predicted probabilities (whiskers – confidence intervals) of attacks during (A) breeding stages and (B) time of the day; alarm calls – (C) breeding stages and (D) time of the day.

abundance of mesopredators in breeding territories (Lourenço *et al.* 2018). The broods of Common Buzzard – the most common raptor in Lithuania (6,000–12,000 pairs; European Environment Agency 2012) – may serve as a source of common prey outside of optimal habitats and/or in areas where they are locally abundant.

Differences in the breeding phenology of a mesopredator may promote coexistence with a superpredator (Rebollo *et al.* 2017), but the breeding cycles of the Common Buzzard and White-tailed Eagle overlap greatly in Lithuania: White-tailed Eagle broods usually hatch in mid-April, while those of the Common Buzzard hatch in mid-May; meanwhile, fledglings of both species begin leaving their nests during the second half of June (Drobėlis 2004). The highest demand for prey was

observed between 7 and 9 weeks in the Golden Eagle (Collopy 1984), which is similar in breeding phenology to the White-tailed Eagle.

This led us to assume that Common Buzzard nestlings grow during the period of the highest prey demand for successfully breeding White-tailed Eagles. The overlap in activity rhythms between superpredators and mesopredators may be one of the factors determining heavier predation on certain species (Petty *et al.* 2003, Lourenço *et al.* 2011). Both species studied here are diurnal, which may favour the White-tailed Eagle in locating the nesting sites of Common Buzzards with broods.

Common Buzzards that were nesting successfully, passively responded to the White-tailed Eagle dummy in the vicinity of their nests, with alarm

calls being observed during only half of the visits, and (mainly mock) attacks being observed in 22% of the visits. Due to different methodological approaches, we are limited to direct comparisons with studies that reported Common Buzzard response to “typical” superpredators, such as the Eagle Owl and Northern Goshawk (e.g., Krüger 2002, Boerner & Krüger 2009). Mueller *et al.* (2016) reported that mock attacks and attacks with physical contact performed by Common Buzzards on an Eagle Owl dummy were frequent during trials (61% to 90% of trials). The antipredator behaviour of a prey species may increase with more frequent predator encounters (Tilgar & Moks 2015, Mueller *et al.* 2016), but we did not detect a relationship between Common Buzzard responses and proximity to White-tailed Eagle nests.

In the Central Lithuanian plot, Common Buzzard nests were located 0.8–14.1 km from the nearest nest occupied by White-tailed Eagle, and more than 21 km away in Northern Lithuania plot. The average distance of White-tailed Eagle feeding flights during the breeding period has previously been recorded as 3.8 km (Struwe-Juhl 2000) but could range between 2.5 km and 15 km from nests (references in Heuck *et al.* 2017). We cannot rule out that Common Buzzards responded to the predator regardless of its proximity because encounters with White-tailed Eagles were rare. On the other hand, birds can recognise predator threat level and adjust their responses accordingly (Arroyo *et al.* 2001, Dutour *et al.* 2016).

Therefore, the lack of association to the proximity to White-tailed Eagles, coupled with the overall non-intensive antipredator behaviour, might indicate that the White-tailed Eagle is not perceived by the Common Buzzard as a dangerous predator. The intensity of brood defence behaviour may be explained by the adult sex as well. Female Common Buzzards mainly attend to the brood, while males provide the food. Brood defence behaviour depends on adult sex, with males being more aggressive towards intruders (Pavel & Bureš 2001, Boerner & Krüger 2009). This might explain the observed higher intensity of aggressiveness when both Common Buzzard adults (probably male and female) reacted to the dummy compared to cases when only one bird (probably female) did.

The Common Buzzard responded most ac-

tively towards the White-tailed Eagle dummy in the second half of June (i.e., when nestlings were closer to fledging). As previously observed among Common Buzzards, brood defence increases with the age of offspring (Krüger 2002), which is the typical pattern among many other altricial species (Onnebrink & Curio 1991; but see Speiser & Bosakowski 1991), and is likely due to the value of nestlings to parents increasing with age and/or because older nestlings are more conspicuous and profitable to predators (Galeotti *et al.* 2000). However, the antipredator responses to the White-tailed Eagle were best explained by the identity of a pair (or separate mates). Recently, strong evidence has suggested that antipredator behaviour is consistent over an individual’s lifetime and is determined by genetic factors (Bize *et al.* 2012). Individual variation in nest defence aggressiveness was also found in the Ural Owl (*Strix uralensis*) (Konttinen *et al.* 2009). The plumage colouration (as a proxy for physiological differences; Karell *et al.* 2017) of Common Buzzard individuals was related to aggressive behaviour against predators (Boerner & Krüger 2009). Males of the Black-tailed Gull (*Larus crassirostris*) that attacked nest predators had higher levels of plasma testosterone compared to non-attacking males (Kazama *et al.* 2011).

