VILNIUS UNIVERSITY
NATURE RESEARCH CENTRE

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The habitat preferences of Common Buzzard (*Buteo buteo*) and interaction with other birds of prey

SUMMARY OF DOCTORAL DISSERTATION

Natural Sciences, Zoology, N 014

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VILNIAUS UNIVERSITETAS GAMTOS TYRIMŲ CENTRAS

Aušra KAMARAUSKAITĖ

Paprastojo suopio (*Buteo buteo*) veisimosi buveinių pasirinkimo skirtumai ir sąveika su kitais plėšriaisiais paukščiais

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SUMMARY

INTRODUCTION

Significance of the study

The Common Buzzard is the most abundant species of birds of prey in Europe (Panek, Hušek, 2014) and Lithuania (Jusys et al., 2012). The populations of Common Buzzard are considered to be overall stable, except for their long-lasting decline in Northern Europe, which may be linked to intensive timber harvesting practices and the resulting changes in the abundance of food resources (Björklund et al., 2015).

Habitat selection is a complex process, determined by habitat characteristics, environmental conditions, intraspecific and interspecific interactions (Brambilla et al., 2010).

Loss and fragmentation of forest habitats are considered to be factors that threaten the survival of forest birds on a global scale, especially birds living in old forests (Hakkarainen et al., 2008). For some species of birds of prey, a suitable nest site is considered to be one of the most critical resources (Radović, Jelaska, 2012), which are destroyed during timber harvesting (Jiménez–Franco et al., 2018). In Lithuania, the annual percentage of timber harvesting between 1998 and 2007 accounted for 66% of the increment (9.7 million cubic meters per year) (Brukas et al., 2011); such harvesting pattern is considered to be intensive. Identifying what determines habitat selection and change in commercially used forests is an essential task for the conservation of forest-dwelling species and the effective management of species' populations.

Competition is considered to be one of the essential biological factors determining the density of animal populations (Sergio et al., 2003; Suhonen et al., 2007), their structure (Sergio et al., 2003), and the extent to which species can coexist (Treinys et al., 2011). Competition is more pronounced at higher tropic levels (Sergio,

Hiraldo, 2008). The Common Buzzard and the Lesser Spotted Eagle *Clanga pomarina* (which is almost two-fold larger in body size) are sympatric species with similar habitat requirements: mature nest stands and visually indistinguishable nests. Moreover, pairs of these species were observed to occupy each other's nests (Skuja, Budrys, 1999). This suggests that there could be competition for nest sites between these raptors.

Superpredation is a widespread phenomenon in large birds of prey (Lourenço et al., 2011) with the potential to form communities of raptors (Serrano, 2000; Petty et al., 2003; Sergio, Hiraldo, 2008; Lourenço et al., 2011) or even vertebrate animal communities in general, through the suppression or release of either mesopredator (Lourenço et al., 2011). The top predator, the White-tailed Eagle *Haliaeetus albicilla*, is known to use nestlings of the Common Buzzard for prey (Müller, Lauth, 2006; Neumann, Schwarz, 2017). White-tailed Eagle populations recover in Europe as well in Lithuania (Nemesházi et al., 2016; Treinys et al., 2016). Such a return of the top predator to ecosystems has the potential to lead to behavioural changes in the mesopredators species as reported in the study of the Common Buzzard and the Eurasian Eagle-Owl *Bubo bubo* in Germany (Mueller et al., 2016).

The aim of the study

The aim of the study is to investigate the habitat preference of the Common Buzzard, its spatio-temporal changes and its interactions with larger species of birds of prey.

Objectives of the study

- To identify factors important to the habitat preference of the Common Buzzard.
- To analyse the habitat preference of the Common Buzzard in different landscapes.

- To compare the preference for nest trees, nest sites and macrohabitats of Common Buzzards in commercial forests in the years between 2002 and 2004, as well as 2017 and 2018.
- To assess the competition between the Common Buzzard and the Lesser Spotted Eagle for nest sites.
- To estimate the brood defence behaviour of the Common Buzzard to the presence of White-tailed Eagle at nest sites during the breeding season.

Defended statements

- The nesting habitat preference of the Common Buzzard is determined by the age and tree species composition of the stand and soil humidity.
- The mature nest site stands are particularly important for the Common Buzzard and preference for them does not differ between landscapes. Other stand variables and distance to the forest edge depends on the forest landscape.
- The use of nest trees and nest sites of Common Buzzard has changed in the years of 2017-2018 compared to the years 2002-2004; however, the location of nest sites in regards to landscape variables remained similar.
- When choosing nest sites, the Common Buzzard did not avoid the larger in body size Lesser Spotted Eagle. Competition for nest sites between the Common Buzzard and the Lesser Spotted Eagle is most likely to happen at the forest edge.
- Proximity to the White-tailed Eagle nest sites did not explain the brood defence behaviour of the Common Buzzard.
- The intensity of the brood defence behaviour of the Common Buzzard to the White-tailed Eagle was mainly influenced by individual characteristics of the Common Buzzard.

Novelty of the study

For the first time, competition for nest sites between the Common Buzzard and the Lesser Spotted Eagle at the local scale has been studied. Moreover, it was the first time that the brood defence behaviour of the Common Buzzard to the top predator White-tailed Eagle was studied using the field experiment approach. The study complemented knowledge about the importance of mature stands in the Common Buzzard nest sites preferences and the plasticity of the habitat preference in relation to the nest tree species, the species composition of the stands, soil characteristics and proximity to the forest edge. Also, for the first time in Lithuania, the patterns of habitat preference of the Common Buzzard were evaluated at different time frames in commercial forests.

Scientific and practical implications of the study

The habitat analysis supplemented the knowledge of habitat elements that are important to the Common Buzzard. The work provides data on the importance of mature stands as an essential component of the nest sites for the Common Buzzard. This study provided additional knowledge of the components of nest sites, whose preference is plastic and varies under different forest landscapes. The estimation of the possible competition between the Common Buzzard and the Lesser Spotted Eagle for nest sites has provided support that it is most likely to occur at the forest edge. The information obtained may be used to complement protection regimes in the Natura2000 sites designated to the Lesser Spotted Eagle. The overall weak brood defence response of the Common Buzzard to the White-tailed Eagle provided evidence that the spread of the top predator did not cause behavioural changes to the mesopredator. While comparing nest sites and macrohabitats of the Common Buzzard in the years between 2002 and 2004, as well as 2017 and 2018, it was found that the use of the nest trees and nest sites changed. However, even as the landscape changed, their location towards the landscape variables remained stable.

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1. STUDY METHODS

1.1 Study area

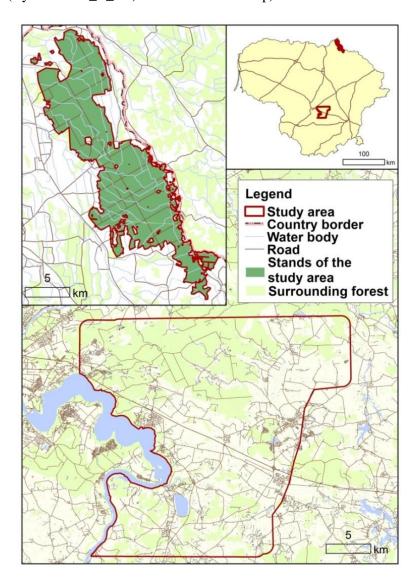
Factors determining the habitat preference of the Common Buzzard have been studied in two areas that are over 130 km apart from each other. The first study area covers forest massifs located in central Lithuania, on the right bank of Kaunas Reservoir (municipalities of Kaišiadorys and Jonava) (hereinafter referred to as the Kaišiadorys forests) (see Fig. 1.1.1.). The second study area covers the Biržai forest massif in northern Lithuania (municipality of Biržai) including smaller forests located in its proximity (hereinafter referred to as the Biržai forest) (see Fig. 1.1.1.).

