CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

FACULTY OF ENVIRONMENTAL SCIENCES

DEPARTMENT OF ECOLOGY

Effects of environmental conditions on the distribution and abundance of the boreal owl in the Czech Republic

Vliv environmentálních podmínek na distribuci a početnost sýce rousného v České republice

DISSERTATION

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CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Environmental Sciences

Ph.D. THESIS ASSIGNMENT

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Thesis title

Effects of environmental conditions on the distribution and abundance of the boreal owl in the Czech Republic

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Objectives of thesis

The main aim of the Ph.D. thesis is to extend our understanding of the distribution and protection of owl species in the Czech Republic, focusing on the boreal owl: the species protected by the European (No. 2009/147/EC, Annex I) and Czech (No. 114/1992 Coll.) directives. The specific aims of the thesis are:

1) to examine the effects of elevation and temperature on the distribution of the boreal owl and other owl species in the Czech Republic using atlas data;

2) to compare the use of nest boxes by the boreal owl in two study areas differed in forest structure (the Ore Mountains and Trebon Basin), considering food supply and other environmental conditions of the specific areas,

3) to examine the effects of food abundance and timing throughout the breeding season and during the day on the spontaneous vocal activity of the boreal owl;

4) to suggest recommendations for:

a) providing nest boxes as alternative nesting opportunities for the boreal owl, and

b) bioacoustic monitoring of boreal owl populations.

Methodology

The distribution of the boreal owl and other owls in the Czech Republic will be evaluated based on the data available from the Atlas of breeding birds in the Czech Republic.

The use of nest boxes will be investigated in the two study areas, the Ore Mts. and Trebon Basin. In these areas, nest boxes will regularly check (between March and July) to record all breeding activities of boreal owls and other animals. In both areas, the food supply of small mammals will be determined by spring snap trapping, and the abundance of boreal owl populations will be estimated based on acoustic monitoring conducted during the breeding season using passive acoustics units.

The proposed extent of the thesis

100 pages

Keywords

atlas data, bioacoustic monitoring, nest boxes, breeding, cavity-nesters, habitat loss, birds of prey

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Recommended information sources

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Prague on 06. 02. 2023

Declaration of originality

I hereby declare that I have independently written the dissertation entitled, Effects of environmental conditions on the distribution and abundance of the boreal owl in the Czech Republic. I have cited all the information sources used in the dissertation, which are listed at the end in the list of sources.

I am aware that my dissertation is subject to Act No. 121/2000 Coll., including copyright, rights related to copyright, and on amendments of some acts, as cited in later regulations, particularly the provisions of Section 35(3) on the use of the thesis.

I am aware that by submitting the dissertation, I agree with its publication under Act No. 111/1998 Coll. regarding universities and the change and amendments of some acts, as amended, regardless of the result of its defence.

With my signature, I also declare that the electronic version is identical to the printed version and that the data stated in the dissertation has been processed in accordance with the GDPR.

Prague, Czech Republic, February 2023   Richard Ševčík

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Abstract

Habitat loss, climate change, and the impact of other environmental factors may pose a potential risk to many species. To understand this risk, we need to monitor population distribution, abundance, and their changes. In this thesis, the combination of atlas data (*Study I*), nest-box monitoring (*Study II*), and bioacoustic monitoring (*Study III*) were used to better understand the factors driving the distribution and abundance of the boreal owl population in the Czech Republic. The most important findings are as follows; first, the Czech boreal owl population, compared to other owl species, prefers to inhabit the highest elevations characterized by cold conditions. Second, the abundance of two boreal owl populations that were monitored based on nest-box occupancy differed in the two habitat types, but it did not differ based on bioacoustic monitoring. Owls readily (8–15%) occupied nest boxes only on mountain plateaus characterized by young blue spruce (*Picea pungens*) and Norway spruce (*Picea abies*) stands, while they use nest boxes only rarely (0–1%) in mature Scots pine (*Pinus sylvestris*) forests in the lowland. Third, the frequency of sampling points in which boreal owls were recorded was higher in the year of increased prey abundance and at the beginning of the breeding season. The duration (the number of minutes per hour) of territorial vocalization of boreal owls increased in the year with a higher food supply later in the breeding season and showed two peaks during the night. The results of the presented work suggest: (1) boreal owls, compared to other species, may be most susceptible to climate changes and forest loss, (2) deployment of nest boxes and associated monitoring should be precisely considered for specific locations, (3) bioacoustic monitoring of boreal owl vocalization shows circadian and seasonal variability and changes greatly under varying food conditions, while simultaneously providing an excellent opportunity for future study. Based on the findings, experiences of my supervisor and collaborators, and a literature review, I also provide individual methodological recommendations for the placement of nest boxes for boreal owls and the monitoring of populations of this species in the Czech Republic.

Keywords: atlas data, bioacoustic monitoring, nest boxes, breeding, cavity-nesters, habitat loss, birds of prey

Abstrakt

Ztráta habitatu, změna klimatu a vliv dalších environmentálních faktorů může do budoucna představovat potenciální riziko pro mnoho druhů. Abychom tomuto riziku porozuměli, musíme monitorovat distribuci, početnost a změny v populacích sledovaných druhů. V této práci je použita kombinace atlasových dat (*studie I*), monitoringu pomocí hnízdních budek (*studie II*) a bioakustického monitoringu (*studie III*), aby se lépe porozumělo faktorům ovlivňujícím distribuci a početnost populací sýce rousného v České republice. Byly zjištěny následující nejdůležitější poznatky. Za prvé, česká populace sýce rousného v porovnání s jinými druhy sov preferuje vyšší nadmořské výšky a nízké teploty. Za druhé, početnost dvou populací sýce rousného monitorovaných na základě obsazenosti hnízdních budek se lišila mezi dvěma habitaty, ale nelišila se na základě bioakustického monitoringu. Sovy ochotně obsazovaly vyvěšené budky pouze v horských oblastech s mladými porosty smrku pichlavého (*Picea pungens*) a smrku ztepilého (*Picea abies*; 8–15 %), zatímco ve vzrostlých nížinných lesích borovice lesní (*Pinus sylvestris*) využívaly budky výjimečně (0–1 %). Za třetí, četnost nahrávacích lokalit, na kterých byl sýc rousný zaznamenán, byla vyšší v roce zvýšené početnosti kořisti a na začátku hnízdní sezóny. Délka teritoriálního houkání sýce rousného (počet minut za hodinu) se zvyšovala v roce s vyšší potravní nabídkou, později v hnízdní sezóně a během noci vykazovala dva vrcholy. Výsledky prezentované práce naznačují, že: (1) sýc rousný může být v porovnání s jinými druhy více náchylný ke změně klimatu a ztrátě lesních porostů, (2) rozmístění hnízdních budek a související monitoring je potřeba zvážit podle specifických podmínek lokalit, (3) bioakustický monitoring vokální aktivity sýce rousného poukazuje na cirkadiánní a sezónní variabilitu a na významné změny vokalizace během odlišných potravních podmínek, a současně poskytuje vynikající příležitost pro navazující výzkumy. Na základě dosažených výsledků, zkušeností mé vedoucí práce a spolupracovníků, a literární rešerše poskytuji také specifická metodická doporučení na vyvěšování hnízdních budek pro sýce rousného a monitoring populací tohoto druhu v České republice.

Klíčová slova: atlasová data, bioakustický monitoring, budky, hnízdění, doupné druhy, ztráta habitatu, dravci

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1. Introduction

Climate change, habitat loss, and modification caused by anthropogenic activities have resulted in significant species declines worldwide (Rosenberg et al. 2019, Sánchez-Bayo and Wyckhuys 2019). Studying and monitoring the effects of selected abiotic and biotic factors on the distribution and abundance of populations provides crucial information for the management and conservation of study species (Williams et al. 2002). A key problem of conservation biology is the difficulty in identifying which species are likely to be at risk in the near future. Conservation measures to prevent declining population abundance, as a rule, focus on critically endangered species, which are characterized by small population size and geographic range, while populations of common species, which can begin to decline rapidly even with relatively small changes in environmental conditions and, thus, disrupt ecosystem structure and function, are often neglected (Gaston and Fuller 2008). By using birds as bioindicators, the results of ornithological surveys can be used to assess the impacts of adverse environmental changes on species occurring in different habitat types and to study their responses to these changes (O'Connell et al. 2000, Egwumah et al. 2017).

The boreal owl (*Aegolius funereus*) is the species studied in this dissertation through the use of different monitoring types. It is a smaller species of montane forest-dwelling owl, which in the Czech Republic inhabits mainly coniferous forests in higher elevations, while it can also nest in mixed or deciduous forest stands of lower elevations (Šťastný et al. 2021). Using four mapping surveys of breeding birds in the Czech Republic, increasing abundance and distribution of this owl between map quadrants have been identified. When comparing two breeding atlases from 1973–1977 and 2014–2017, up to 43.7% increase in the occupancy of map quadrants by the boreal owl was recorded (Šťastný et al. 2021). On the other hand, rapid declines in boreal owl populations in response to the influence and change of environmental conditions such as global warming and habitat loss or modification have been reported by many studies in Southern and Northern Europe (e.g., Solonen 2004, Hipkiss et al. 2013, Kouba et al. 2020, Shurulinkov et al. 2021). Therefore, it is necessary to find out what effect environmental conditions have on the distribution and abundance of

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breeding populations of the boreal owl in the Czech Republic so that we can effectively prevent any possible reduction in the abundance of this owl in our region. Most important, the degradation of old-growth forests is causing a reduction in breeding opportunities for the boreal owl, which uses the cavities left by the black woodpecker (*Dryocopus martius*) in these forests (Korpimäki and Hakkarainen 2012). Nest boxes are installed to support populations of this species (Korpimäki and Hakkarainen 2012, Zárybnická et al. 2015d). However, studies on the effect of environmental conditions on the use of nest boxes in different habitat types have not yet been conducted for this species. Finally, in order to estimate the abundance of nocturnally vocally active species, such as the boreal owl, it is necessary to determine what environmental factors influence their spontaneous vocalizations (Conway et al. 2008, Zuberogoitia et al. 2018). This information is essential for acoustic monitoring.

Aims of the dissertation

The main aim of the Ph.D. thesis is to extend our understanding of the distribution and protection of owl species in the Czech Republic, focusing on the boreal owl: the species protected by the European (No. 2009/147/EC, Annex I) and Czech (No. 114/1992 Coll.) directives. The specific aims of the thesis are:

1) to examine the effects of elevation and temperature on the distribution of the boreal owl and other owl species in the Czech Republic using atlas data;
2) to compare the use of nest boxes by the boreal owl in two study areas differed in forest structure (the Ore Mts. and Trebon Basin), considering food supply and other environmental conditions of the specific areas;
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   (a) providing nest boxes as alternative nesting opportunities for the boreal owl, and
   (b) bioacoustic monitoring of boreal owl populations.