Our results indicate some support for the response probability being influenced by the time of day, although our results were inconsistent for alarm calls and attacks. Bize *et al.* (2012) also determined that antipredator behaviour varied throughout the day, thereby suggesting some behavioural plasticity. To our knowledge, daytime-dependent brood defence has rarely been tested (though see Honza *et al.* 2004); therefore, we are limited in our interpretation of possible reasons for this observed trend in daytime patterns. However, the low probability of mock attacks during morning hours could be also related to the absence of males near nests at that time, as females are less likely to perform attacks compared to males (Boerner & Krüger 2009).

Notably, adult raptors were nearly absent from the diet sample. Apart from Common Buzzard nestlings, only two individuals (one fledgling Tawny Owl and one adult Common Kestrel) were found and likely represent random prey items. Although the prey remains identification method has

its biases in terms of representing the prey consumed (Lewis *et al.* 2004), no evidence of preying on other mesopredators (e.g., Northern Goshawks, Honey Buzzards (*Pernis apivorus*), Lesser Spotted Eagles (*Clanga pomarina*), Black Kites (*Milvus migrans*), Red Kites (*Milvus milvus*), among others) that breed in the regions included in this study was found. Therefore, the recently recovered White-tailed Eagle population in boreal and temperate ecosystems is not likely to suppress mesopredator populations by direct removal of adult individuals as, for example, is the case for the recovered Northern Goshawk, which was suggested to contribute to the decline of Common Kestrel population (Petty *et al.* 2003, Hoy *et al.* 2017). Additionally, we found that the Lesser Spotted Eagle (a mesopredator) coexists with more abundant White-tailed Eagle in the coastal area of Lithuania without any obvious adverse effects on its population dynamics (Dementavičius *et al.* 2019). No substantial evidence exists to expect that the White-tailed Eagle returning to the natural ecosystems may strongly reshape avian mesopredator communities through lethal or non-lethal interactions. However, tests for these interactions in different regions could provide a deeper understanding of the role of this recovered large avian predator.

Acknowledgments. We are grateful to Kaunas Tadas Ivanauskas Zoological Museum for the opportunity to use reference collections. We are also thankful to two anonymous reviewers and associate editor for their valuable comments on the early version of the manuscript.

Mitä ravintoanalyysi ja poikasten puolustaminen paljastavat merikotkan ja hiirihaukan vuorovaikutuksesta?

Viimeaikaiset tutkimukset viittaavat siihen, että merikotka – runsastunut huippupeto – voi käyttää saaliinaan nk. mesopredaattoreita ja niiden poikasia. Tässä tutkimuksessa selvitettiin merikotkan ja mesopredaattori hiirihaukan vuorovaikutusta (i) analysoimalla merikotkan ravintoaineistoa ja (ii) kokeellisesti selvittämällä pesivien hiirihaukkojen reaktioita lähestyvään merikotkaan. Hiirihaukan poikasten jäännöksiä oli havaittavissa 9%:ssa onnistuneista merikotkapesinnöistä, kun taas muiden

petolintujen jäännökset olivat hyvin harvinaisia. Hiirihaukan predaatiossa oli vaihtelua merikotkarien ja habitaattien välillä, mikä viittaisi alueelliseen vaihteluun saalistuspaineessa.

Vain noin puolet hiirihaukoista reagoi keinotekoiseen merikotkaan pesien läheisyydessä, mutta reagointi ei riippunut pesivien merikotkien läheisyydestä. Hiirihaukkojen reagointi (varoitusäänet, hyökkäykset) oli voimakkaampaa pesinnän loppuvaiheessa, mutta tämä vaikutus johtui lähinnä riien välisistä eroista, ja täten viittaa siihen että aggressiivisuudessa on yksilöiden välistä vaihtelua. Tulosten perusteella voidaan todeta, että merikotka saalistaa hiirihaukkoja, ainakin tietyissä ympäristöolosuhteissa, ja että hiirihaukan poikue voi olla helppo saalis merikotkalle, koska vain osa emoista puolustaa pesiä merikotkia vastaan.