1.1.1 Study area – the Kašiadorys forests

Only forest land (22,662 ha) has been attributed to the study area; forest stands cover 21,492 ha of this territory. Stands dominated by spruces (*Picea abies*) and birches (*Betula pendula*) predominate here, together forming more than 50% of the forest cover. The average age of forest stands is 51.4 years \pm 35.9 (SD), and middleaged and young stands prevail (32% and 28% respectively). The area is dominated by temporarily soaked soils and soils of normal humidity (79%), as well as fertile and highly fertile soils. Seventy-eight per cent of the forested area is attributed to group IV commertial forests.

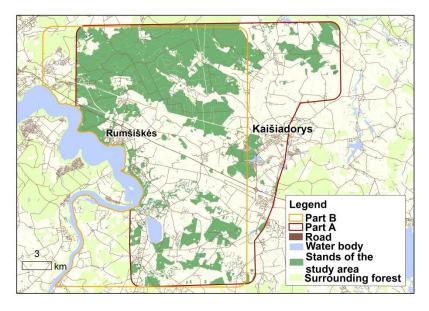
Two parts were set in this study area: the first part was set for comparative analysis of the habitat preference of the Common Buzzard with control stands and with habitats of the Lesser Spotted Eagle (hereinafter referred to as part A of the Kaišiadorys forests' study area) (the setting principles are described in Selection of control stands in Chapter 1.2.), and the second part – for analysis of Common Buzzard nest sites occupied in the years 2002-2004 and 2017-2018 (hereinafter referred to as part B of the Kaišiadorys forests' study area) (see Figure 1.1.1.1.).

Fig. 1.1.1. The study areas in Biržai forest (top) and Kaišiadorys forests (bottom) (data of State Forest Cadastre of the Republic of Lithuania (2017), and the Geo-referential spatial data sets at scale 1:10000 – GDR10 (layer PLOTAI), GDR250 (layer Border), GDR50 (layer RIBOS P LT) were used in this map).



Part B of the Kaišiadorys forests' study area was set based on the distribution of nests of the Common Buzzard in the years 2002-2004 and 2017-2018 (hereinafter referred to as the years of 2002 and 2017 respectively).

Fig. 1.1.1.1. Parts A and B of Kaišiadorys forests' study area (the only wooded forest land) (data of State Forest Cadastre of the Republic of Lithuania (2017) and the Geo-referential spatial data set GDR10 (layer PLOTAI) were used in this map).



1.1.2 Study area – the Biržai forest

The Biržai forest (area $\sim 17,000$ ha) is located in the Mūša-Nemunėlis Lowland, which is characterized by flat terrain (Česnulevičius, 2010). The average age of the Biržai forest stands is 47 years \pm 29 (SD). Stands dominated by birch and spruce cover 44% and 27% of the forests, respectively. Nearly 54% of the Biržai forest is covered by young and middle-aged stands. The largest part of the forest grows on fertile and highly fertile soaked soils. Ninety-

three per cent of the forest stands is attributed to group IV commercial forests.

1.1.3 Software used in the study

Statistical calculations were made using R v.3.5.1 software. R packages used: MuMIn (Bartoń, 2018), rsq (Zhang, 2018), lme4 (Bates et al., 2019). Nest site and macrohabitat data were obtained using ArcGIS ArcMap 10.2.2 software. The average nearest neighbour analysis was performed using the "Average Nearest Neighbour" tool of ArcGIS ArcMap 10.2.2 software. Graphs were created using Microsoft Excel 2010 software. Statistical functions used: STDEV. P, CONFIDENCE. T, AVERAGE.

1.2 Study methods for habitat preference of the Common Buzzard in comparison with control stands and habitats of the Lesser Spotted Eagle

Search for nests. The initial data on the Common Buzzard nest location in the Biržai forest was provided by ornithologist Saulis Skuja. The nest occupancy check-ups were carried out during field work in the spring and summer in the years of 2014-2015.

The initial data on the Common Buzzard nest location in the Kaišiadorys forests was provided by ornithologist Deivis Dementavičius. The author of the dissertation carried out field work to assess the nest occupancy of the Common Buzzard and the exact location of the nests in the Kaišiadorys forests in the summer and autumn of 2017. A description of each nest was provided, and the species of bird of prey occupying the nest was identified. If the species of bird of prey that occupied the nest was not identified in 2017, the re-inspection was carried out in the spring of 2018.

The data on the nest sites of the Lesser Spotted Eagle in both study areas was obtained during the implementation of the project "Conservation of the Lesser Spotted Eagle (*Aquila pomarina*) in Lithuanian Forests" (Eagles in the forest, No. LIFE09 NAT/LT/000235). The search for nest sites during this project was

carried out between 2011 and 2014 by monitoring the behaviour of birds in open areas and by mapping potential bird nest sites. Following this, the potential nest sites were examined, the exact coordinates were obtained and descriptions of the nests were provided.

If a pair of birds of prey used several nests in their breeding territory during the study years, only one nest, the last one to be occupied, was included in the analysis. Altogether, this study analyzed 27 nests occupied by the Common Buzzard, 21 nests occupied by the Lesser Spotted Eagle in the Kaišiadorys forests, as well as 53 Common Buzzard nests and 26 Lesser Spotted Eagle nests located in the Biržai forest.

Selection of control stands. Stands were selected using the random point method by randomly generating points into forest stands of the study areas. Stands with random points were considered as Control stands.

The area for the generation of random points in the Kaišiadorys forests was defined based on the distribution of Common Buzzard and Lesser Spotted Eagle nests (Part A of Kaišiadorys forests' study area). In the Biržai forest, random points were generated in the forest area, as shown in Figure 1.1.1.

Random points were generated only in forest stands, regardless of their age or tree species composition; this included clear cut areas. The minimum distance between the points was 500 m, according to the minimum distance between the nests of two breeding pairs of the Common Buzzard in the Biržai forest. Twenty-seven random points were generated in the Kaišiadorys forests and fifty-three in the Biržai forest. Random points were generated using ArcGIS ArcMap 10.2.2 software (tool "Create random points").

Habitat data. In the Kaišiadorys forests, 13 variables were used for both bird species (see Table 1.2.1.). In the Biržai forest, 14 variables were used for the Common Buzzard and 13 variables for the Lesser Spotted Eagle (see Table 1.2.1.). The impact of interspecies competition on the distribution of the Common Buzzard

pairs was not tested in the Kaišiadorys forests due to the methodological data collection approach.

During the fieldwork, five nest platform placement positions of the Common Buzzard and the Lesser Spotted Eagle were distinguished in the tree (Drobelis, 2004). After summarising the data, the nest placement positions were grouped into three categories: on the trunk fork (on the trunk fork and on the trunk curve), on the side branches (on the side branches at the trunk and on the side branches away from the trunk) and on the top branches.

The tree species composition of the stand has been extracted from the formula of the first layer of trees in the stand (see below for source). The fertility of the soil in the stands was determined based on the soil fertility index, as defined by the second letter of the forest site (e.g., d in "Nd" index). Five points have been used (i.e., a = 1, b = 2, c = 3, d = 4, f = 5), where 1 is the poorest soil and 5 is the most fertile. The humidity of the stands was determined by the first letter of the forest site. Soil humidity indices were assigned numerical values ranging from 1 to 5 (slope = 1, normally irrigated = 2, temporarily soaked = 3, bog = 4, waterlogged = 5), i.e. 1 for the driest soils and 5 for the most humid.

Information about 5-12 variables of stands (Table 1.2.1.) in the State Forest Cadastre of the Republic of Lithuania is provided with the accuracy of forest inventory compartments. These are determined by tree species, age, density, site type and other characteristics.

Statistical data analysis. The Chi-square test was used to determine the homogeneity of the proportions of nest tree species and the nest platform placement in trees of Common Buzzard in the Kaišiadorys and the Biržai forests. The five groups for trees with nests in each area were used classified as 1) oak (*Quercus robur*), 2) birch, 3) spruce, 4) black alder (*Alnus glutinosa*) and 5) others (i.e., aspen (*Populus tremula*), pine (*Pinus sylvestris*), ash (*Fraxinus excelsior*) and maple (*Acer platanoides*)). Three groups described above were used in the analysis of nest platform positions in trees.