2. Literature review

2.1 Population monitoring

The current biodiversity crisis, manifested by global species loss, affects many taxonomic groups across different regions around the world (e.g., Sala and Knowlton 2006, Rosenberg et al. 2019, Sánchez-Bayo and Wyckhuys 2019). Over the past century, increased rates of species extinction have been recorded, primarily due to anthropogenic impacts resulting in habitat modification and loss, climate change, and the spread of invasive species (Butchart et al. 2010, Ceballos et al. 2015). Changes in the distribution and abundance of individual species and their populations can differ, especially at local scales (Sax and Gaines 2003). Severe declines in local biomass and changes in species distribution have been observed, for example, in birds (e.g., Chamberlain and Fuller 2000, Inger et al. 2014, Rosenberg et al. 2019). On the other hand, some studies show an increase in their local biodiversity (e.g., Inger et al. 2014, Rosenberg et al. 2019). However, as a result, there is an overall decline in bird populations and their biodiversity, which has been observed in many regions worldwide (e.g., Inger et al. 2014, Stanton et al. 2018, Rosenberg et al. 2019, Li et al. 2020). A major problem in conservation is the high degree of difficulty in identifying which species are currently at risk of extinction or whether a species that, in many cases, is common but could be threatened in the near future (Gaston and Fuller 2008). Many species are typically identified as "at risk" only once they become rare. From the 1960s to the 1990s, Europe saw a dramatic decline in bird populations inhabiting agricultural landscapes as a result of agricultural intensification (Fuller et al. 1995, Gregory et al. 2005, Burns et al. 2021). For example, the grey partridge (*Perdix perdix*) used to be a common bird of agricultural areas throughout Europe but is now rare. Within a decade, its population has declined by up to 80% in some European countries (Kuijper et al. 2009). Another example of a formerly common species that have experienced dramatic declines of up to 94% and local extinctions over the last two decades is the little owl (*Athene noctua*) in the Czech Republic (Chrenkova et al. 2017). Therefore, monitoring the changing status of selected species populations is one of the key approaches to assessing and understanding the anthropogenic influences at work and associated environmental factors (Balmford et al. 2003).

Monitoring distribution, abundance, density, presence, absence, or breeding success are some of the most crucial indicators describing how terrestrial animal populations respond to environmental change (Williams et al. 2002, Egwumah et al. 2017). Systematic long-term monitoring of changes and trends in population can contribute to the actual conservation of declining or threatened species, document and refine the effectiveness of conservation measures, and detect incipient negative impacts associated with anthropogenic activity (Goldsmith 2012). Therefore, a significantly negative population trend tells us that negative environmental factors are acting on the monitored population, which could even drive the species to regional extinction if the factor's influence remains unchanged (Owens and Bennett 2000). Conservation measures of ecosystems and populations themselves are assessed primarily through the so-called bioindicator species that respond quickly to environmental changes. The bioindicator species are mostly well studied, cover different levels of the ecological pyramid in every environment, and are easily detectable (Padoa-Schioppa et al. 2006).

Birds are significant ecological bioindicators (Egwumah et al. 2017). A characteristic of many bird species is their quick response to environmental changes, therefore, allowing for the detection of such changes in a short time frame (Bibby et al. 2000, Stephens et al. 2016). Birds of prey, including owls play a crucial role in ecosystems as apex predators (integrating a range of specialist and generalist food chains) that are highly sensitive to environmental change at both macrogeographic (e.g., effect of climate change on the population of migratory birds of prey; Bildstein 2001, Sullivan et al. 2016), and microgeographic scales (e.g., effect of habitat loss and fragmentation on reproductive success of owl; Hinam and St. Clair 2008). It is relatively easy to monitor numerical and demographic changes of raptors and owls because of their top position in the food chain, in response to changing environmental conditions and the influence of environmental factors caused by anthropogenic activity (Kovács et al. 2008). For example, in owls, it has been found that the mere occurrence of the boreal owl and the Eurasian pygmy owl (*Glaucidium passerinum*) can be a reliable indicator of high biodiversity in forest ecosystems because they prefer to breed in structurally complex mature forest habitat, which supports high levels of biodiversity (Sergio et al. 2006, Askeyev et al. 2020). Monitoring populations is often carried out through long-term projects using professional and amateur ornithologists (called Citizen Science), which produce large and complex datasets that contain valuable information about the

occurrence, abundance, and distribution of species on Earth (Gibbons et al. 2007). These datasets can be employed to understand the influence of environmental factors, whether man-made or natural, that affect populations over large areas. However, it does not have to be only qualitative changes, as environmental quality can also be assessed by quantitative characteristics. For example, Lodenius and Solonen (2013) found that raptor feathers can be a reliable indicator of the degree of heavy metal pollution in the environment.

2.2 Citizen Science

Citizen Science is a term frequently used today; however, people only rarely realize that scientists and the public has been cooperating for decades, especially in ornithology (Zárybnická in verb). In Citizen Science, people from the non-scientific community, i.e., the general public, are involved in generating new scientific information (Bonney and Dickinson 2012). For example, public involvement in the scientific community plays a key role in monitoring populations of common and endangered species worldwide. For these volunteers, the primary motivation is to contribute to scientific understanding and conservation. For scientists, Citizen Science provides an opportunity to collect complex and large-scale data that would be impossible to obtain given limited resources and time (Dickinson et al. 2010). Although the quality of data collected through Citizen Science is limited (Fraisl et al. 2022), technology and software in the form of online applications make it possible to engage large numbers of the public in scientific projects while providing quality data. For example, the large number of participants ensures peer review of collected data, and species identification applications help refine species identification (Dickinson et al. 2010, Wood et al. 2022). Scientific projects involving public participation are most often in Environmental Science, Ecology, and Biodiversity Conservation, where the public is predominantly involved in data collection but also in the actual evaluation and interpretation of results (Kullenberg and Kasperowski 2016). These data often provide information of comparable quality to that collected only by professionals (Szabo et al. 2012). The longest tradition and history of Citizen Science can be found in ornithology, with thousands of amateur and professional ornithologists globally interested in the field (Greenwood 2007). Additionally, Citizen Science often represents the only practical way to achieve the geographic scale needed to document

ecological patterns and to address ecological questions at scales relevant to the distribution and movements of all bird species (e.g., Lee and Hammer 2022), including their migratory patterns (e.g., Martín et al. 2020), disease spread (e.g., Kain and Bolker 2019), population trends at broad scales (e.g., Fink et al. 2019, Lee and Hammer 2022), and to determine the impacts of environmental processes such as climate change (e.g., Newson et al. 2016, Sullivan et al. 2016).

One of the most important outputs of ornithological projects are atlases of the breeding distribution of birds (e.g., Birds of the Vratza Mountains. II. Breeding Bird Atlas, Czech Breeding Atlas 2014 - 2017, European Breeding Bird Atlas 2; Georgiev and Milchev 2000, Keller et al. 2020, Šťastný et al. 2021). In the Czech Republic, the creation of breeding birds' atlases is the longest-running Citizen Science project. So far, four atlases have been published through the coordinating department of the Faculty of Environmental Sciences of the Czech University of Life Sciences Prague, mapping the distribution of breeding birds in the Czech Republic in 1973–1977, 1985–1989, 2001–2003, and 2014–2017 (Šťastný et al. 2021). The breeding atlases mainly document and depict the distribution of individual species along a geographical gradient such as latitude and longitude. Because atlases have relatively standardized monitoring methods and are repeated over time, the data allow for assessing change in distribution, i.e., within latitude and longitude, or examining changes in abundance of monitored species over long periods of time (e.g., Chamberlain and Fuller 2001, Lemoine et al. 2007, Zuckerberg et al. 2009). For example, Brommer (2004) found a northward range boundary shift for 116 bird species occurring mainly in the southern part of Finland by comparing two Finnish atlases. However, the potential of these atlas data is still underestimated (Donald and Fuller 1998, Dunn and Weston 2008). These comprehensive datasets can be used, for example, to understand the effect of environmental factors such as elevation, climate, and land cover on species distribution within a single macrogeographic unit and to reveal potential threats to now common species within a single region due to rapid habitat degradation or change due to anthropogenic activity and climate in many areas. However, such information is often hidden in maps and breeding atlas databases, and further analyses addressing these factors within a single region are sparse (Donald and Fuller 1998, Milanesi et al. 2017).

2.3 Distribution of species – the effect of abiotic factors

Understanding the abundance and distribution patterns of species at large spatial scales is one of the primary goals of biogeography and macroecology (Gaston and Blackburn 2000). While latitude and longitude are among the leading macroecological factors that fundamentally influence the distribution of species and ecosystems on Earth at large spatial scales as well (Merriam 1892, Andrewartha and Birch 1954, Gaston and Blackburn 2000), elevation can influence these parameters at local scales (Gaston and Blackburn 2000, Storch et al. 2003). Across the elevational gradient, environmental conditions change substantially. In particular, high elevated sites are characterized by coldness, short breeding season, and low food availability (Sasvári and Hegyi 2011, Boyle et al. 2016, Zárybnická et al. 2017b). As a result, the species richness and density usually decrease along an elevation gradient. These patterns appear to differ within and among taxonomic groups and climates (Boyle et al. 2016). For example, Thiollay (1996) found that the total species richness of South American diurnal raptors richness fell sharply with elevation. Similarly, Hawkins (1999) found that forest birds' richness strongly decreases above approximately 1300 m in eastern Madagascar. Below this elevation, species richness is about constant or declines slightly. On the other hand, the richness of salamanders and lichens increases with elevation (Wake et al. 1992, Grytnes et al. 2006). Elevation can also play a significant role in the distribution and density of owl populations because temperature, habitat structure, reproductive success, predation risk, and food availability change with increasing elevation (Hawkins 1999, Sergio et al. 2004, Marchesi et al. 2006, Sergio et al. 2009, Sasvári and Hegyi 2011, Boyle et al. 2016). For example, Dalbeck and Heg (2006) found a negative effect of increasing elevation on the reproductive success of the eagle-owl (*Bubo bubo*) associated with low temperature, egg incubation, and food availability. A limiting factor for the distribution of the barn owl (*Tyto alba*) is that higher elevations are associated with extreme climatic conditions, therefore, mortality increases with increasing elevation (Taylor 1994). Some studies have looked at the effect of elevation on the distribution of owls, which have mainly focused on one species and a particular range (e.g., Alegre et al. 1989, Sergio et al. 2004, Dalbeck and Heg 2006, Marchesi et al. 2006, Pačenovský and Shurulinkov 2008, Gottschalk et al. 2011, Sasvári and Hegyi 2011, Zárybnická et al. 2017b). The studies assessing the elevational segregation of particular owl species within the whole community

occupying a large geographical area (area of the whole country) are ultimately lacking, although they are essential due to the rapidly changing state of the environment caused by the influence of anthropogenic activity.

Species' presence can also often be influenced by microclimatic and microhabitat conditions like temperature, humidity, light intensity, vegetation composition, or vegetation structure (Rajpar and Zakaria 2011, Ray et al. 2016). High habitat heterogeneity, which in large part provides considerable variation in the availability of food resources and nesting sites, affects demographic parameters (Both 1998, Penteriani et al. 2002, Pakkala et al. 2006), as well as the dynamics of entire populations (Ferrer and Donázar 1996, Pakkala et al. 2006). The distribution of birds, including owls, also varies significantly with changes in habitat structure and heterogeneity, although particular species show different responses (Hanzelka and Reif 2016, Morelli et al. 2019b). For example, populations of forest-dwelling animal species can be affected by forest characteristics such as tree diameter and a height above the ground, age of forest stands, forest canopy coverage, or amount of deadwood, and respond very quickly to their loss caused by forest degradation or fragmentation or intensive forest management (Petty and Avery 1990, Fuller 1995, Schmiegelow and Monkkonen 2002, Vaillancourt et al. 2008, Nikolov et al. 2022). Also, boreal and many mountain forests face a considerable decrease in their structural and compositional heterogeneity as a result of historic and recent forest management activities (Arnett et al. 2010, Bouget et al. 2014). The occurrence of cavity-nesting owl species is often significantly limited by the availability of suitable habitats in old-growth forest stands (Newton 1994, Barbaro et al. 2016), and also the food availability itself, the main driver of reproductive patterns, can be considerably influenced by forest stand structure (Zárybnická et al. 2017a). For example, the population size and viability of boreal and pygmy owls are driven by the presence of old-growth coniferous forests with suitable tree cavities (Hakkarainen et al. 2008, Barbaro et al. 2016). It was found that boreal owl prefers to breed in dense and high coniferous forests (high forest canopy coverage and tree diameter) rather than mixed or deciduous forests to avoid the risk of being mobbed by small birds or killed by diurnal birds of prey (Bye et al. 1992, Korpimäki and Hakkarainen 2012, Nikolov et al. 2022). Additionally, the reproductive success of the boreal owl and the survival of individuals during winter increases with increasing proportions of dense coniferous forest stands (Laaksonen et

al. 2004, Hakkarainen et al. 2008, Korpimäki and Hakkarainen 2012). Furthermore, nest predation risk was found to be lower in coniferous forest stands than in deciduous forest stands (especially early in the season before tree leafing; Zárybnická et al. 2017c). However, in Europe, the proportion of coniferous forests usually increases with increasing latitude and elevation (e.g., Kolář et al. 2017). Therefore, it is unclear if the effect of elevation separated from habitats still affects the distribution of boreal owls.