References

- Arroyo, B., Mougeot, F. & Bretagnolle, V. 2001: Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). — Behavioral Ecology and Sociobiology 50: 109–115.
- Bartoń, K. 2019: MuMIn: Multi-Model Inference. R package version 1.43.6. <https://CRAN.R-project.org/package=MuMIn>.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015: Fitting Linear Mixed-Effects Models Using lme4. — Journal of Statistical Software 67: 1–48.
- Bize, P., Diaz, D. & Lindström, J. 2012: Experimental evidence that adult antipredator behaviour is heritable and not influenced by behavioural copying in a wild bird. — Proceedings of the Royal Society B: Biological Sciences 279: 1380–1388.
- Björklund, H., Santangeli, A., Blanchet, F.G., Huitu, O., Lehtoranta, H., Lindén, H., Valkama, J. & Laaksonen, T. 2016: Intraguild predation and competition impacts on a subordinate predator. — Oecologia 181: 257–269.
- Boerner, M. & Krüger, O. 2009: Aggression and fitness differences between plumage morphs in the common buzzard (*Buteo buteo*). — Behavioral Ecology 20: 180–185.
- Brown, J.L. 1969: Territorial behavior and population regulation in birds. — The Wilson Bulletin 81: 293–329.
- Chakarov, N. & Krüger, O. 2010: Mesopredator Release by an Emergent Superpredator: A Natural Experiment of Predation in a Three Level Guild. — PLOS One 5: e15229.
- Collopy, M.W. 1984: Parental care and feeding ecology of Golden Eagle nestlings. — The Auk 101: 753–760.
- Dementavičius, D. 2007: White-tailed Eagle (*Haliaeetus albicilla*) in Lithuania: population numbers and trends