Table 1.2.1. Habitat variables used and sources of their data in the analysis of Common Buzzard and Lesser Spotted Eagle nest sites. Abbreviations: K – Kaišiadorys forests (part A); B – Biržai forest; State Forest Cadastre – State Forest Cadastre of the Republic of Lithuania; GDR10 – Geo-referential spatial data set at scale 1:10000.

No.	Habitat variable	Study area	Data source
1	Nest tree species	K, B	Fieldwork
2	Height from ground, m	K, B	Fieldwork
3	Nest tree trunk circumference, cm	K, B	Fieldwork
4	Nest platform position in the tree	K, B	Fieldwork
5	Age of the stand, years	K, B	State Forest Cadastre (2013, 2017)
6	The proportion of spruce in the stand	K, B	State Forest Cadastre (2013, 2017)
7	The proportion of birch in the stand	K, B	State Forest Cadastre (2013, 2017)
8	The proportion of black alder in the stand	K, B	State Forest Cadastre (2013, 2017)
9	The proportion of aspen in the stand	K, B	State Forest Cadastre (2013, 2017)
10	The proportion of oak in the stand	K, B	State Forest Cadastre (2013, 2017)
11	Soil fertility of the stand (1 to 5)	K, B	State Forest Cadastre (2013, 2017)
12	Soil humidity of the stand (1 to 5)	K, B	State Forest Cadastre (2013, 2017)
13	Shortest distance to the forest edge, m	K, B	GDR10
14	Shortest distance to the nest of a Lesser Spotted Eagle, m	В	GDR10

The analysis of the homogeneity of the proportions of nest tree species and the nest platform positions in trees of the Common Buzzard and the Lesser Spotted Eagle was performed analogously.

For comparison of the nest tree trunk circumference and the height of the nest from the ground, the generalized linear mixed models (GLMMs) were used. Using GLMMs, the nest sites of the Common Buzzard in the Kaišiadorys and the Biržai forests were compared, as well as the nest sites of the Common Buzzard and the Lesser Spotted Eagle in both study areas. The first model set was formed, in which the dependent variable was the buzzard nest site in the study area (i.e., 0 – nest site of Common Buzzard in the Biržai forest, 1 – nest site of Common Buzzard in the Kaišiadorys forests). The explanatory fixed effect variables were the circumference of the nest tree and the height of the nest from the ground (and all combinations between them); the tree species was included as the random variable. The second model set was formed where the dependent variable was the nest site of bird species (i.e., 0 – nest site of the Lesser Spotted Eagle, 1 – nest site of the Common Buzzard) and the explanatory fixed and random variables were the same as described above. In the construction of the GLMMs, binomial error structure and logit link function were used.

Generalized linear models (GLMs) were used to compare Common Buzzard and Lesser Spotted Eagle nest sites with each other, raptors nest sites with the control stands and Common Buzzard nest sites between the study areas.

In comparing Common Buzzard nest sites with control stands (control stand - 0, nest site - 1), GLMs (binomial distribution, logit link function) were constructed using explanatory habitat variables Nos. 5-13 (Table 1.2.1) (and all combinations between them). The sample consisted of 80 Common Buzzard nests and 80 control stands.

For the comparison of nest sites of the Common Buzzard in the Kaišiadorys (n = 27) and the Biržai (n = 53) forests, all combinations of explanatory habitat variables Nos. 5-13 (Table 1.2.1) were used in

GLMs (binomial distribution, logit link function). In these models, the dependent variable was the nest sites of the Common Buzzard in the study area (i.e., 0 – nest site of Common Buzzard in the Biržai forest, 1 – nest site of Common Buzzard in the Kaišiadorys forests).

GLMs with combinations of all possible habitat variables Nos. 5-9 and Nos. 11-13 (Table 1.2.1.) were compiled for a comparative analysis of the nest sites of the Common Buzzard and the Lesser Spotted Eagle. The sample consisted of 80 Common Buzzard nests and 47 Lesser Spotted Eagle nests. In these constructed GLMs (binomial distribution, logit link function) the nest sites of raptors were included as the response variable (i.e., 0 – nest site of Lesser Spotted Eagle, 1 – nest site of Common Buzzard).

In order to better understand the overlap of the nest sites of the Common Buzzard and the Lesser Spotted Eagle, the nest sites of latter were also compared to the control stands. GLMs (binomial distribution, logit link function) were compiled with the combinations of all possible habitat variables Nos. 5-9 and Nos. 11-13 (Table 1.2.1.). The response variable was the nest site (i.e., 0 – control stand, 1 – nest site of the Lesser Spotted Eagle). The sample consisted of 47 Lesser Spotted Eagle nests and 80 control stands.

Before performing the GLMs, explanatory variables were checked for pairwise correlation by calculating Pearson's correlation coefficients. Only the explanatory variables of control stands were compared with each other. However, no strong correlations (i.e., coefficients ≥ 0.6 or \leq -0.6) between the variables studied were found.

To estimate whether the Common Buzzard avoids the Lesser Spotted Eagle, GLM was constructed where the nest site was the response variable (i.e., 0 – control stand, 1 – nest site of Common Buzzard) and the nearest distance to the Lesser Spotted Eagle nest was the explanatory variable. In the GLM binomial distribution and logit link function was used.

AICc and Δ AICc were used for model selection. Only models with Δ AICc \leq 2 were selected as supported by the data (Burnham, Anderson, 2002):

$$\Delta AICc = AICc_i - AICc_{min}$$

Where $AICc_i$ – AICc, of which $\Delta AICc$ value is calculated, $AICc_{min}$ – the minimum AICc value from the set of models. This gives a subset of the best models that are further analysed.

Akaike weights (w_i) were also calculated for each model of the best models subset $(\Delta AICc \le 2)$:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2}\Delta_r)}$$

 w_i values range from 0 to 1; higher w_i values indicate the higher weight of the model in that set of models.

For subset models with a similar weight, the model averaging procedure was performed to determine the relative importance values (RIV) of explanatory variables.

In order to determine how well the variance of explanatory variables included in the model predict the variance of the dependent variable around the average, coefficient of determination (R^2) was calculated for the models.

The average nearest neighbour analysis was used to determine the spatial distribution type of the Common Buzzard and the Lesser Spotted Eagle in the Biržai forest. This analysis is performed by measuring the distance from the specific points (in this case – nests) to their closest neighbours (Euclidean distances are measured – distances in a straight line)

The confidence interval (CI) shown in the graphs in the Results chapter is calculated for the population mean μ . In all cases, the 95% confidence level was used.

1.3 Methods for comparative analysis of Common Buzzard habitats occupied in 2002 and 2017

Nest data. Thirty-seven occupied nests were identified in the years of 2002-2004 and 28 in the years of 2017-2018.

Habitat variables. The habitat variables were divided into three, separately analysed groups: nest tree, nest site and macrohabitat (see Table 1.3.1.). In the cases when the same Common Buzzard nest was occupied for several years in the same period, only one occupancy of a nest was used as sample unit for that period.

The habitat variables Nos. 3-10 (see Table 1.3.1.) are described in the Habitat data section of the chapter 1.2. Mature stands in macrohabitats were selected according to the age limits of mature trees, covered in the Forest Felling Rules (oak \geq 121-year-old; birch, black alder, lime (*Tilia cordata*), hornbeam (*Carpinus betulus*) \geq 61-year-old; grey alder (*Alnus incana*), willow (*Salix sp.*) \geq 31-year-old; common aspen \geq 41-year-old; spruce \geq 71-year-old; pine, ash, elm (*Ulmus glabra*) \geq 101-year-old). The stand data were obtained from the databases of years 2003 and 2017 of the State Forest Cadastre of the Republic of Lithuania. The data source of geo-referential spatial data sets at scale 1:10000 and CORINE land cover database – geoportal.lt.