2.4 Distribution of species – the effect of biotic factors

In many cases, interspecific competition has a significant effect on the distribution of many animals, including owls (Hakkarainen et al. 1997, Peterson and Robins 2003). Intraguild interactions not only affect the distribution of species but can also have a significant effect on their population dynamics (Newton 1998, Heikkinen et al. 2007). One of the factors that allow two competing species to coexist in the same area may be elevation (Vrezec and Tome 2004a). Segregation of species by elevation may aid in the coexistence of competitively weaker owl species in one area with competitively stronger species (Vrezec 2003, Vrezec and Tome 2004a). The effect of interspecific competition is often linked to the availability of suitable habitat (Glutz von Blotzheim and Bauer 1980, Storch et al. 2003, Francis and Saurola 2004, Chamberlain et al. 2016). High habitat heterogeneity often allows for the coexistence of a competitively weaker and stronger species without large negative effects (Lundberg 1980b, Vrezec and Tome 2004b, Bolboaca et al. 2013). For example, the boreal owl strictly avoids the territory of the tawny owl (*Strix aluco*), but due to the heterogeneity of the environment, it can inhabit a relatively small area without serious adverse effects (Vrezec and Tome 2004b). Due to habitat degradation and modification, and the effects of climate change, competition between species that currently coexist in a relatively small area due to habitat heterogeneity and the elevational gradient being disrupted. For example, in North America, a population decline of spotted owls (*Strix occidentalis*) was recorded due to the expansion of their competitor barred owls (*Strix varia*), which was facilitated by habitat modification (Livezey 2009, Yackulic et al. 2019). In Europe, an interchange in the occupancy of the territories of the boreal owl by the tawny owl has been observed (Brambilla et al. 2020, Pačenovský and Kürthy 2022). In fact, changing climatic conditions and habitat modification may impact the

distribution of boreal owl populations depending on interspecific competition with the tawny owl.

2.5 Nest boxes

The availability of suitable tree cavities is crucial for survival of the secondary cavity-nesting species (Newton 1994, Mikusiński et al. 2018). However, secondary cavity-nester populations are negatively affected, and declining because of the loss of availability of nest sites due to intensive forest management or the decline of primary cavity-excavator populations (e.g., Newton 1994, Remm and Lõhmus 2011, Mikusiński et al. 2018, van der Hoek et al. 2020). Small birds use tree cavities excavated by both small and large Picidae woodpeckers (van Balen 1984, Lambrechts et al. 2010) or cavities formed by the decay in old-growth forests by natural environmental processes (Bunnell 2013, van der Hoek et al. 2017). However, large-sized birds such as owls find the conditions more difficult due to the limited availability of cavities with suitable large-sized entrances excavated by large primary-cavity nesters (Lambrechts et al. 2012). For example, the European great tit (*Parus major*) prefers nesting holes with an entrance diameter between 3.5–5.9 cm (Lambrechts et al. 2010), but it also commonly breeds in smaller or larger cavities (van Balen et al. 1982, Maziarz et al. 2015, Charter et al. 2016). Contrarily, boreal owls depend on the availability of nest holes at least 7.0–8.0 cm (López et al. 2010, Korpimäki and Hakkarainen 2012). In European forests, such large-sized natural cavities are excavated predominantly by the black woodpecker (Glutz von Blotzheim and Bauer 1980, Korpimäki and Hakkarainen 2012, Brambilla et al. 2020). When the black woodpecker population declines, the populations of the secondary-cavity nesters decrease, too (Korpimäki and Hakkarainen 2012, Mikusiński et al. 2018).

The abundance of secondary-cavity nesting species can also decrease depending on the reduction of the heterogeneity of old-growth forest stands, which, compared to intensively managed forests, contain the highest density of primary and secondary cavities (mainly in deciduous and pine forest; Newton 1998, Moning and Müller 2008, Wesołowski 2011, Walankiewicz et al. 2014). For example, over the past 35 years, a high degradation of old-growth forests has occurred in North America, including a reduction in older age classes and a simplification of forest structure and composition, resulting in a reduced availability of breeding habitat for 66% of the 54 most common

forest species. The habitat loss was associated with population declines (Betts et al. 2022). In Europe, these old-growth forests have been destroyed and converted to managed forests by intensive forest management over the last century (Bengtsson et al. 2000). Due to the decrease in availability of nest sites for secondary cavity-nesters, nest boxes are used as one of the conservation tools, that increases breeding density of their population (Newton 1994).

Nest boxes of all shapes and sizes are used by many secondary cavity-nesting animals for nesting or roosting, especially, birds including owls (Lambrechts et al. 2012). Mainly in the last century, wooden nest boxes have frequently been used as an efficient tool to support the availability of nest opportunities for secondary cavity-nesting species (Newton 1994, Lambrechts et al. 2010, Lambrechts et al. 2012). If nest boxes are regularly maintained, they provide nesting opportunities of better quality than natural cavities, which often suffer from environmental processes like water leaking (Llambías and Fernandez 2009, Hruška 2020). Apart from the increase of nesting opportunities, nest boxes also allow us to monitor the breeding population to better understand breeding, trophic ecology, life-history strategies, and interspecific interactions among species that would be impossible to observe in natural-cavity populations (Korpimäki and Hakkarainen 2012, Lambrechts et al. 2012, Barker and Wolfson 2013, Zárybnická et al. 2013, Zárybnická et al. 2015e). Several studies show that the use of nest boxes is, in many cases, a common management practice and brings many positives during the non-breeding or breeding season (e.g., Møller 1989, Mainwaring 2011, Libois et al. 2012, Fay et al. 2019). Some studies have shown that the application of nest boxes results in population density increase (e.g., Fargallo et al. 2001, Libois et al. 2012, Fay et al. 2019) or in increased reproductive success and decreased predation rates mainly due to management and design of nest boxes (e.g., Møller 1989, Fargallo et al. 2001, Griffith et al. 2008). For example, the distribution of nest boxes may be essential for the survival of the boreal owl population in the damaged parts of the Ore Mts. in the Czech Republic (Zárybnická et al. 2015d). Last but not least, nest boxes provide suitable structures to mount camera devices for nest monitoring, making available information for research and educational material for schools and the public (e.g., Zárybnická et al. 2016, Kubizňák et al. 2019, Zárybnická 2020). However, some studies also describe the negatives associated with the use of

these artificial nest sites (Schlaepfer et al. 2002, Mänd et al. 2005, Klein et al. 2007, Mainwaring 2011).

Under specific conditions, nest boxes can work as an ecological trap. In such a case, nest boxes are attractive for birds but ultimately, they are detrimental and can cause their population to decline (Schlaepfer et al. 2002, Mänd et al. 2005). For example, for wood ducks (*Aix sponsa*), placing nest boxes in suboptimal habitats negatively affected the reproduction of breeding pairs due to an increase in the level of intraspecific brood parasitism (Semel and Sherman 2001). Contrarily, Mänd et al. (2005) found that placing nest boxes in an optimal habitat of great tits causes a supra-optimal breeding density leading to reduced reproductive success due to increased competition for resources. Some studies also indicate that breeding pairs switch from natural cavities to artificial boxes (e.g., Newton 1994, Lõhmus and Remm 2005). However, the willingness to occupy nest boxes varies among species (boreal owl vs. pygmy owl; Glutz von Blotzheim and Bauer 1980) and can differ substantially in various environments (Lambrechts et al. 2010, 2012). For example, an occupancy rate of nest boxes for the tawny owl in two study areas in Great Britain reached 32.6% (n = 193 nests/nest box-years) and 17.4% (n = 46 nests/nest box-years) during 1979–1985 and varies from 0.0% to 45.6% during seasons (Petty 1987). The author explains the differences in occupancy of the boxes to the changing availability of food and the supply of cavities. Differences in the use of nest boxes across different regions around the world have also been noted in the boreal owl (see subsection 2.7.4), and it is, therefore, necessary to determine how effective the boxes are for secondary cavity-nesting owls and what environmental factors influence their use in different types of environments.

2.6 Bioacoustic monitoring

For animals, communication is one of the key mechanisms that maintain bonds between individuals of the same or different species (Smith 1977, Bradbury and Vehrencamp 2011). Birds communicate using visual and acoustic signals, with many species using predominantly vocalizations, in which they use a wide range of sounds from calls to songs to defend and mark territories, attract mates, discourage and warn predators, forage for food, and make contact with members of their social group (Marler and Slabbekoorn 2004, Catchpole and Slater 2008, Bradbury and Vehrencamp

2011, Sabol et al. 2022). Human acoustic observations are a well-established research method for monitoring many bird species used to detect vocally active individuals (e.g., Gregory and Strien 2010, Egwumah et al. 2017). There are two long-standing methods most commonly used to detect biodiversity and abundance in bird populations. These include line transect and point transect. Both methods are based on visual and acoustic recordings of all species along a predefined route or spaced points in a selected map quadrant. In the case of line transects, the recording of individuals is continuous, whereas point transect is based on manual counts of birds at precisely defined points for a selected unit of time (Gregory et al. 2004, Volpato et al. 2009). These methods have been used in many different regions and habitats around the world, and the monitoring is primarily carried out by human observers (e.g., Reif et al. 2006, Alexander et al. 2017). However, in many cases, they can be limited by various factors. These include mainly errors in correct species identification, lack of expert observers, and the correct choice of a given method depending on the type of habitat and the species being monitored. Another potential shortcoming of both methods may lie in the tendency of observers to place transects along paths that may affect the species being monitored (Gregory et al. 2004). Additionally, playback provocation, which can be used during line and point monitoring of birds, is used to census elusive species, thus, improving their detection probability (Hardy and Morrison 2000, Navarro et al. 2005). This technique consists of broadcasting conspecific calls to elicit the reply of respective species (Johnson et al. 1981, Worthington-Hill and Conway 2017). This is particularly useful for those species that exhibit territorial behavior because they will be more inclined to respond by defending their territories (Pilla et al. 2018). It is known that factors such as habitat, seasonality, time of day, and weather can influence response rates during playback surveys (Hardy and Morrison 2000, Currie et al. 2002, Johnson et al. 2009). However, these factors can be eliminated by using long-term sound recordings, which can provide more extensive, comprehensive, and accurate datasets on the presence and abundance of individual species in study area (Celis-Murillo et al. 2009, Kulaga and Budka 2019).