- 1900–2007. — *Acta Zoologica Lituanica* 17: 281–285.
- Dementavičius, D., Rumbutis, S., Vaitkuvienė, D., Dagys, M. & Treinys, R. 2019: No adverse effects on Lesser Spotted Eagle breeding in an area of high White-tailed Eagle density. — *Journal of Ornithology* 160: 453–461.
- Drobėlis, E. 2004: Lietuvos miškų plėšrieji paukščiai. — Aplinkos ministerija, Vilnius. (In Lithuanian)
- Dutour, M., Lena, J.-P. & Lengagne, T. 2016: Mobbing behaviour varies according to predator dangerousness and occurrence. — *Animal Behaviour* 119: 119–124.
- Ekblad, C.M.S., Sulkava, S., Stjernberg, T.G. & Laaksonen, T.K. 2016: Landscape-scale gradients and temporal changes in the prey species of the White-tailed Eagle (*Haliaeetus albicilla*). — *Annales Zoologici Fennici* 53: 228–240.
- European Environment Agency 2012: Birds population status and trends at EU 27 and Member State level <https://bd.eionet.europa.eu/article12/>
- Galeotti, P., Tavecchia, G. & Bonetti, A. 2000: Parental defence in Long-eared Owls *Asio otus*: effects of breeding stage, parent sex and human persecution. — *Journal of Avian Biology* 31: 431–440.
- 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.
- Heuck, C., Herrmann, C., Schabo, D.G., 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.
- Honza, M., Grim, T., Capek, M. Jr., Moksnes, A. & Ruškaf, E. 2004: Nest defence, enemy recognition and nest inspection behaviour of experimentally parasitized Reed Warblers *Acrocephalus scirpaceus*. — *Bird Study* 51: 256–263.
- Hoy, S.R., Petty, S.J., Millon, A., Whitfield, D.P., Marquiss, M., Anderson, D.I.K., Davison, M. & Lambin, X. 2017: Density-dependent increase in superpredation linked to food limitation in a recovering population of northern goshawks *Accipiter gentilis*. — *Journal of Avian Biology* 48: 1205–1215.
- Kamarauskaitė, A., Skuja, S. & Treinys, R. 2019: Nesting Habitat Overlap between the Common Buzzard *Buteo buteo* and the Lesser Spotted Eagle *Clanga pomarina* for Conservation Planning in Natura 2000 Sites. — *Bird Study* 66: 224–233.
- Karell, P., Bensch, S., Ahola, K. & Asghar, M. 2017: Pale and dark morphs of tawny owls show different patterns of telomere dynamics in relation to disease status. — *Proceedings of the Royal Society B: Biological Sciences* 284: 20171127.
- Kazama, K., Niizuma, Y., Sakamoto, K.Q. & Watanuki, Y. 2011: Factors affecting individual variation in nest-defense intensity in colonially breeding Black-tailed Gulls (*Larus crassirostris*). — *Canadian Journal of Zoology* 89: 938–944.
- Konttinen, P., Pietiäinen, H., Huttunen, K., Karell, P., Kolunen, H. & Brommer, J.E. 2009: Aggressive Ural owl mothers recruit more offspring. — *Behavioral Ecology* 20: 789–796.
- 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.
- Krüger, O. 2002: Interactions between common buzzard *Buteo buteo* and goshawk *Accipiter gentilis*: trade-offs revealed by a field experiment. — *Oikos* 96: 441–452.
- Lewis, S.B., Fuller, M.R. & Titus, K. 2004: A comparison of 3 methods for assessing raptor diet during the breeding season. — *Wildlife Society Bulletin* 32: 373–386.
- Löhmus, A. 2001: Habitat selection in a recovering Osprey *Pandion haliaetus* population. — *Ibis* 143: 651–657.
- Lourenço, R., Delgado, M.M., Campioni, L., Goytre, F., Rabaça, J.E., Korpimäki, E. & Penteriani, V. 2018: Why do top predators engage in superpredation? From an empirical scenario to a theoretical framework. — *Oikos* 127: 1563–1574.
- Lourenço, R., Penteriani, V., Rabaça, J.E. & Korpimäki, E. 2014: Lethal interactions among vertebrate top predators: a review of concepts, assumptions and terminology. — *Biological Reviews* 89: 270–283.
- Lourenço, R., Santos, S.M., Rabaça, J.E. & Penteriani, V. 2011: Superpredation patterns in four large European raptors. — *Population Ecology* 53: 175–185.
- Lüdecke, D. 2018: sjmisc: data and variable transformation functions. — *Journal of Open Source Software* 26: 754.
- Lüdecke, D. 2019a: sjPlot: data visualization for statistics in social science. R package version 2.6.3. <https://CRAN.R-project.org/package=sjPlot>.
- Lüdecke, D. 2019b: sjlabelled: labelled data utility functions (Version 1.1.0). <https://CRAN.R-project.org/package=sjlabelled>.
- Mac Sharry, B. 2012: User manual for range tool for article 12 (birds directive) and article 17 (habitats directive). — European Topic Centre on Biological Diversity, Paris.
- Malinauskas, V. 1998: Kaišiadorių rajono gyvūnyjos atlasas 1986–1997. — Gamtos pasaulis, Vilnius. (in Lithuanian)
- Mammen, U. & Stubbe, M. 2002: Jahresbericht 2001 zum Monitoring Greifvögel und Eulen Europas. — Jahresbericht. Monitoring Greifvögel Eulen Europas 14: 1–111. (In German)
- Mebs, T. & Schmidt, D. 2006: Die Greifvögel Europas, Nordafrikas und Vorderasiens: Biologie, Kennzeichen, Bestände. — Kosmos, Stuttgart. (In German)
- Michel, V.T., Jiménez-Franco, M.V., Naef-Daenzer, B. & Grübler, M.U. 2016: Intraguild predator drives forest