Control stands. Control stands in Part B of the Kaišiadorys forests' study area were generated based on the same criteria as specified in the Selection of control stands section of Chapter 1.2. Points for this analysis were generated into stands at least 45 years and 55 years old for periods of years of 2002-2004 and 2017-2018, respectively, based on the youngest stands used by Common Buzzard for nesting in these periods. This created two sets of mature control stands for years 2002-2004 (n = 37), according to the data of the State Forest Cadastre (2003), and for years 2017-2018 (n = 28), according to the data of the State Forest Cadastre (2017).

Statistical data analysis. The Chi-square method was used to determine the homogeneity of the Common Buzzard nest tree

Table 1.3.1. Variables used and the sources of their data in the comparative analysis of Common Buzzard habitats, occupied in the years 2002 and 2017. Abbreviations: State Forest Cadastre – State Forest Cadastre of the Republic of Lithuania, GDR10 – Geo-referential spatial data set at scale 1:10000, CORINE – CORINE land cover database.

No.	Habitat variable	Study level	Data source
1	Nest tree species	Nest tree	Fieldwork
2	Age of the stand, years	Nest site	State Forest Cadastre (2003, 2017)
3	Soil humidity of the stand (1 to 5)	Nest site	State Forest Cadastre (2003, 2017)
4	Soil fertility of the stand (1 to 5)	Nest site	State Forest Cadastre (2003, 2017)
5	The proportion of oak in the stand	Nest site	State Forest Cadastre (2003, 2017)
6	The proportion of birch in the stand	Nest site	State Forest Cadastre (2003, 2017)
7	The proportion of aspen in the stand	Nest site	State Forest Cadastre (2003, 2017)
8	The proportion of spruce in the stand	Nest site	State Forest Cadastre (2003, 2017)
9	The proportion of black alder in the stand	Nest site	State Forest Cadastre (2003, 2017)
10	The proportion of pine in the stand	Nest site	State Forest Cadastre (2003, 2017)
11	The proportion of mature stands (%) in	Macrohabitat	State Forest Cadastre (2003, 2017)
	macrohabitat forests		
12	Shortest distance to the road, m	Macrohabitat	GDR10
13	Shortest distance to the body of water, m	Macrohabitat	GDR10
14	Shortest distance to the forest edge, m	Macrohabitat	State Forest Cadastre (2003, 2017)
15	Shortest distance to the arable land, m	Macrohabitat	CORINE (2000, 2018)
16	Shortest distance to the pasture, m	Macrohabitat	CORINE (2000, 2018)

species in the years of 2002 and 2017 by comparing the percentage of distribution of oak, birch, aspen, spruce, black alder and pine within these periods.

Generalized linear models (GLMs) (binomial distribution, logit link function) were used for comparative analysis of Common Buzzard habitats, as well as between mature control stands during different periods. For these comparisons, three sets of models have been compiled using the same explanatory variables (i.e., Nos. 2-9 in Table 1.3.1.) and all their combinations, with different dependent variables, were included. First models group included a dependent variable consisting of mature control stands in the year 2002 (value – 0) and nest sites of Common Buzzard in the year 2002 (value – 1). The second models group included the dependent variable consisting of mature control stands in the year 2017 (value – 0) and Common Buzzard nest sites in the year 2017 (value – 1). The third model group included the dependent variable consisting of mature control stands in the year 2002 (value – 0) and mature control stands in the year 2017 (value – 1).

For the comparison of macrohabitats, another three sets of models have been compiled analogously using the same three dependent variables as desribed above and the explanatory variables Nos. 10-16 listed in Table 1.3.1.

Before the GLM analysis, explanatory variables were tested for pairwise correlations (Pearson's correlation) by analysing only the control stands of years 2002 and 2017. Strong correlations (\geq 0.6 or \leq -0.6) were found for the proportion of black alder and the soil humidity of the stand, as well as between the proportion of pine and the soil fertility of the stand. As a result, the proportions of black alder and pine in the stands were removed from further analysis.

Model selection was based on the Akaike information criterion adjusted for small samples (AICc), Δ AICc (only models with Δ AICc \leq 2 were selected) and Akaike weight (calculated for subset Δ AICc \leq 2 models). For subset of models with a similar weights, the model averaging procedure was performed to determine the relative

importance values (RIV) of explanatory variables. Coefficients of determination were also calculated for all models included in subset. Confidence interval (CI) is provided in the graphs shown in the Results chapter.

1.4 Methods of the experiment for determining the response of Common Buzzard to White-tailed Eagle

The experiment was performed in the year 2018 to determine the Common Buzzard (mesopredator) brood defence behaviour towards superpredator White-tailed Eagle in the vicinity of nests. The experiment was performed in the Kaišiadorys forests (inhabited by the White-tailed Eagle since ca. 1995) and the Biržai forest (uninhabited by the White-tailed Eagle). In both areas, the experimental groups consisted of 14 pairs of the Common Buzzard that occupied nests for the breeding season. The occupancy of these nests was determined throughout April and May of 2018 (in the Biržai forest, occupancy was determined by the ornithologist Saulis Skuja, and in the Kaišiadorys forests – by A. Kamarauskaitė).

The course of the experiment. At the nest of each pair of the Common Buzzard, the dummy of a perching White-tailed Eagle was displayed for thirty minutes together with a voice playback (according to Lourenço et al., 2011). The dummy was placed at a distance of 17-115 m from the nest (distance was measured using the Garmin Oregon 600 GPS receiver); the distance depended on the characteristics of the stand. The dummy was placed at the height of one metre from the ground (on the tripod) (Lourenco et al., 2011) in the area, thereby providing good visibility to observe flying birds (Boerner, Krüger, 2008). The White-tailed Eagle dummy and the playback equipment were placed as quickly as possible in order to minimise disturbance of the Common Buzzards (Lourenço et al., 2011). The dummy was transported under cover and was uncovered at the site of the experiment, only after all the equipment had been installed and immediately before the observer went to the cover. The observer (A. Kamarauskaitė) was wearing a body and face covering

camouflage outfit throughout the experiment. At the time of recording the behaviour of the buzzards, the observer was hiding not far from the dummy in order to minimize visibility, while still ensuring a clear view of the dummy and the surrounding environment.

The recorded voice of the White-tailed Eagle (male) was used in the experiment (White-tailed Eagle (Haliaeetus albicilla), Terje Kolaas, XC338144), access: www.xeno-canto.org/338144. The first 15 seconds of this record was used. Link to licence: https://creativecommons.org/licenses/by-nc-nd/4.0/. The playback calls of the White-tailed Eagle was played for 15 minutes from the start of the experiment on the same volume of the speakers (Marshall Kilburn), while being placed under the dummy to attract the attention of Common Buzzard to the White tailed-Eagle as a hostile intruder (Boerner, Krüger, 2008). Registration of the behaviour of Common Buzzard was started only after the playback calls of the White-tailed Eagle had begun (Boerner, Krüger, 2008). The response behaviour of Common Buzzard was registered by one observer (A. Kamarauskaitė) for 30 minutes. Visits in random order to the nest sites were carried out from 8 a. m. to 9 p. m.

The treatment with the White-tailed Eagle dummy was conducted over three stages during the breeding season at each Common Buzzard pair nest: Stage I - the second half of incubation (hereinafter the early stage); Stage II - late incubation - recently hatched nestlings (hereinafter the middle stage); and Stage III - 2-3 week old nestlings changing down feathers to the feather body cover (hereinafter the late stage).

During the experiment the following variables were recorded: the time of the Common Buzzard's first and last response, the number of alarm calls, the number and time of attacks at different heights (i.e., <5 m; <10 m; >10 m – below trees; and above trees), the number of adult birds responding, in addition to other types of activities of the Common Buzzard. Following this, the responses of the Common Buzzard to the predator's dummy were scored (response scale):

- 0 no response;
- 1 unexpressed response (the bird showed no signs of aggression but appeared next to the dummy);
 - 2 response by alarm calls;
 - 3 response by highly active alarm calls, on-site flights;
- 4 response by alarm calls, on-site flights, attacks on the dummy (at a distance of more than 10 m to the dummy);
- 5 response by alarm calls, on-site flights, attacks on the dummy (at a distance of below than 10 m to the dummy).