Bioacoustics deals with the sounds of animal communication that are recorded, stored, and later analyzed (Vallee 2017). Bioacoustic monitoring uses modern technologies, including sound recording (Blumstein et al. 2011), which allows us to record and detect vocal activity over large ultrasonic to infrasonic wavelengths (Whytock and

Christie 2017) and over long-time intervals (Frommolt 2017, Whytock and Christie 2017). Acoustic methods effectively help us detect the presence or absence of a species at a given location, its abundance (Fischer et al. 1997, Haselmayer and Quinn 2000, MacSwiney et al. 2008), and distinct variations in vocal spectrum and style (Forstmeier and Balsby 2002, Brunner and Pasinelli 2010, Halfwerk et al. 2011). Additionally, the vocalization of different species carries considerable scientific information about various features of their biology and ecology (Catchpole and Slater 2008, Blumstein et al. 2011, Bradbury and Vehrencamp 2011). Bioacoustic monitoring improves the detection of individuals, their age, and gender (Blumstein et al. 2011, Teixeira et al. 2019) and reduces disturbance to sensitive species (e.g., Abrahams 2019). The use of autonomous recorders also reduces the need for trained observers and potentially per-survey costs, which could allow for more frequent and spatially extensive surveys than traditional observer-based approaches (Hill et al. 2017, Shonfield et al. 2018). Permanent audio records are valuable data source for the detection of changes in species distributions and biodiversity in areas with increasing anthropogenic disturbance (Shonfield and Bayne 2017). Furthermore, the performance of autonomous recorders compared to trained professional human observers in avian studies about estimating of species richness, abundance, and the presence or absence of target species has been evaluated in a wide range of habitats, and the final conclusions of these studies are more in favor of bioacoustic monitoring or comparable (Wimmer et al. 2013, Zwart et al. 2014, Shonfield and Bayne 2017). With the advantages described above and the further development of automatic recognition, passive acoustic surveys using an autonomous recording unit are becoming an important tool for studying and monitoring owls (for details see, Shonfield et al. 2018).

In nocturnal bird species, including owls, vocalizations play a critical role in their communication, behavior, and biology (König and Weick 2008, Odom and Mennill 2010, Bradbury and Vehrencamp 2011). Most owl species are difficult for human observers to detect visually due to their nocturnal habits, cryptic coloration, and occurrence at low densities. Therefore, vocalization is an essential characteristic of determination. Owls, mainly males, use territorial vocalizations to defend territories or attract mates during the breeding season in early spring (e.g., Ganey 1990, Penteriani 2002, Odom and Mennill 2010). Females usually respond with a contact call, yet, during the non-breeding season, they may produce territorial calls to a lesser extent

(Zuberogoitia and Martínez 2000, Reid et al. 2022). Due to its nocturnal lifestyle, territorial hooting is used to recognize the quality of the hooting individual. For example, Redpath et al. (2000) and Hardouin et al. (2007) found a relationship between the frequency of owl vocalizations and the weight or degree of parasitism of a vocally active individual. Territorial hooting is typically highest during spring and is used by ornithologists monitoring owl populations to determine abundance and distribution or identify territories and individuals (e.g., Nagy and Rockwell 2012, Vrezec and Bertoncelj 2018, Zuberogoitia et al. 2018).

It is important to identify environmental factors affecting spontaneous owl calling because territorial vocalizations are used to estimate the owl population (Worthington-Hill and Conway 2017, Zuberogoitia et al. 2018). The vocal activity of owls, including the boreal owl (see subsection 2.7.6), varies due to the influence of local abiotic and biotic factors. For example, one factor is the time of year with peak vocal activity during the breeding season (Slagsvold 1977, Clark and Anderson 1997, Amrhein et al. 2002, Kloubec and Čapek 2012). Another factor affecting vocal activity may be the time of day, with higher activity during dusk and dawn (Kloubec and Pačenovský 1996, Clark and Anderson 1997, Mougeot and Bretagnolle 2000, Kloubec 2007). The vocal activity of nocturnal bird species can also be influenced by climatic conditions (Slagsvold 1977, Lengagne and Slater 2002), the presence of suitable nesting sites, unpaired individuals (Galeotti and Pavan 1993, Amrhein et al. 2002, Kloubec 2007), or interspecific competition (Crozier et al. 2006, Zuberogoitia et al. 2008, Lourenco et al. 2013). The vocal activity of nocturnal bird species can also be influenced by food supply and availability, although such studies are rare (e.g., Lundberg 1980a, Swengel and Swengel 1995). Therefore, it is crucial to determine what environmental factors may influence the spontaneous vocal activity of the species under study in the face of ever-changing environmental conditions.

2.7 Boreal owl

The boreal owl is a small, nocturnal avian predator that occupies, in seven subspecies, the circumpolar Holarctic area, which corresponds well with the natural range of Norway spruce (*Picea abies*). In Europe, the center of the boreal owl's range is an area of high latitudes and elevation where the species frequently inhabits mature and dense Norway spruce coniferous forests (Korpimäki and Hakkarainen 2012). In Central and

Southern Europe, this owl inhabits mainly coniferous forests, but it can also occur in deciduous or mixed forest of spruce, European beech (*Fagus sylvatica*), or non-native blue spruce (*Picea pungens*) forest stands (Šťastný et al. 2006, Castro et al. 2008, Korpimäki and Hakkarainen 2012, Zárybnická et al. 2015d, Zárybnická et al. 2017b, Zárybnická et al. 2017c). In Europe, this threatened species, European directive 2009/147/EC, Annex I, exhibits foraging, habitat, and nest-site specialization (Morelli et al. 2019a). Southern and Central Europe hold some of the European glacial relict populations of boreal owls inhabiting higher elevations, which are at the southernmost edge of their distribution range, especially in Southern Europe (e.g., Spain, Italy). However, in Northern and Southern Europe, many studies have recorded changes in the abundance and distribution of boreal owl populations in response to the influence and change in environmental conditions such as global warming and habitat loss or modification (e.g., Solonen 2004, Hipkiss et al. 2013, Kouba et al. 2020, Shurulinkov et al. 2021).

2.7.1 Northern population of boreal owl

Boreal owls face a long-term decline in the boreal forests of northern Europe (e.g., Hörnfeldt et al. 2005, Saurola 2009, Hipkiss et al. 2013, Elts et al. 2019, Kouba et al. 2020), which is mainly attributable to the loss of mature and old-growth forests offering refuges against larger predators or reduced availability of primary and alternative prey (Korpimäki 2021). For example, Hörnfeldt et al. (2005) and Hipkiss et al. (2013) show that the breeding population of the boreal owl has declined by 75% compared to the peak densities from the mid-1980s to the early 2000s in Sweden. Declines in boreal owl populations have also been recorded in Finland (e.g., Saurola 2009), and was associated with the decline of fledgling production (Kouba et al. 2020). Even in Northern Europe, climate change and rising temperatures are thought to have an indirect negative impact on the northern populations of this boreal species. Increases in daily temperatures affect the duration and height of snow cover, which in turn, affects the abundance and population cycles of the main prey of the boreal owl, *Microtus* voles (Hipkiss et al. 2013, Mysterud 2016). Increasing temperatures can be detrimental to the overwintering vole, as their survival rate decreases in years with mild winters (Aars and Ims 2002, Solonen 2004). Deep snow cover provides effective insulation for overwintering voles, which can also breed under snow (Norrdahl and

Korpimäki 2002). On the other hand, during milder winters, when the snow cover melts and refreezes, voles are unable to effectively use the space under the snow to forage for food and defend themselves against predators (Aars and Ims 2002, Hörnfeldt 2004, Solonen 2004). Consequently, their mortality increases, leading to a more pronounced decline in populations during winter periods and negatively disrupting vole population cycles in Northern Europe (Aars and Ims 2002, Hörnfeldt 2004). For this reason, that the combination of influences acting on populations of the boreal owl in Northern Europe has led to a decline in the abundance of this species.

2.7.2 Southern population of boreal owl

In Southern Europe, a decline in the abundance of boreal owl populations has also been recorded (e.g., Shurulinkov et al. 2021). Changes in the distribution and a significant decline in abundance of this species in response to increasing temperature are predicted by many studies in Southern Europe (Castro et al. 2008, Brambilla et al. 2015, Brambilla et al. 2017, Brambilla et al. 2020, Shurulinkov et al. 2021, Cerman et al. 2022). It is an owl that has clear preferences for cooler and more humid climatic conditions (Castro et al. 2008). Furthermore, Cerman et al. (2022) found that the maximum temperature of the warmest month of the year was crucial for the boreal owl in the Balkan Peninsula, as populations of this species did not occur in areas where temperatures were above 31 °C. Rajković et al. (2013), in turn, point out that up to 71% of the territories of the Serbian population were located mainly on the northern and northwestern slope exposures. Such oriented slopes typically provide smaller tree density, higher humidity, and cool native boreal climatic conditions (Hayward et al. 1993). Additionally, a Bulgarian study reported that boreal owl territories have disappeared from slopes exposed to the south, southwest, and southeast directions (Shurulinkov et al. 2021). Furthermore, in Italy, climate impacts are predicted to cause the loss of up to 65% of the current optimal special protection habitat by 2050, which may cause a significant decline in boreal owl abundance in southern European countries.

2.7.3 Populations of the boreal owl in the Czech Republic

In the Czech Republic, the boreal owl, protected by Decree No. 395/1992 Coll. of the Act No. 114/1992 Coll. on Nature and Landscape Protection, Annex III, inhabits

dense, old-growth coniferous forests, especially spruce forests of higher elevations, rather than deciduous and mixed forests of lower elevations, but this preference may change over the process of tree leafing (Šťastný et al. 2006, Zárybnická et al. 2015d, Zárybnická et al. 2017c). The focal point of the boreal owl's distribution in the Czech Republic is in border areas that have been affected by air pollution in the past, especially the Ore Mts. and Jizerské hory Mountains (Fig. 1). These locations have the advantage of large areas of open land and loose forest cover, which provide this owl with a high prey supply of small mammals, mainly *Microtus* voles and *Apodemus* mice (Zárybnická et al. 2015d, Zárybnická et al. 2017b). Based on four mapping surveys of breeding populations of the boreal owl in the Czech Republic, it was found that quadrate occupancy increased from 10% in 1973–1977 to 23% in 1985–1989, 37% in 2001–2003, and to 54% in 2014–2017 (Fig. 1). The size of the boreal owl population was estimated at 550–800 breeding pairs in 1985–1989. However, this number increased to 1500–2000 pairs in 2001–2003 and to 1700–2500 pairs in 2014–2017 (Šťastný et al. 2021). Additionally, Kopij (2011) attributes the previously recorded increased abundance and occurrence of this species at lower elevations in the Czech Republic to the increasing interest of amateur and professional ornithologists who have become actively involved in monitoring breeding birds in this area since the early 1970s. Although the expansion of this boreal species to lower elevations has been recorded in recent years, core sites of occurrence in the Czech Republic still represent higher elevations along the frontiers (Zárybnická et al. 2017b).

Figure 1. Distribution map of the boreal owl in the Czech Republic in 2014–2017 (Šťastný et al. 2021).