- edge avoidance of a mesopredator. — *Ecosphere* 7: e01229.
- Morosinotto, C., Villers, A., Thomson, R.L., Varjonen, R. & Korpimäki, E. 2017: Competitors and predators alter settlement patterns and reproductive success of an intraguild prey. — *Ecological Monographs* 87: 4–20.
- Mueller, A.K., Chakarov, N., Hesecker, H. & Krüger, O. 2016: Intraguild predation leads to cascading effects on habitat choice, behaviour and reproductive performance. — *Journal of Animal Ecology* 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 für Meckl-Vorp* 45: 399–401. (In German)
- Nadjafzadeh, M., Hofer, H. & Krone, O. 2016: Sit-and-wait for large prey: foraging strategy and prey choice of White-tailed Eagles. — *Journal of Ornithology* 157: 165–178.
- Neumann, J. & Schwarz, J. 2017: Seeadlerpaar mit besonderer Vorliebe für junge Mäusebussarde – Teil 3. — *Großvogelschutz im Wald (Jahresberichte 2017)*: 28–30. (In German)
- Onnebrink, H. & Curio, E. 1991: Brood defense and age of young: a test of the vulnerability hypothesis. — *Behavioral Ecology and Sociobiology* 29: 61–68.
- Pavel, V. & Bureš, S. 2001: Offspring age and nest defence: test of feedback hypothesis in the meadow pipit. — *Animal Behaviour* 61: 297–303.
- Petty, S.J., Anderson, D.I.K., Davison, M., Little, B., Sherratt, T.N., Thomas, C.J. & Lambin, X. 2003: The decline of Common Kestrels *Falco tinnunculus* in a forested area of northern England: the role of predation by Northern Goshawks *Accipiter gentilis*. — *Ibis* 145: 472–483.
- Polis, G.A., Myers, C.A. & Holt, R.D. 1989: The ecology and evolution of intraguild predation: potential competitors that eat each other. — *Annual Review of Ecology and Systematics* 20: 297–330.
- R Core Team 2019: R version 3.6.0. — R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Rebollo, S., Martknez-Hesterkamp, S., Garça-Salgado, G., Pérez-Camacho, L., Fernández-Pereira, J.M. & Jenness, J. 2017: Spatial relationships and mechanisms of coexistence between dominant and subordinate top predators. — *Journal of Avian Biology* 48: 1226–1237.
- Reif, V., Tornberg, R., Jungell, S. & Korpimäki, E. 2001: Diet variation of common buzzards in Finland supports the alternative prey hypothesis. — *Ecography* 24: 267–274.
- Rytönen, S. & Soppela, M. 1995: Vicinity of sparrowhawk nest affects willow tit nest defense. — *The Condor: Ornithological Applications* 97: 1074–1078.
- Sjindor, A., Alexe, V., Marinov, M., Dorofencu, A., Domşa, C. & Kiss, B.J. 2015: Nest-site selection, breeding success, and diet of white-tailed eagles (*Haliaeetus albicilla*) in the Danube Delta, Romania. — *Turkish Journal of Zoology* 39: 300–307.
- Sergio, F. & Hiraldo, F. 2008: Intraguild predation in raptor assemblages: a review. — *Ibis* 150: 132–145.
- Sergio, F., Marchesi, L. & Pedrini, P. 2003: Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. — *Journal of Animal Ecology* 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? — *Animal Behaviour* 74: 1607–1616.
- Serrano, D. 2000: Relationship between Raptors and Rabbits in the Diet of Eagle Owls in Southwestern Europe: Competition Removal or Food Stress? — *Journal of Raptor Research* 34: 305–310.
- Speiser, R. & Bosakowski, T. 1991: Nesting Phenology, Site Fidelity, and Defense Behavior of Northern Goshawks in New York and New Jersey. — *Journal of Raptor Research* 25: 132–135.
- Struwe-Juhl, B. 2000: Funkgestützte Synchronbeobachtung – eine geeignete Methode zur Bestimmung der Aktionsräume von Großvogelarten (Ciconiidae, *Haliaeetus*) in der Brutzeit. — *Populations Ökologie Greifvogel und Eulenarten* 4: 101–110. (In German)
- Struwe-Juhl, B. 2003: Why do White-tailed eagles prefer coots? — *In Sea eagle 2000* (ed. Helander, B., Marquiss, M. & Bowerman, B.): 317–325. Swedish Society for Nature Conservation (SNF), Stockholm.
- Sulkava, S., Tornberg, R. & Koivusaari, J. 1997: Diet of the white-tailed eagle *Haliaeetus albicilla* in Finland. — *Ornis Fennica* 74: 65–78.
- Tilgar, V. & Moks, K. 2015: Increased risk of predation increases mobbing intensity in tropical birds of French Guiana. — *Journal of Tropical Ecology* 31: 243–250.
- Treïnys, 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. — *Journal of Ornithology* 157: 311–323.
- Whitfield, D.P., Marquiss, M., Reid, R., Grant, J., Tingay, R. & Evans, R.J. 2013: Breeding season diets of sympatric White-tailed Eagles and Golden Eagles in Scotland: no evidence for competitive effects. — *Bird Study* 60: 67–76.
- Whitfield, D.P., Reid, R., Haworth, P.F., Madders, M., Marquiss, M., Tingay, R. & Fielding, A.H. 2009: Diet specificity is not associated with increased reproductive performance of Golden Eagles *Aquila chrysaetos* in Western Scotland. — *Ibis* 151: 255–264.
- Wickham, H. 2016: ggplot2: Elegant Graphics for Data Analysis. — Springer-Verlag, New York.
- Zuberogoitia, I., Martknez, J.E., Zabala, J., Martknez, J.A., Azkona, A., Castillo, I. & Hidalgo, S. 2008: Social interactions between two owl species sometimes associated with intraguild predation. — *Ardea* 96: 109–113.