The experiment was performed under favourable weather conditions: without rain and without excessive wind speeds. In the event of highly aggressive attacks with direct contact to the dummy, the experiment was terminated (Lourenço et al., 2011), to avoid the risk of injury to birds following contact with the dummy and to prevent damage to the dummy itself. The experiment was also terminated when the weather deteriorated; for instance, in the event of rainfall.

The number of nestlings in the brood and the success of breeding were determined by A. Kamarauskaitė in early July of 2018, as the nestlings were already standing in a nest or had started to fly, while still frequently visiting the nest or its vicinity.

Statistical data analysis. Only the visits where breeding was successful during the experiment have been used (i.e., incubation was happening) or where nestlings were present in the nest at the time. The following data was removed from the analysis: three pairs in the Biržai forest (no signs of clutches or broods), one treatment in Stage III in the case of dead nestlings in the Kaišiadorys forests and one treatment in Stage I in the case where distance to the dummy in the Kaišiadorys forests was too large. The approximate time of death of nestling was determined by comparing the plumage development of nestling remains found close to the nest with the plumage development observed in other nestlings during visits. The final sample consisted of 73 visits and 25 pairs (14 in the Kaišiadorys forests and 11 in the Biržai forest).

The experiment data was analysed using GLMMs (binomial distribution, logit link function). Two sets of models were constructed to analyse the Common Buzzard's response to the White-tailed Eagle. In the first model set, the dependent variable was the reaction by alarm calls $(0 - if no or single call observed, 1 - if <math>\geq$ 3 calls observed). In the second set, the dependent variable was the reaction by attacks (0 - no attacks performed, 1 - at least one attackobserved). The fixed explanatory variables (and all combinations between them) that were included in both sets of models where: the distance from the Common Buzzard nest to the nearest White-tailed Eagle nest, the time of day (morning – 8 a.m.-10 a.m., daytime – 10.01 a.m.-4.30 p.m., evening - 4:31-9 p.m.), the distance from the dummy to the Common Buzzard nest, and the stage of the breeding season (I, II, III, see above for description). All these models included the same random effect - the identity of the Common Buzzard pair.

GLMs were used to determine if the size of the brood (one nestling or ≥ 2 nestlings) and the number of responding adults (one or two birds) (explanatory variables) could explain the response scale (dependent variable) of the Common Buzzards.

Models have been selected using AICc, $\Delta AICc \leq 2$ and model weights. The effect of explanatory variables on the dependent variable was determined by calculating R^2 adapted to GLMMs ($R^2_{\rm GLMM}$). The Confidence Interval (CI) is provided in the graphs shown in the Results chapter..

2. RESULTS

2.1 Habitat preference of the Common Buzzard

A subset of five GLMs with $\Delta AICc \leq 2$ (see Table 2.1.1.) showed that the nest sites of the Common Buzzard differed from the control stands. The probability that the stand would be occupied by the Common Buzzard increases as the age of the stand increases, as well as when the proportion of oak, birch, aspen and black alder in the stand increases, while the humidity of the forest stand soil decreases (see Figure 2.1.1.).

Fig. 2.1.1. The comparison of the Common Buzzard nest sites (B) (n = 80) with the the control stands (C) (n = 80) by the age of the stands, the humidity of the soil, and the proportion of oak, birch, aspen, and black alder in the stand. Mean 95%CI Abbreviations: CI – confidence interval.

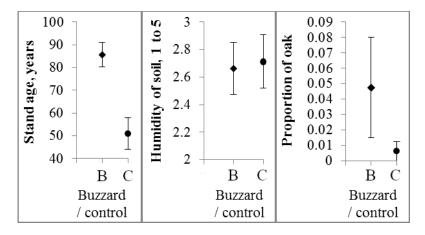
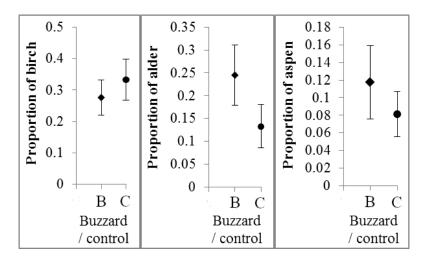


Fig. 2.1.1. (continued).



The Common Buzzard habitats in the Kaišiadorys forests and the Biržai forest differed in the per cent distribution of the nest tree species that were used ($\chi^2 = 73.46$, df = 4, p < 0.0001) and the nest platform placement in trees ($\chi^2 = 32.2$, df = 2, p < 0.0001). In the Kaišiadorys forests, Common Buzzards mainly built their nests in oaks and on side branches, whereas in the Biržai forest, nests were built mainly in birches and on trunk forks (see Figure 2.1.2.).

Between the study areas, the habitats did not differ in the circumference of the nest trees trunk and the height of the nest platform from the ground. The highest-rated model in the model set was a null model (Δ AICc = 0.00, weight – 0.53).

A subset of eight models ($\Delta AICc \leq 2$) obtained by comparing the Common Buzzard nest sites in the Kaišiadorys forests and the Biržai forest showed that the nest sites differed between the study areas in all of the variables studied, except in the variable representing the age of the stands (see Table 2.1.1.).

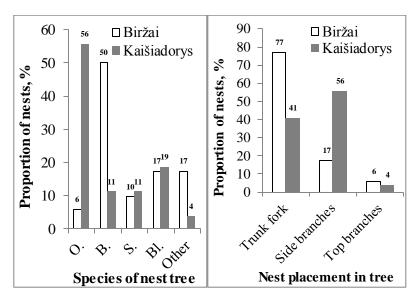
Table 2.1.1. Summaries of subsets (\triangle AICc \le 2) of models for comparison of the Common Buzzard nest sites with control stands and Common Buzzard nest sites in the Kaišiadorys forests and the Biržai forest. "+" and "-" refer to the increase and the decrease in the variable values of Common Buzzard nest sites, compared to the control stands and in values of Common Buzzard nest sites in the Kaišiadorys forests, and further compared to the Common Buzzard nest sites in the Biržai forest. Abbreviations: Age – age of the forest stand, O., B., A., S., Bl. – the proportion of oak, birch, aspen, spruce, black alder in stand composition, Fertility, Humidity – fertility, the humidity of stand soil, Forest edge – distance to the forest edge.

Models		Explanatory variables								Weight
Buzzard vs. control stand	Age	O.	B.	A.	Fertility	Humidity S	S. Bl.			
Model No. 1	+	+	+	+		_	+	37	0.00	0.32
Model No. 2	+	+	+	+		- +	+	38	0.13	0.30
Model No. 3	+	+	+	+	+	_	+	38	1.75	0.13
Model No. 4	+	+	+	+	+		+	37	1.83	0.13
Model No. 5	+	+		+		_	+	36	1.94	0.12
RIV	1.00	1.00	0.88	1.00	0.26	0.87 0	.30 1.00			

Table 2.1.1. (continued).

Models	odels Explanatory variables								ΔAICc	Weight
Kaišiadorys vs. Biržai	O.	B.	A.	Fertility	Humidity	Bl.	Forest edge			
Model No. 1	+			_	+		_	55	0.00	0.18
Model No. 2	+		+	_	+		_	58	0.03	0.18
Model No. 3	+				+		_	52	0.41	0.15
Model No. 4	+	_		_	+		_	58	0.73	0.13
Model No. 5	+		+		+		_	55	1.08	0.11
Model No. 6	+		+	_	+	+	_	60	1.40	0.09
Model No. 7	+	_	+	_	+		_	60	1.48	0.09
Model No. 8	+	_			+		_	55	1.50	0.09
RIV	1.00	0.30	0.46	0.66	1.00	0.09	1.00			

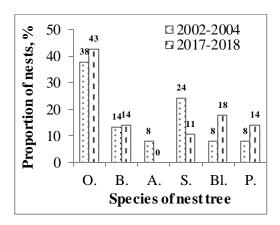
Fig. 2.1.2. The comparison of Common Buzzard nest tree species and nest platforms placement in the Kaišiadorys forests (n = 27) and in the Biržai forest (n = 52). Abbreviations: O. – oak, B. – birch, E. – spruce, Bl. – black alder, Other – aspen, pine, ash, maple.