● confirmed breeding
● probable breeding
• possible breeding
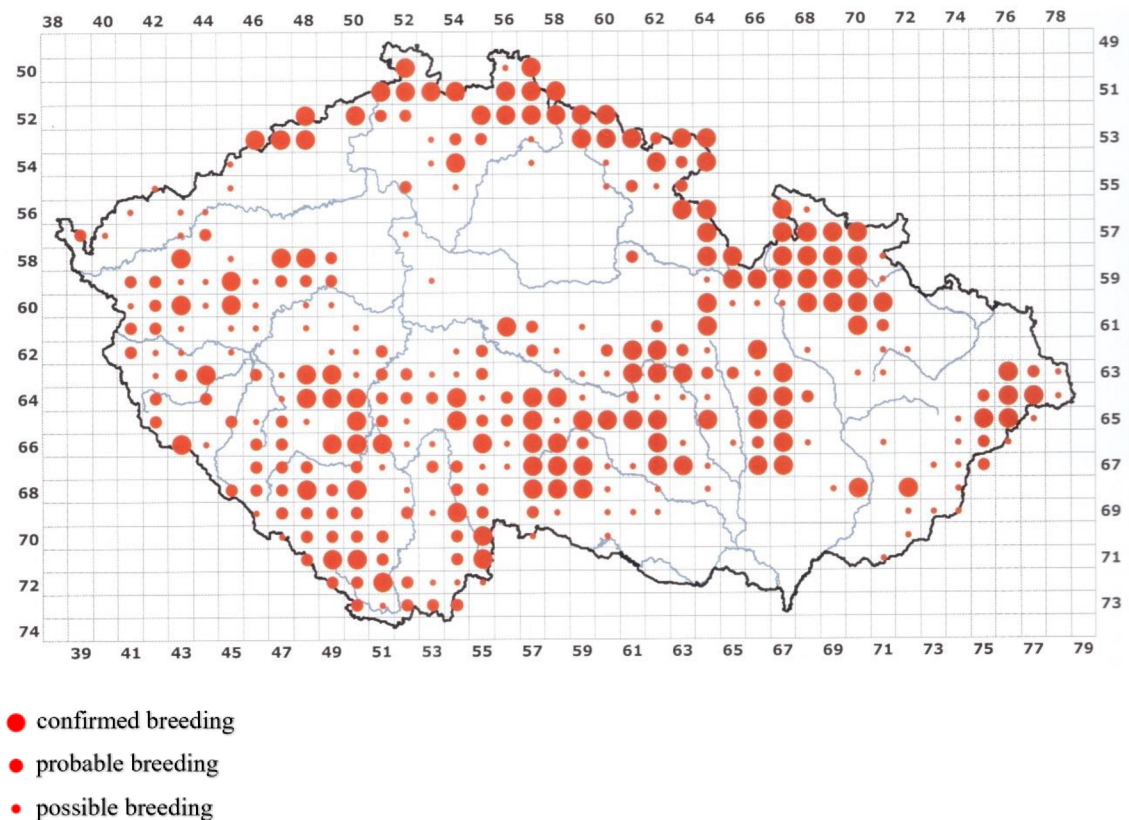
2.7.4 Breeding opportunities of the boreal owl

The boreal owl is a forest specialist secondary cavity-nester and, therefore, uses cavities excavated by black woodpeckers. If the population of this keystone species declines, then many secondary cavity users, including the boreal owl, will decline along with it (Korpimäki and Hakkarainen 2012). Additionally, cavities excavated by black woodpeckers also occur more frequently in mature deciduous and mixed forests while less abundant in intensively managed spruce forests (Miller 2010, Wesołowski 2011, Walankiewicz et al. 2014). However, the boreal owl often breeds in nest boxes, which have started to be used in areas with decreased availability of natural nest site due to the increase and conservation of their population (Korpimäki and Hakkarainen 2012, Zárybnická et al. 2015d). Many studies based on research of nest-box-using populations show the influence of many abiotic and biotic factors (e.g., habitat, breeding period, or interspecific and intraspecific competition), which affect the timing of breeding, clutch size, reproductive success, home range size, and parental

care of boreal owls (Vrezec 2003, Vrezec and Tome 2004b, Zárybnická et al. 2013, Zárybnická and Vojar 2013, Zárybnická et al. 2015d, Kouba et al. 2017). However, nest box occupancy varies in the boreal owl over the Holarctic region, reaching the nest box occupancy of 0–66% (for details, see Table 1). For example, Hayward et al. (1993) explain the reluctance to occupy nest boxes to the availability of sufficient natural cavities. Sonerud (1985) points to a decrease in occupancy rates as a function of increasing predation rates and the age of the boxes. On the other hand, it has been reported that pairs nesting in nest boxes produce more fledglings than those using natural cavities (Korpimäki 1984). However, the effect on the utilization of nest boxes by boreal owls and the breeding performance of this species under different habitat quality and environmental conditions is poorly studied.

Table 1. The utilization of nest boxes by the boreal owl in Europe, North America, and Asia; the state, locality, elevation, period, the number of boxes, nests, box-years, and the nest box occupancy (expressed as the proportion of occupied nest boxes of checked boxes). The way how authors described their results varied hugely. Therefore, we present the information on the number of boxes, nests, and nest box occupancy from long-term studies either as a sum counted for the entire study period (marked as 'total') or a yearly mean (marked as 'mean') with minimum (min) and maximum (max) values.

State	Locality	Elevation	Period	No. of boxes/year	No. of box-years	No. of nests			Nest box occupancy (%)				Authors
						Total	Min	Max	Total	Mean	Min	Max	
Canada	Southern Yukon		1984–96	13–105	573	6			1				(Mossop 1997)
Canada	Alberta region	470–920	2016	169	169	4			2				(Domahidi et al. 2020)
USA	Alaska	90–150	1995–97	36	108	29			27				(Whitman 2001)
USA	Alaska	200–650	2005–06	91, 108	199	23			12				(Whitman 2008)
USA	Alaska	110–690	2015	200	200	27			14				(Anderson 2017)
USA	Rocky Mts.	1700	1985–88	45	180	3			2				(Hayward et al. 1993)
USA	Idaho	1520–2140	1988–90	283–450	1016					4			(Hayward et al. 1992)
USA	Rocky Mts.		1995–01	250–450						1			(Koopman et al. 2007)
China	Lianhuashan Mts.		2003–07	67	335		4	7			6	10	(Fang et al. 2009)
Sweden	Västerbotten		1980–84	500	2500	525	4	201	21		1	40	(Löfgren et al. 1986)
Sweden	Västerbotten		1981–82, 1984–85	44–149		330	5	99		30	6	66	(Hörnfeldt and Nyholm 1996)
Sweden	Västerbotten		1998–99	300	600	84					15	22	(Hipkiss et al. 2002)
Sweden	Västerbotten		2006–07	273, 275	548	47			9		2	15	(Hipkiss et al. 2013)

Country	Location												Reference
Finland	Kauhava region	30–120	1966–85	35–450	4577	352	2	63	8		2	22	(Korpimäki 1987)
Finland	Kauhava region	30–120	1966–08	hundreds	677	104			15				(Korpimäki and Hakkarainen 2012)
Czech Rep.	Ore Mts.	730–960	2000–03	100	400	72	10	26	18		10	26	(Drdáková 2003)
Czech Rep.	Šumava Mts.	500–1300	1984–05	211	4448	316			7				(Zárybnická et al. 2017b)
Czech Rep.	Šumava Mts.	500–1100	1992–02	395		250				6	4	8	(Zárybnická et al. 2015a)
Czech Rep.	Šumava Mts.	400–1378	1978–02		5006	299				6			(Kloubec 2003)
Czech Rep.	Krkonoše Mts.		1985–86	40, 60	100	1			1		0	2.5	(Flousek 1988)
Switzerland, France	Jura Mts.	1000–1600	1985–14	64–116	2550	425	2	39	17		3	55	(Ravussin et al. 2015)
Germany	Kaufunger Wald	250–580	1965–84	60	1200	76			6				(Schelper 1989)
Germany	Harz Mts.	450–850	1979–91	250	3250	390			12				(Schwerdtfeger 1994)
Germany	Olpe	430–580	1981–10	4–64	1034	187	0	20	18		0	56	(Hunke 2011)
Italy	Cansiglio Highland		1989–20	80–100	2400	93			4				(Mezzavilla and Lombardo 2013)
Serbia	Kopaonik National Park	800–2017	2011–13	63	189	9			5				(Rajković 2018)

2.7.5 Food supply of boreal owl

Food availability plays a critical role in the reproduction and life-history strategies of boreal owls. Food availability influences breeding density, laying date, clutch size, sex allocation, nestling fitness, fledgling productivity, predation of boreal owl's nests, and home range size (Hipkiss and Hörnfeldt 2004, Korpimäki and Hakkarainen 2012, Zárybnická et al. 2015b, Zárybnická et al. 2015c, Zárybnická et al. 2015e, Kouba et al. 2017). The most abundant prey of boreal owl consists of small rodents (König and Weick 2008). In Northern Europe, the boreal owl feeds predominantly on voles of the genus *Microtus* (field vole, *M. agrestis*, and common vole, *M. arvalis*) and voles of the genus *Myodes* (bank vole, *M. glareolus*), with their availability varying significantly between years (Sonerud 1986, Korpimäki and Hakkarainen 2012). *Microtus* vole populations are subject to regular three or four-year cycles in Northern Europe, with more stable populations in the temperate zone (Zárybnická et al. 2015e, Zárybnická et al. 2017a). In the Czech Republic, the main prey of the boreal owl are mice of the genus *Apodemus* (i.e., wood mouse, *Apodemus sylvaticus*, and yellow-necked mouse, *Apodemus flavicollis*) and *Microtus* voles (i.e., field and common vole). However, during a year with low availability, the boreal owl can switch to alternative food sources such as mainly *Sorex* shrews (common shrew, *S. araneus* and pygmy shrew, *S. minutus*) and birds (Korpimäki and Hakkarainen 2012, Zárybnická et al. 2013). In years with low availability of its main prey, the boreal owl alters its hunting area and moves from open areas to closed forests, where it seeks out and hunts bank voles, which are considered its most important alternative prey in northern Scandinavia (Korpimäki 1988, Korpimäki and Hakkarainen 2012).

2.7.6 Territorial vocalization

The boreal owl usually breeds from March to July (Korpimäki and Hakkarainen 2012, Zárybnická et al. 2012) and, during this period, it makes a territorial call to defend its territory and attract females (Vacík 1991, Kloubec 2007). The vocalizations of the boreal owl can be heard from January to May, with peaks in the early breeding season from March to April (Vacík 1991, Kloubec 2007). The prolonged, so-called territorial call of the boreal owl is emitted by males from the start of courtship to the early incubation period. The function of this vocalization is often related to pair formation and communication (Korpimäki and Hakkarainen 2012). The vocal activity of this owl

usually begins 30 to 60 minutes after sunset, with a peak phase around midnight (Kloubec and Pačenovský 1996). Additionally, unpaired males may hoot throughout the night (Korpimäki 1981). So far, vocal activity is affected by climatic conditions such as wind, rain, or snow, while the influence of temperature, cloud cover, and phase of the lunar cycle has not been demonstrated (Mikkola 1983, Palmer 1987, Kloubec and Pačenovský 1996, Korpimäki and Hakkarainen 2012). Moreover, vocalizations of boreal owls are usually detectable up to a distance of 0.5–1 km or 1–3 km during more suitable weather conditions (Vacík 1991, Kloubec and Pačenovský 1996). Some studies have suggested that vocal activity may be influenced to some extent by food supply (Palmer 1987, Kloubec and Pačenovský 1996), certain times of the night (Kloubec et Pačenovský 1996), the density of the breeding population (Kloubec 1986, König et al. 1999), or interspecific competition (Hakkarainen and Korpimäki 1996). However, individual studies have usually focused separately on particular effects, without a comprehensive approach and verifying the specific food availability in the field allowing us to understand the relative significance of individual factors to boreal owl vocalization.

2.8 Aims of the dissertation

The distribution of owls breeding in the Czech Republic is primarily known in terms of latitudinal and longitudinal distribution. However, studies dealing with the influence of other environmental factors, namely, elevation and associated climatic conditions and habitat, on the distribution of owl populations throughout the Czech Republic using atlas data have not yet been carried out. Therefore, the influence of selected abiotic factors on breeding populations in the Czech Republic is addressed in this doctoral thesis (*Study I*) using data from the Breeding Atlas.