2.2 Comparison of Common Buzzard habitats occupied in 2002 and 2017 in the Kaišiadorys forests

Nest tree species level. Common Buzzard nests that were occupied in the year 2002 (n = 37) and 2017 (n = 28) significantly differed in the proportions of nest tree species ($\chi^2 = 32.7$, df = 5, p < 0.0001). The greatest differences were observed in the proportions of spruce and black alder. In 2017, nesting in spruces decreased by 13% and increased by 10% in black alders, compared to the proportion of nests occupied in 2002. No nests in the aspens were found in 2017, compared to the nest trees in 2002 (see Figure 2.2.1.)

Fig. 2.2.1. Common Buzzard in the year 2002 and year 2017 statistically significantly differed in the per cent distribution of nest tree species occupied. Abbreviations: O. – oak, B. – birch, A. – aspen, S. – spruce, Bl. – black alder, P – pine.



Nest site level in the year 2002. As a result of the GLMs analysis, a set of ten models with a $\Delta AICc \leq 2$ was obtained by comparing the Common Buzzard nest sites occupied in 2002 with the mature control stands of that time (see Table 2.2.1.). The explanatory variables with the highest RIVs in the models set were the proportion of aspen in the stand (RIV 0.91) and the fertility of the stand soil (RIV 0.93). Coefficients of determination for models varied between 5% and 14%. These results indicated that the Common Buzzard nest sites in 2002 tended to differ from mature control stands, in terms of the higher proportion of aspen in the stands and higher soil fertility of the stands.

Macrohabitat level in the year 2002. According to statistical analyses, the macrohabitats of the Common Buzzard did not differ from the environment surrounding mature control stands in 2002, because the null model was the highest-ranked one (i.e., $\Delta AICc = 0.00$).

Nest site level in the year 2017. The results of the statistical analysis revealed that the Common Buzzard nest sites that were

occupied in 2017 did not differ from mature control stands. The highest ranked model was a null model ($\Delta AICc = 0.00$).

Macrohabitat level in the year 20017. A set of three GLMs with $\Delta \text{AICc} \leq 2$ was obtained by comparing the macrohabitats of the Common Buzzard with the environment surrounding mature control stands in 2017 (see Table 2.2.1.). The explanatory variables with the highest RIVs in this model set were the distances to the nearest pasture (RIV 0.78) and to the nearest road (RIV 1.00). Coefficients of determination (R^2) for these models supported by the data ranged between 7% and 15%. Based on the results, the Common Buzzard macrohabitats in 2017 tended to differ from mature control stands by the smaller distance to the pasture (p = 0.07 in average model) and significantly by a greater distance to the road (p = 0.04 in average model).

Mature control stands in the years 2002 and 2017. When comparing the mature control stands in the year 2002 with the mature control stands in the year 2017, a set of six models with $\Delta AICc \leq 2$ was obtained (see Table 2.2.2.). Althogether, four variables were included in the model set, but the highest RIV (i.e., 1.00) was found for the age of the stand. According to results, mature control stands in the year 2017 were older compared with mature control stands in 2002 (p = 0.04 in average model) (see Figure 2.2.2.).

Macrohabitat level in the years 2002 and 2017. When comparing the environment surrounding mature control stands in 2002 and in 2017, a set of six models with $\Delta AICc \le 2$ was obtained (see Table 2.2.2.). The highest RIV (i.e., 1.00) was found for the distance to the nearest pasture. Results indicate, that in 2017, the mature stands were more distant from the pastures compared to the mature stands in 2002 (p = 0.04 in average model) (see Figure 2.2.2).

In summary, when comparing the nest sites of the Common Buzzard with the mature control stands, it was found that, as the mature stands grew older in the forest landscape, the age of the stands occupied by the Common Buzzard increased accordingly.

However, the Common Buzzard maintained a similar distance to the nearest pasture in the year 2017, as it did in 2002, although in the year 2017 mature stands were available further away from pastures compared to the situation in 2002 (see Figure 2.2.2.).

Fig. 2.2.2. Changes in Common Buzzard habitats (B) (diamond) and mature control stands (B) (circle) in years 2002 (grey) and years 2017 (black). Abbreviations: Distance to pasture – distance to nearest pasture, CI – confidence Mean 95%CI interval.

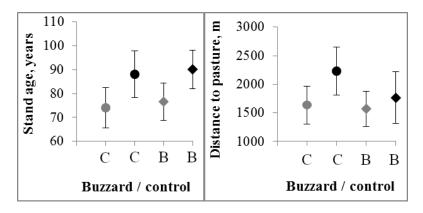


Table 2.2.1. Summaries of models for comparison of the Common Buzzard habitats with mature control stands in the Kaišiadorys forests in the years 2002 and 2017. "+" and "-" mean the increase or decrease in the variable values of the Common Buzzard habitats compared to mature control stands. Abbreviations: Age – age of the forest stand, O., B., A., S. – proportion of oak, birch, aspen, spruce in stand composition, Fertility, Humidity – fertility, humidity of stand soil, Distance to arable land, Distance to pasture, Distance to road – distance to the nearest arable land, pasture, road.

Buzzard vs.		Explanatory variables of nest site R^2								Weight
mature control stand in 2002	Age	O.	B.	A.	Humi- dity	Ferti- lity	S.	_		
Model No. 1				+		+		10	0.00	0.173
Model No. 2	+			+		+		12	0.18	0.158
Model No. 3	+			+	+	+		14	1.08	0.101
Model No. 4	+			+		+	_	14	1.30	0.090
Model No. 5				+	+	+		11	1.30	0.090
Model No. 6						+		5	1.34	0.089
Model No. 7			_	+		+		11	1.43	0.085
Model No. 8				+		+	_	11	1.68	0.075
Model No. 9				+				5	1.69	0.074
Model No. 10		+		+		+		10	1.97	0.065
RIV	0.35	0.06	0.08	0.91	0.19	0.93	0.17			

Table 2.2.1. (continued).

Buzzard vs.	Explanatory	variables of mac	R^2	ΔAICc	Weight	
mature control	Distance to arable	Distance to	Distance to	_		
stand in 2017	land	pasture	road			
Model No. 1		_	+	13	0.00	0.504
Model No. 2	+	_	+	15	1.18	0.279
Model No. 3			+	7	1.69	0.216
RIV	0.28	0.78	1.00			

Table 2.2.2. Summary of models for comparing mature control stands in 2002 and in 2017 in the Kaišiadorys forests. "+" and "-" mean the increase or decrease in the variable values of the mature control stands in 2017 compared to mature control stands in 2002. Abbreviations: Age – age of the forest stand, B., S. – the proportion of birch and spruce in the stands, Humidity – the soil humidity of the stand, Mature stands – the proportion of mature stands from all the stands in macrohabitat (i.e., within 1 km radius), Distance to water body, Forest edge, Distance to arable land, Distance to pasture, Distance to road – the distance to the nearest water body, to the forest edge, to the arable land, to the pasture and to the road.

Mature control stand in 2017	Explanatory variables of nest site				R^2	ΔAICc	Weight
vs. mature control stand in 2002	Age	B.	Humidity	S.			
Model No. 1	+			_	11	0.00	0.254
Model No. 2	+				7	0.41	0.207
Model No. 3	+		+		10	0.78	0.172
Model No. 4	+	+			9	1.23	0.137
Model No. 5	+		+	_	12	1.25	0.136
Model No. 6	+	+		_	11	1.97	0.095
RIV	1.00	0.23	0.31	0.48			

Table 2.2.2. (continued).

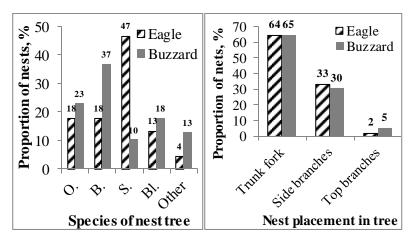
Mature control	Explanatory variables of macrohabitat						R^2	ΔAICc	Weight
stand in 2017 vs. mature control stand in 2002	Mature stands	Distance to arable land	Distance to pasture	Distance to road	Forest edge	Distance to water body	_		
Model No. 1			+				8	0.00	0.283
Model No. 2			+	_			9	0.77	0.193
Model No. 3			+		_		9	1.35	0.144
Model No. 4	_		+				9	1.51	0.133
Model No. 5			+				8	1.64	0.124
Model No. 6		_	+			+	8	1.67	0.123
RIV	0.13	0.12	1.00	0.19	0.14	0.12			

2.3 Comparison of habitats of the Common Buzzard and the Lesser Spotted Eagle

The Common Buzzard and the Lesser Spotted Eagle significantly differed by the per cent distribution of the nest tree species occupied ($\chi^2 = 41.59$, df = 4, p < 0.0001). The Common Buzzard built 60% of all its nests in birches and oaks, and the proportion of any other tree species was less than 20%. Meanwhile, the Lesser Spotted Eagle has built almost half of its nests in spruces and no more than 18% in any other tree species (see Figure 2.3.1.).

However, there was no statistically significant difference between the bird species according to the placement of the nest platform in the tree ($\chi^2=1.43$, df = 2, p = 0.49) (see Figure 2.3.1.). Neither did the two species differ according to the circumference of the nest tree trunk and the height of the nest from the ground (the null GLMM: $\Delta AICc=0.00$).

Fig. 2.3.1. The nest tree species and placement of the nest platform in the tree of the Common Buzzard (n = 79) and the Lesser Spotted Eagle (n = 45). Abbreviations: O. – oak, B. – birch, S. – spruce, Bl. – black alder, Other – aspen, ash, pine, maple.



Four models were supported by the data ($\Delta AICc \leq 2$) as a result of the GLMs analysis that compared the Common Buzzard and the Lesser Spotted Eagle nest sites (see Table 2.3.1.). Following the models averaging procedure, the highest RIVs were determined for the soil humidity of the stand (1.00), the proportion of black alder in the stand (0.81) and the nearest distance to the forest edge (1.00).

The nest sites of the Common Buzzard differed from the nest sites of the Lesser Spotted Eagle in lower soil humidity of the stand (average model p=0.02), and the higher proportion of black alder in the stands, as well as with greater distance to the forest edge (average model p<0.0001) (see Figure 2.3.2.).

Fig. 2.3.2. The soil humidity of the stand, proportion of black alder in the stands and distance to the forest edge in the nest sites of the Common Buzzard (B) (n = 80) and the Lesser Spotted Eagle (E) (n = 47). Abbreviations: CI – Mean 95%CI confidence interval.

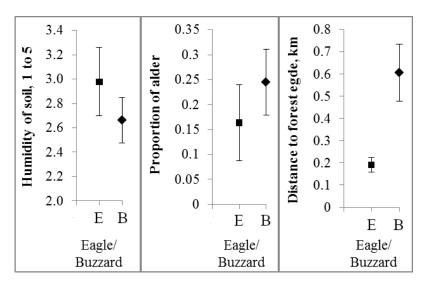


Table 2.3.1. Summaries of models subset (\triangle AICc ≤ 2) for comparison of Common Buzzard nest sites with the nest sites of Lesser Spotted Eagle. "+" and "-" mean the increase and decrease of the variable values of Common Buzzard nest sites relative to the nest sites of the Lesser Spotted Eagle. Abbreviations: B., Bl. – the proportion of birch and black alder in the stands, Humidity – soil humidity of the stand, Fertility – soil fertility of the stand, Forest edge – distance to the forest edge.

Models	Explar	Explanatory variables						Weight
Buzzard vs. Eagle	B.	Fertility	Humidity	Forest edge	Bl.			
Model No. 1			_	+	+	28	0.00	0.448
Model No. 2			_	+		25	1.70	0.192
Model No. 3		_	_	+	+	28	1.81	0.181
Model No. 4	+		_	+	+	28	1.83	0.180
RIV	0.18	0.18	1.00	1.00	0.81			

No differences have been established between the Common Buzzard nest sites and control stands in Biržai forest by distance to the nearest occupied Lesser Spotted Eagle nest (the highest-ranked model was a null model, $\Delta AICc = 0.00$, weight -0.70). This shows that the Common Buzzard did not avoid the Lesser Spotted Eagle when occupying the nest sites in the Biržai forest.

The analysis of the average nearest neighbour showed that the distribution of the Common Buzzard pairs in the Biržai forest corresponds to the random distribution (z-score = 0.97, p = 0.33) (mean distance between pairs 1.28 km \pm 0.52 (SD), minimum - 0.5 km, n = 53). The distribution of the Lesser Spotted Eagle pairs in the Biržai forest had a trend of regular distribution (z-score = 1.77, p = 0.08) (mean distance between pairs 2.01 km \pm 0.97 (SD), minimum - 0.65 km, n = 26).

2.4 The response of the Common Buzzard to the top predator White-tailed Eagle

The Common Buzzard responded by alarm calls to the White-tailed Eagle dummy on 49% of visits (n = 73). The average number of calls per visit with alarm calls was 166 ± 146 (SD). In 10% of the visits, the response to the dummy was recorded but without alarm calls. In 22% of the visits, the buzzards attacked the dummy of the White-tailed Eagle (average number of attacks was 6 ± 5 (SD)). Eighty-four per cent of Common Buzzard pairs studied (n = 25) responded with alarm calls in at least one of the stages of the experiment, while 36% of pairs responded with attacks.

The pairs of the Common Buzzard, with one nestling in brood, were not statistically significantly different from the pairs with 2-3 nestlings, according to the response scale towards the dummy of the White-tailed Eagle (see Table 2.4.1.).

The response scale of the Common Buzzard towards the predator dummy was statistically significantly different between the visits when reacted only one member of Common Buzzard pairs (40% of visits with response observed; n = 43) and both members (60%) (see

Table 2.4.1.). During the visits, when both members of the pair took part in the brood defence behaviour, the response scale to the White-tailed Eagle dummy was an average 1.6 times greater compared to cases when only one bird participated.

Table 2.4.1. Summaries of generalized linear models (GLMs) to determine the relationship between the response scale of the Common Buzzard pairs, the number of nestlings, and the number of adult birds involved in the response

Models	Explanatory variable Number of nestlings					
Dependent variable	Effect	SE	p			
Response scale	-0.14	± 0.19	0.46			
Models	Explanatory variable					
Models	Number	of responding	g adult birds			
Dependent variable	Effect	SE	р			
Response scale	0.47	± 0.17	0.006			

Two models ($\triangle AICc \le 2$) were obtained from an analysis of the generalised linear mixed effect models to investigate what may have influenced the response of the Common Buzzard to the dominant predator by alarm calls (see Table 2.4.2.). The highest-ranked model $(\Delta AICc = 0.00, weight - 0.56)$ included only one fixed variable, the breeding stage. The second model (\triangle AICc = 0.49, weight - 0.44) included two fixed variables, the breeding stage and the time of day. According to the best model, the highest probability of a Common Buzzard responding to the White-tailed Eagle dummy by alarm calls is when nestlings are at a late stage of breeding (GLMM: p = 0.008), rather than when they are in the early stage of breeding. However, there was no significant difference between the early and middle stages within the breeding period (GLMM: p = 0.33). The breeding stage explained 13% (i.e., marginal R^2) of alarm call probability variation. The second model, additionally to the aforementioned variable, indicated that the probability of response by alarms calls during evening hours tended to be higher compared to morning hours

(GLMM: p=0.08). However, the probability of response was similar between morning and daytime hours (GLMM: p=0.42). The marginal R^2 for this second ranked model is 21%. In both models, a Common Buzzard pair identity was included as a random variable, and in both models, conditional R^2 was greater than 50%. This conditional coefficients of determination indicated that the identity of the Common Buzzard pair had an important influence on the observed response of the Common Buzzard to a dominant predator by alarm calls.