Despite the popularity of nest boxes among amateur and professional ornithologists, studies comparing the occupancy rate and life-history traits of populations breeding in nest boxes and natural cavities in different environments are scarce. Moreover, boreal owl nest boxes are an effective conservation tool only in suitable habitats characterized, for example, by the low availability of nest holes (Brambilla et al. 2013). Inappropriate distribution of nest boxes can also reduce breeding success or occupancy of these artificial nest sites (Gottschalk et al. 2011, Brambilla et al. 2013). That is why this doctoral thesis deals with the influence of environmental factors on the use of nest

boxes by boreal owls in two biotopically different areas (***Study II***) and based on the results obtained, experiences of my supervisor and collaborators, and literature reviews providing practical guides for deploying nest boxes for the boreal owl in the Czech Republic.

When monitoring populations of vocally active species, estimating their population size and determining territories, it is important to identify how environmental factors affect species' spontaneous vocal behavior (Zuberogoitia et al. 2018). It is known that the vocalization of the boreal owl is influenced by many abiotic and biotic factors (e.g., Palmer 1987, Hakkarainen and Korpimäki 1996, Kloubec and Pačenovský 1996). However, many studies investigating the influence of environmental factors on the vocal activity of the boreal owl have used the standard method of vocal registration by individual observers during selected parts of the night, and often using voice provocation, which can alter the result (Kissling et al. 2010). Thus, I examine the influence of ever-changing environmental factors on the spontaneous vocal activity of the boreal owl is addressed in my final study (***Study III***). I also provide recommendations for effective bioacoustic monitoring of local populations of the boreal owl in Czech conditions.

3. Results of studies

3.1 Study I.

The effect of environmental variables on owl distribution in Central Europe: A case study from the Czech Republic

Richard Ševčík, Jan Riegert, Karel Šťastný, Jan Zárybnický, Markéta Zárybnická

Authors contribution:

M. Zárybnická and J. Zárybnický conceived and designed the research topic and settled research questions.

J. Riegert, M. Zárybnická, and **R. Ševčík** performed the analyses and created figures.

M. Zárybnická, **R. Ševčík**, and J. Riegert wrote the manuscript.

K. Šťastný contributed the data.

J. Zárybnický and M. Zárybnická synthesized the data.

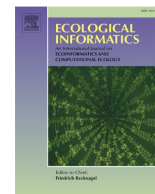**R. Ševčík**, M. Zárybnická, J. Riegert, K. Šťastný, and J. Zárybnický edited the manuscript.

The effect of environmental variables on owl distribution in Central Europe: A case study from the Czech Republic

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A B S T R A C T

Species distributional data from atlas projects collected by volunteers and professionals play an essential role in ecology and biodiversity conservation. Atlas data primarily allow evaluating longitudinal and latitudinal gradients in species distribution. However, the effects of additional factors such as elevation and associated climatic conditions and landscape structure are rarely assessed. We used the original data from the Atlas of birds breeding in the Czech Republic in terms of the presence and absence (0/1) of breeding occurrence of seven owl species in 604 mapping quadrates (each quadrate 12.0 × 11.1 km in size) to assess the effect of elevation (reaching from 100 to 1100 m a.s.l.) and temperature on the distributional patterns of the owls. Using a multivariate spatial analysis with latitude and longitude as space predictors and landscape structure as covariates, we found that elevation and temperature significantly affected owl distribution; the model explained 94.8% of the variability ($p = 0.002$). Only the boreal owl (*Aegolius funereus*) showed a clear preference for the highest elevation, and simultaneously, boreal and pygmy (*Glaucidium passerinum*) owls preferred the coldest environments. Eagle owl (*Bubo bubo*) and tawny owl (*Strix aluco*) most often occupied low and middle elevation of moderate temperatures. Barn owl (*Tyto alba*) and long-eared owl (*Asio otus*) inhabited the warmest areas in low elevations. Finally, little owl (*Athene noctua*) most often occurred in the lowest elevations of intermediate temperatures. We have documented that the elevation and associated climate conditions can work as an effective predictor to assess distributional preferences of owl species based on atlas data. The findings can be helpful when the management of owls' habitats is considered and implemented. For example, the results of our case study suggest that the boreal owl can be susceptible to global warming and intensive logging at high elevations.

1. Introduction

Broad-scale bird monitoring projects are the longest-running and largest citizen science programs (for review, see Gibbons et al., 2007) and play an important role in ecology and biodiversity conservation studies (Herrando et al., 2019; Robertson et al., 2010; Whittaker et al., 2005). Distributional data from breeding bird atlases usually provide reliable and high-quality datasets collected by standardized methods over regions (e.g., Atlas of Breeding Birds of Wallonia; Jacob et al., 2010), countries (e.g., Atlas of Breeding Birds in the Czech Republic; Šťastný et al., 2006), and continents (e.g., The EBCC Atlas of European Breeding Birds; Hagemeijer and Blair, 1997; eBIRD). However, the potential of atlas data is still undervalued (for review, see Donald and Fuller, 1998; Dunn and Weston, 2008). For example, atlas data used to

be displayed as the 2D-maps, documenting geographical patterns in species distribution along latitude and longitude. Still, the effect of additional factors such as elevation and associated climatic conditions and land cover on species distribution is hidden in the maps. Although some atlases have included translucent plastic films to indicate the distributional patterns of individual species to additional effects (e.g., Kloubec et al., 2015; Šťastný et al., 2006), comprehensive analyses of other factors are scarce (Donald and Fuller, 1998; Dunn and Weston, 2008; Milanesi et al., 2017).

Geographical factors — especially latitude, longitude, and elevation — firmly control species distribution (Storch et al., 2003). While latitudinal effects work on a broad geographical (horizontal) scale, elevation effects can be evident on a small (vertical) scale as a result of temperature and habitat gradients (Barry, 2008; Chamberlain et al.,

2016; Kolář et al., 2017; Londoño et al., 2017; McCain, 2009; Nagy and Grabherr, 2009). It has been shown that species diversity decreases with increasing distance from the equator in various animal taxa, including birds (Darwin, 1859; Hawkins et al., 2003). This effect has been explained, for example, by the decrease of primary productivity and habitat diversity towards northern latitude (Kerr and Packer, 1997; Rohde, 1992). Elevational diversity gradients have commonly been reported as decreasing in species diversity (e.g., Brown and Lomolino, 1998; Stevens, 1992; Terborgh, 1977). However, the effect of local environmental conditions can shift the peak of species diversity at any specific elevation, apart from the highest elevation (for details, see McCain, 2009; Rahbek, 2005). This effect can be explained by low temperature, habitat structure, short breeding season, low food availability, and higher predation risk at higher elevations (Boyle et al., 2016; Hawkins, 1999; Marchesi et al., 2006; McCain, 2009; Sergio et al., 2004, 2009).

The studies dealing with the relationship between the elevational gradient and animal distribution have usually focused on particular species in specific environments. For example, the effect of elevation was studied in particular owl species, including Eurasian eagle owl *Bubo bubo* (Eifel region, Germany, Dalbeck and Heg, 2006; Trento region, Italy, Sergio et al., 2004), tawny owl *Strix aluco* (Trento region, Italy, Marchesi et al., 2006; Duna-Ipoly National Park, Hungary, Sasvári and Hegyi, 2011a), boreal owl *Aegolius funereus* (Šumava Mts., Czech Republic, Zárybnická et al., 2017a), little owl *Athene noctua* (catchment area of the Nidda River, Hesse, Germany, Gottschalk et al., 2011), barn owl *Tyto alba* (Province of León, Spain, Alegre et al., 1989), and Eurasian pygmy owl *Glaucidium passerinum* (Rila Mts., Bulgaria and Slovakia, Pačenovský and Shurulinkov, 2008). The rare studies have documented the differentiation of elevational distribution of two or three coexisting species. For example, it has been reported that tawny owl preferred to occupy lower elevations than boreal and Ural owls *Strix uralensis* (Mt. Krim, Slovenia Vrezec, 2003; Vrezec and Tome, 2004a). Similarly, tawny and Ural owls segregated their elevational distribution due to competitive exclusion (Slovenia Mts. Vrezec and Tome, 2004b). However, the studies assessing the elevational segregation of particular owl species within the whole community occupying a large geographical area are completely lacking.

The distribution of birds, including owls, also varies significantly with changes in habitat structure and heterogeneity, although particular species show different responses (Hanzelka and Reif, 2016; Morelli et al., 2019). One of the most sensitive groups to habitat changes is forest-dwelling animal species that usually suffer from the loss of forest area and intensive forest management (Schmiegelow and Monkkonen, 2002). For example, the population size and viability of boreal owl and pygmy owl are driven by the presence of old-growth coniferous forests (Barbaro et al., 2016; Hakkarainen et al., 2008; Zárybnická et al., 2017a; Zárybnická et al., 2017b). These habitats are necessary to provide suitable conditions for breeding and foraging these species; mainly, they provide safe shelters and a sufficient amount of tree cavities (Barbaro et al., 2016; Baroni et al., 2020; Hakkarainen et al., 2008). However, in Europe, the proportion of coniferous forests usually increases with increasing latitude and elevation (e.g., Kolář et al., 2017; Zárybnická et al., 2017a). Therefore, it is unclear if the effect of elevation separated from habitats still affects the distribution of owls.

We aimed to perform a multivariate spatial analysis of the data from the Atlas of breeding birds in the Czech Republic (Šťastný et al., 2006) as a case study to find the effect of elevation and climatic conditions on the distribution patterns of Czech owls. More specifically, we used the original data from the Atlas of breeding birds in terms of the presence and absence (0/1) of breeding occurrence of seven owl species in 604 mapping quadrates (each quadrate 12.0×11.1 km in size) to assess the effect of elevation (reaching from 100 to 1100 m a.s.l.), temperature, and rainfall on the owls' distribution. To remove the impact of additional factors, we included latitude and longitude as space predictors and landscape structure as covariates. We also aimed to discuss the

biological results of our study to point the species that may be susceptible to habitat and clime changes.

2. Material and methods

2.1. Atlas data

We used the data from the Atlas of birds breeding in the Czech Republic in 2001–2003 (Šťastný et al., 2006). These data include the occurrence (presence/absence) of nine owl species in 628 mapping quadrates (each quadrate of 12.0×11.1 km in size) distributed between 100 and 1100 m a. s. l. (Fig. 1). We assessed the occupancy of quadrates only when the breeding of owl species was confirmed (i.e., we only included quadrates marked as "D"), as recommended by (Moudrý et al., 2017). We assessed only such quadrates where breeding of at least one owl species was confirmed, counting a total of 604 mapping quadrates. We used a quadrate as a data unit for analyses.

Into analyses, we included the distribution of seven owl species — boreal owl, Eurasian pygmy owl, tawny owl, long-eared owl (*Asio otus*), barn owl, little owl, and Eurasian eagle owl. We excluded short-eared owl (*Asio flammeus*) and Ural owl from the analyses because they occupied only one and three quadrates, respectively. In general, the landscape structure that owl species occupy in the Czech Republic varies. While boreal, pygmy, tawny, long-eared, and eagle owls most often inhabit a variety of forest habitats from lowlands to mountains, little and barn owls are rather synanthropic species occupying agricultural areas in the lower elevation (Hudec and Šťastný, 2005). Additionally, the home range size of owl species varies from less than 1 km^2 to more than 32 km^2 depending on a variety of factors, including the owl species, habitat structure, food availability, the age and sex of individuals, and time of the year (e.g., Henrioux, 2000; Kouba et al., 2017; Šálek and Lövy, 2012; Strøm and Sonerud, 2001).