Table 2.4.2. Summaries of GLMMs subsets (\triangle AICc \le 2) to estimate effect of the breeding stage and time of the day to the probability of the Common Buzzard response by alarm calls or attacks on the White-tailed Eagle dummy. "+" – explanatory variable included in the model. Abbreviations: m – marginal R^2 , c – conditional R^2 .

Models	Explanatory variables		R^2		ΔAICc	Weight
Response by alarm calls	Breeding stage	Time of day	m	c		
Model No. 1	+		13	54	0.00	0.561
Model No. 2	+	+	21	60	0.49	0.439
Response by attacks						
Model No. 1	+	+	10	99	0.00	1.00

The probability that the Common Buzzard will attack the White-tailed Eagle dummy was explained by the one model supported by the data ($\Delta \text{AICc} \leq 2$). This model included the breeding stage and the time of the day as explanatory fixed variables (see Table 2.4.2.). Based on the results of this model, the probability of attacks was higher in the late breeding stage when compared to the early stage (GLMM: p=0.04), while it also tended to be higher in the middle breeding stage compared to the early breeding stage (GLMM: p<0.1). The probability of attacks tended to be higher in the daytime (GLMM: p=0.055) and evening (GLMM: p=0.057) compared to morning hours. However, as the conditional (90%) and marginal (10%) R^2 indicates, the identity of the pair of the Common Buzzards

had the most significant influence on the occurrence of attacks on the dummy of the top predator.

3. DISCUSSION

The importance of mature stands for Common Buzzards in nest sites that was found in this study has also been observed in other studies (Selås, 1997 (Norway); Bielański, 2006 (Poland); Zuberogoitia et al., 2006 (Spain); Väli, 2015 (Estonia)). In general, mature forests are considered to be a vital component of breeding habitats of birds of prey (Poirazidis et al., 2007), including the widespread Common Buzzard.

Plasticity of the Common Buzzard in breeding habitats was also observed in previous studies in Lithuania (Skuja, Budrys, 1999; Drobelis, 2004). Habitat plasticity was also observed in some other diurnal birds of prey such as Hen Harrier (*Circus cyaneus*) (Paprocki et al., 2015) and Osprey (*Pandion haliaetus*) (Monti et al., 2018).

The Common Buzzard is the most common and abundant species of birds of prey in Europe (Panek, Hušek, 2014). It is likely that the plasticity in breeding habitat use is one of the reasons for the high numbers of the Common Buzzard populations across range.

The proportion of the nest tree species that was used has shifted between analyzed periods. The number of nests in oaks has increased in the year 2017, thereby reflecting an increased importance of the large nest trees for the Common Buzzard. According to a study conducted in Lithuania in the years 1995 and 2009, the number of Black Stork nests in oaks increased from 67% to 75%, although oaks were rare in Lithuanian forests during both investigation periods (Treinys et al., 2016). Barrientos, Arroyo (2014) found that the diameter of the nest tree was the most crucial parameter for the Common Buzzard, the Short-toed Snake-eagle (*Circaetus gallicus*), the Northern Goshawk (*Accipiter gentilis*) and the Booted Eagle (*Aquila pennata*), thereby leading the species to prioritize trees of larger circumference.

The strong overlap in breeding habitats between the Common Buzzard and the Lesser Spotted Eagle was found in this study. Furthermore, the Common Buzzard did not avoid the larger in body

size Lesser Spotted Eagle (1-2.2 kg (www.hbw.com)) when occupying the nests. These findings may best explain that both species have been observed to be occupying and breeding in each other's nests (Drobelis, 2004; Skuja, Budrys, 1999; Väli, 2003).

The return of the top predator White-tailed Eagle to the area did not cause behavioural changes for the mesopredator, the Common Buzzard, because the distance to the nearest nest site of the superpredator did not explain the brood defence behaviour of the mesopredator. These results are the opposite of what was found with the Common Buzzard and the Eurasian Eagle-Owl (superpredator), due to the finding that when the latter recolonised the area, the intensity of Common Buzzard's aggression towards this top predator increased (Mueller et al., 2016). The White-tailed Eagle prey only on the Common Buzzard's nestlings, but the Eurasian Eagle-owl prey on both, adults and nestlings. This finding may explain the difference in the Common Buzzard's behavior towards the two superpredator species.

The increase in intensity of the Common Buzzard's brood defence behaviour towards the superpredator's advancement during breeding season has also been determined by Krüger (2002). However, Boerner and Krüger (2008) did not find that the age of the nestlings influenced the intensity of aggression of the Common Buzzard towards the Eurasian Eagle-Owl. The results of the experiment indicated that Common Buzzards distributed the efforts of rearing nestlings based on a cost-benefit ratio, i.e. weighing the likelihood of being injured or dying in a collision with a large predator with the prospect of reproduction in the future, as well as the age of nestlings (Krüger, 2002).

The number of Common Buzzard nestlings did not affect the intensity of aggression towards the predator in adult birds, as shown by the results of this study and the studies carried out by Boerner and Krüger (2008) and Krüger (2002). The opposite situation was observed with Ural Owls (*Strix uralensis*), as the pairs with larger clutches were more aggressive (Kontiainen et al., 2009).

The difference in the response of Common Buzzard pairs to the White-tailed Eagle may have been due to factors such as different colour morphs, age, experience and temperament of individuals. Boerner and Krüger (2008) found that the scale of aggression of the Common Buzzard to the superpredator varied among the morphs. Moreover, Møller and Nielsen (2014) found that the nest protection intensity of the Northern Goshawk (*Accipiter gentilis*) females depended on their age.

Individual animal behaviour is relatively inflexible (Kontiainen et al., 2009). Animals often exhibit stable patterns of aggressiveness, courage and activity in different environments (van Oers et al., 2003; Bell, 2007; Réale et al., 2007; Kontiainen et al., 2009). Furthermore, temperament-restricted behavioural plasticity can lead to an individual being characterised by a particular type of behaviour in different situations (Bell, 2007).

CONCLUSIONS

- The breeding habitat preferences of Common Buzzard are determined by age, tree species composition and soil humidity of the stand.
- 2. The breeding habitats of the Common Buzzard located in the different landscapes did not differ only in the age of the stands (mean 86 years \pm 25 (SD)). While the tree species composition of the stand, humidity and fertility of the soil and the distance to the forest edge depended on the forest landscape characteristics.
- 3. As the landscape changed, the plasticity of the nest tree use and nest site characteristics, but not nest sites location in the landscape, was observed.
- 4. The Common Buzzard does not avoid the Lesser Spotted Eagle when choosing nest sites.
- 5. The Common Buzzard and the Lesser Spotted Eagle used the same tree species for nesting but at different frequencies. Other nests, nest trees properties and tree species composition of the stands were similar between raptors. Nest sites differed in the humidity of the soil and distribution in forests; nest sites of buzzard were distributed throughout the forest, in drier soils, and eagles nested only close to the forest edge, in stands on wetter soils.
- 6. The brood defence behaviour of the Common Buzzard towards the White-tailed Eagle did not differ between the areas inhabited and uninhabited by this superpredator.
- 7. The intensity of the Common Buzzard's brood defence behaviour to the White-tailed Eagle is mostly explained by individual differences, the age of the nestlings and the number of responding adults of the pair.

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LIST OF PUBLICATIONS

Scientific publications:

- 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(2): 224–233.
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