2.2. Elevational data

We calculated the mean, minimal, and maximal elevation for every quadrate based on Czech topographic base maps (ZABAGED 2002–2006, Czech State Administration of Land Surveying and Cadastre) using ArcGIS Desktop 10.8 (ESRI, 2020). Most quadrates ($n = 543$, 89.9%) reached mean elevation between 200 and 600 m a. s. l. (Fig. 2a). Mean elevation strongly correlated with minimal (Spearman's rank correlation coefficients, $r_s = 0.88$) and maximal (0.93) elevation (Fig. 2b). Therefore, we included only mean elevation into analyses.

2.3. Habitat data

For each quadrate, we calculated landscape structure as the proportions of coniferous forest, mixed forest, deciduous forest, open area, and urban area based on CORINE land cover 2010 (European Environment Agency) using ArcGIS Desktop 10.8 (ESRI, 2020). Mean elevation correlated with the proportions of most habitat types and particular habitat types related to each other (Table 1, Fig. 3a-e). The proportions of coniferous forests strongly increased with increasing elevation, while the proportion of open areas steeply increased with decreasing elevation (Fig. 3a-b). We included the percentages of particular habitat types for each quadrate as a covariate into analyses.

2.4. Climatic data

We calculated the mean daily temperature and mean daily rainfall for each quadrate in April and May (i.e., breeding season) based on daily measurements from meteorological stations in Czech counties ($n = 78$) using ArcGIS Desktop 10.8 (ESRI, 2020). We used daily measurements from one meteorological station of each county provided by the Czech Hydrometeorological Institution. Temperature and rainfall negatively correlated (Spearman's rank correlation coefficients, $r_s = -0.71$,
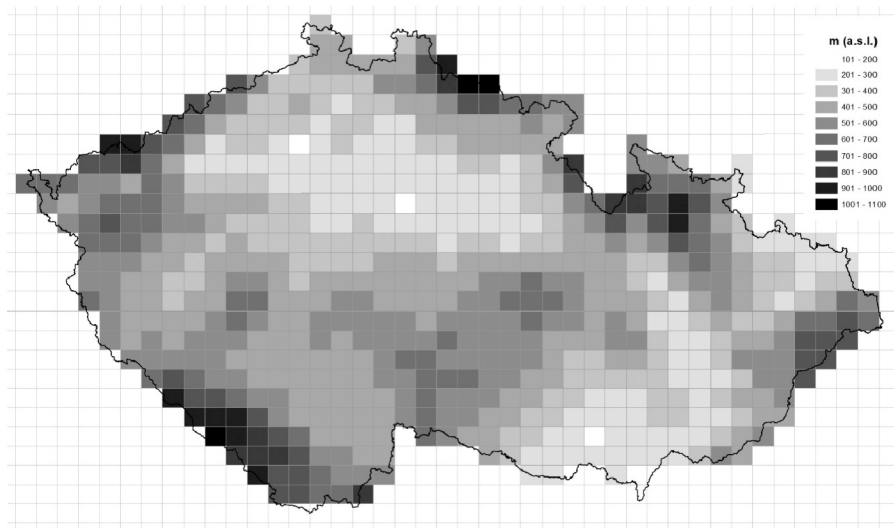
Fig. 1. The distribution of mapping quadrates (12.0 × 11.1 km, *n* = 628) used in the Atlas of birds breeding in the Czech Republic in 2001–2003 (Šťastný et al., 2006) in relation to mean elevation of each quadrate (data extracted from Czech topographic base maps).
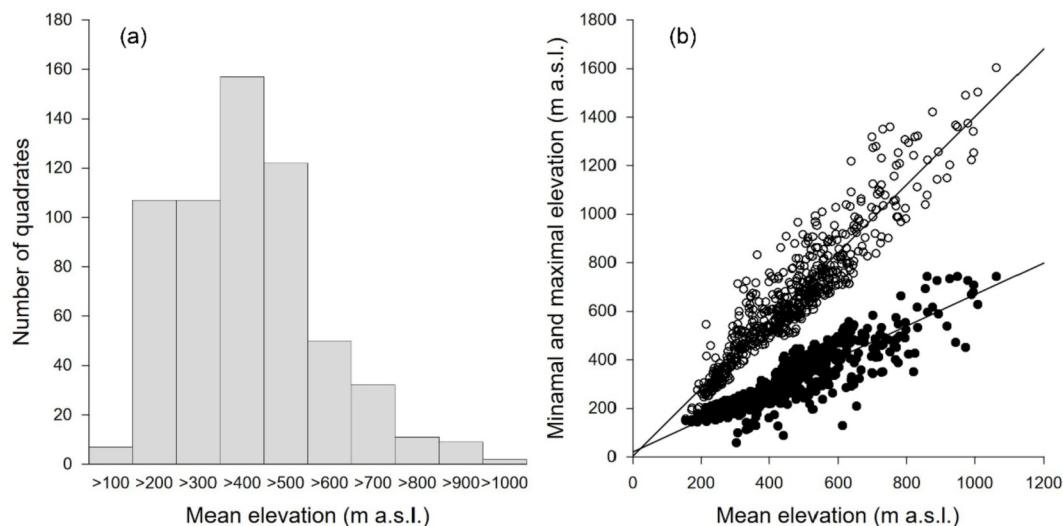
Fig. 2. (a) The distribution of mapping quadrates included in the analysis (a total of 604 quadrates) within a 100-m elevational band and (b) the correlation between mean elevation and minimal (black circle, Spearman's rank correlation coefficients, $r_s = 0.88$) and maximal (white circle, 0.93) elevation of each quadrate.

Table 1

Spearman's rank correlation coefficient matrix ($p < 0.05$) among the proportions of particular land covers (coniferous forest, mixed forest, deciduous forest, open area, and urban area), elevation (mean, minimal, and maximal elevation), and climatic conditions (temperature and rainfall) calculated for each mapping quadrate ($n = 604$). The strongest correlations with the correlation coefficient > (±) 0.70 are in bold.

	Coniferous forest	Deciduous forest	Open area	Mixed forest	Urban area	Mean altitude	Min altitude	Max altitude	Daily temperature	Daily rainfall
Coniferous forest	1.00									
Deciduous forest	−0.37	1.00								
Open area	−0.64	−0.17	1.00							
Mixed forest	−0.02	0.23	−0.61	1.00						
Urban area	−0.43	0.08	0.03	−0.01	1.00					
Mean altitude	**0.75**	−0.29	−0.57	0.22	−0.41	1.00				
Min altitude	**0.74**	−0.39	−0.37	−0.05	−0.44	**0.88**	1.00			
Max altitude	0.66	−0.19	−0.60	0.33	−0.36	**0.93**	**0.71**	1.00		
Daily temperature	−0.47	0.32	0.26	−0.04	0.22	−0.56	−0.49	−0.54	1.00	
Daily rainfall	0.34	−0.20	−0.23	0.04	−0.08	0.35	0.30	0.40	**−0.71**	1.00

Fig. 3. Relationships between the mean elevation of particular mapping quadrates (*n* = 604) divided within a 100-m elevat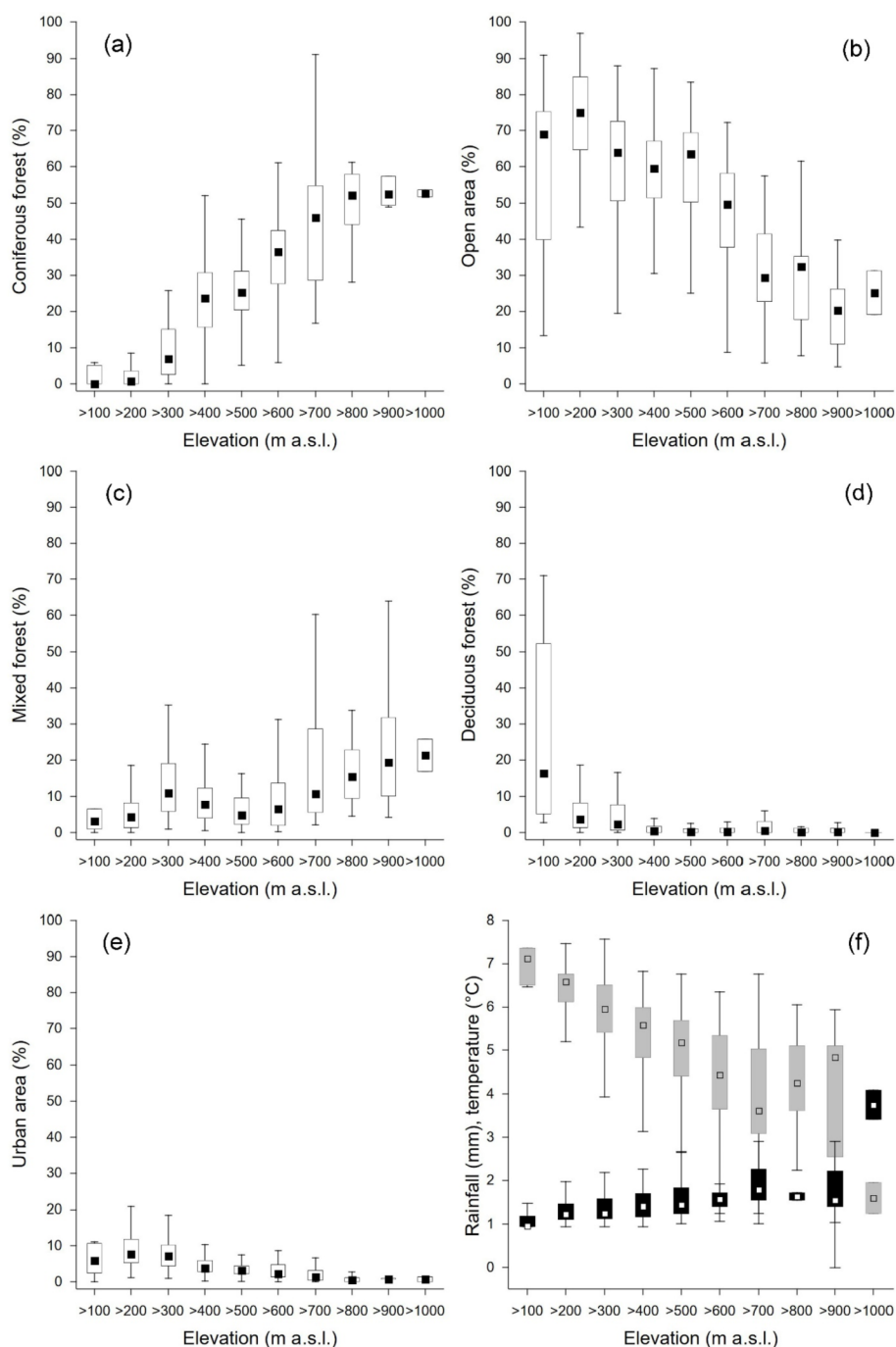ional band and the proportion of a) coniferous forest, b) open area, c) mixed forest, d) deciduous forest, and e) urban area of particular mapping quadrates and f) the mean daily temperature and rainfall (April–May) of particular mapping quadrates.

Table 1, Fig. 3f). Simultaneously, we found correlations between elevation and temperature and between elevation and rainfall; however, the correlation coefficients did not exceed ±0.56 (Table 1, Fig. 3f).

2.5. Statistical analyses

We performed a multivariate analysis to examine the effect of primary predictors, i.e., elevation (mean elevation) and climate conditions (mean daily temperature and rainfall) on the breeding occurrence of seven owl species (0/1). We removed Ural and short-eared owls from the analysis (see above). We included land cover (the proportions of coniferous forest, mixed forest, deciduous forest, open area, and urban area in

each quadrate) as covariates and latitude and longitude as space predictors. We conducted the multivariate analysis using variance partitioning by principal coordinate analysis of neighbour matrices (PCNM) in Canoco 5 (ter Braak and Šmilauer, 2012), the method recently recommended by Marrot et al. (2015). The multivariate analysis has enabled us to separate the effect of space predictors (i.e., the geographical position of sampling squares) and covariates (the proportions of particular land covers) from the effect of the primary predictor (Legendre and Legendre, 2012) that was represented by mean quadrate elevation. Each multivariate analysis included nine steps: (1) primary predictor test (i.e., preliminary test of the overall effect of the primary predictor on the dataset); (2) primary predictor selection by

partial redundancy analysis (RDA), using forward selection based on partial Monte-Carlo permutation tests; (3) principal coordinate analysis (PCoA) based on Euclidean distances (i.e., finding the main space predictors based on latitude and longitude coordinates); (4) PCNM for all predictors (i.e., preliminary test of the overall effect of space predictors on the dataset, including covariates); (5) PCNM selection (i.e., the choice of space predictors based on coordinates, using forward selection and partial Monte-Carlo permutation tests); (6) spatial effects analysis (i.e., assessing the amount of variability explained by space predictors); (7) primary predictor effects analysis (i.e., assessing the amount of variability explained by the primary predictor); (8) joint effects analysis (i.e., evaluating the amount of variability explained by both (i.e., primary and space) predictor types); and (9) removal of spatial effects (Šmilauer and Lepš, 2014). Statistical significance was obtained by Monte-Carlo permutation tests using a forward selection of factors.

3. Results

Tawny and long-eared owls were the most frequent owl species breeding in 352 and 308 mapping quadrates (58.3% and 51.0% of all mapping quadrates, respectively), followed by the Eurasian eagle owl ($n = 238$, 39.4%), barn owl ($n = 184$, 30.5%), and boreal owl ($n = 114$, 18.9%). Eurasian pygmy and little owls were the most less frequent species breeding in 66 (10.9%) and 38 (6.3%) quadrates, respectively (Table 2). The distribution of owls covered the entire elevational range between 100 m and 1100 m a. s. l. Barn owl (mean elevation: 326.4 ± 101.1 m a. s. l.) and little owl (377.2 ± 143.3 m a. s. l.) occupied the quadrates located at the lowest elevation, followed by long-eared owl (405.2 ± 140.3 m a. s. l.), tawny owl (431.7 ± 146.1 m a. s. l.), and eagle owl (474.6 ± 110.0 m a. s. l.). Boreal owl (629.1 ± 161.4 m a. s. l.) and pygmy owl (560.1 ± 159.6 m a. s. l.) occupied the most elevated quadrates (for details, see Table 2). Simultaneously, boreal and pygmy owls occupied the quadrates with the highest proportion of coniferous forests (36.1% and 35.0%) and the lowest daily temperature (4.7 °C and 4.8 °C, Table 2). In contrast, barn owl, little owl, and long-eared owl occurred in the warmest quadrates (6.0 °C, 5.7 °C, and 5.7 °C) with the highest proportion of open areas (71.0%, 64.0%, and 62.4%, Table 2).

Using a multivariate analysis, we found the significant effect of elevation (PCNM analysis, pseudo-F = 14.3, $p = 0.002$, Fig. 4) and temperature (pseudo-F = 2.5, $p = 0.016$) on owl distribution. The effect of rainfall was not significant (pseudo-F = 1.1, $p = 0.368$). The first (elevation) and second (temperature) ordination axes explained 94.8% of the variability. According to variance partitioning, elevation and temperature explained 32.6% of the variability, space predictors 63.3% of the variability, and the shared fraction was 4.2%. Elevation negatively correlated with the first ordination axis (correlation coefficient −0.61) and temperature (−0.37) with the second axis. Along the axes, the owl species showed an obvious distributional pattern. Only the boreal owl showed a clear preference for the highest elevation with cold temperatures. Pygmy owl preferred cold temperatures in middle and low elevation. Eagle owl and tawny owl most often occupied middle and low elevation of moderate temperatures. Barn owl and long-eared owl frequently occupied low elevation of warmest temperatures. Finally, little owl most often occurred in the lowest elevation of intermediate temperatures (Fig. 4).

4. Discussion

Using the multivariate analysis with latitude and longitude included as space predictors and landscape structure as covariates, we found the distributional pattern of owl species along elevational and temperature gradients. Rainfall did not influence the owl distribution; however, it significantly correlated with temperature.

Table 2

The number and proportion of mapping quadrates in which particular owl species were breeding in 2001–2003 in the Czech Republic (data from the Atlas of birds breeding in the Czech Republic; Šťastný et al., 2006). The average (± SD) of mean, minimal, and maximal elevation, the proportion of coniferous forest, mixed forest, deciduous forest, open area, and urban area, and mean daily temperature and rainfall during April and May of occupied quadrates (i.e., the quadrates in which breeding was confirmed) are presented. Relevant data for the Czech Republic are also shown.

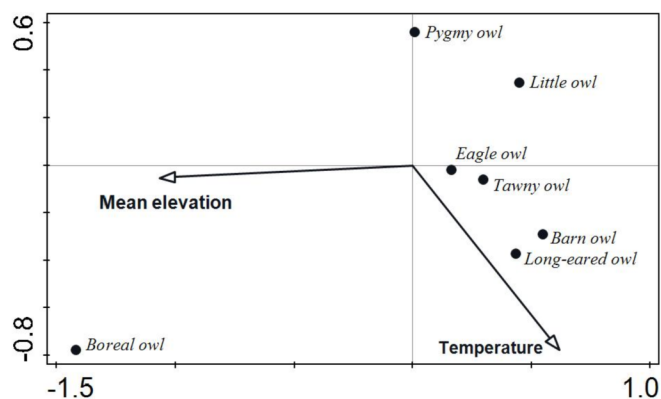| Species/area	Occupied quadrates			Mean elevation (m a.s.l.)	Minimal elevation (m a.s.l.)	Maximal elevation (m a.s.l.)	Coniferous forest (%)	Deciduous forest (%)	Open area (%)	Mixed forest (%)	Urban area (%)	Daily temperature (°C)	Daily rainfall (mm)
Boreal owl	No.	114	Mean	629.1	430.1	890.9	36.1	1.4	46.0	12.2	3.5	4.7	1.7
	%	18.9	SD	161.4	128.0	252.2	16.5	2.9	19.4	14.2	3.6	1.4	0.6
Eurasian pygmy owl	No.	66	Mean	560.1	395.2	775.1	35.0	1.6	48.5	10.0	3.8	4.8	1.6
	%	10.9	SD	159.6	112.6	264.7	14.9	3.7	17.5	12.1	2.9	1.3	0.6
Eurasian eagle owl	No.	238	Mean	474.6	333.1	659.8	23.1	2.2	59.0	9.9	5.0	5.3	1.5
	%	39.4	SD	110.0	99.6	168.2	14.0	4.3	14.3	9.4	4.4	1.1	0.5
Tawny owl	No.	352	Mean	431.7	302.1	606.1	19.2	4.1	59.9	9.5	6.6	5.5	1.5
	%	58.3	SD	146.1	107.6	228.4	15.7	7.4	16.3	8.9	6.6	1.3	0.5
Long-eared owl	No.	308	Mean	405.2	294.4	556.7	17.2	4.1	62.4	8.1	7.2	5.7	1.4
	%	51.0	SD	140.3	113.4	200.6	16.2	7.5	16.0	7.5	7.3	1.2	0.4
Little owl	No.	38	Mean	377.2	255.9	546.9	13.9	3.9	64.0	9.0	8.3	5.7	1.3
	%	6.3	SD	143.3	107.0	206.1	16.1	4.7	17.3	9.3	6.1	1.1	0.3
Barn owl	No.	184	Mean	326.4	229.6	464.2	8.2	5.6	71.0	7.3	7.3	6.0	1.3
	%	30.5	SD	101.1	71.6	159.3	10.4	7.1	12.5	6.5	4.8	0.9	0.3
Czech Republic	No.	604	Mean	460.9	320.2	647.8	21.3	3.5	58.2	10.3	6.0	5.3	1.5
	%	100	SD	165.6	121.8	248.6	17.3	6.7	18.4	10.3	6.4	1.3	0.5

Fig. 4. The multivariate analysis based on principal coordinate analysis of neighbour matrices (PCNM). The effect of elevation and temperature on the breeding occurrence of owl species within the 12.0 × 11.1 km quadrates (*n* = 604 quadrates) in the Czech Republic. Latitude and longitude were included as spatial predictors and the proportion of particular landscape structures as covariates. I and II axes explained 94.8% of the variability together.

4.1. Boreal owl

We found that only the boreal owl showed a clear preference for the highest elevations and cold temperatures. Similar findings were documented by Czech local studies in the Šumava Mountains and the Ore

Mountains (Zárybnická et al., 2015a; Zárybnická et al., 2015b; Zárybnická et al., 2017a) and most of the European bird atlases (for details, see Table 3). In Spain, boreal owl prefers the areas with a higher number of freezing days and higher precipitations (Castro et al., 2008). Hayward et al. (1993) also found that boreal owl individuals roost at colder places and cool themselves using gular fluttering (observed already at temperature 18–23 °C). Boreal owl exhibits an excellent cold resistance due to effective insulation allowing the species to inhabit colder ambient temperatures, while it may suffer from physiological stress at higher temperatures (Hayward et al., 1993; Hohtola et al., 1994). These findings support the suggestion that central and southern European boreal owl populations are a relict of colder ages (Brambilla et al., 2015).

The boreal owl exhibits a circumpolar Holarctic range inhabiting Eurasian and North American coniferous forests (Korpimäki and Hakkarainen, 2012). It mainly prefers to occupy mature and dense Norway spruce forests in Northern (Hakkarainen et al., 2008; Korpimäki and Hakkarainen, 2012) and Central Europe (Zárybnická et al., 2015a; Zárybnická et al., 2017a; Zárybnická et al., 2017b). It finds safe shelters and suitable foraging and breeding conditions in this habitat (Hakkarainen et al., 2008; Zárybnická et al., 2015a). In Europe, the proportion of coniferous forests usually increases with increasing elevation (Kolář et al., 2017; Zárybnická et al., 2017a), which is supposed as a crucial factor for the species distribution. However, in our study, we have found that boreal owl's occurrence probability increased with increasing elevation even though we removed the effect of land cover.

The preference of boreal owl for high elevation occurs despite the

Table 3
The southern and northern limits of latitudinal distribution (i.e., confirmed or probably breeding occurrence according to Hagemeijer and Blair, 1997) and elevational distribution (minimal, maximal, and most common occurrence) of the European owl species.

Species	Latitude		Elevation			Country
	Southern limit	Northern limit	Minimum	Maximum	Most common	
Barn owl	36° N	56° N	200	1000	400–600	Switzerland (Schmid et al., 1998)
			300	400		Great Britain (McCafferty, 1993)
				900		Germany (Gedeon et al., 2014)
				900		Poland (Sikora et al., 2007)
				500	< 150	Austria(Berg and Rottraut, 2002)
Little owl	36° N	55° N	200	600	400–600	Switzerland (Schmid et al., 1998; Walasz and Mielczarek, 1992),
				500		Central Europe (Bauer and Berhold, 1996)
				600		Switzerland (Bauer and Berhold, 1996)
				900		Poland (Sikora et al., 2007)
				200		Austria(Kloibhofer and Lugmair, 2012)
					< 100	Germany(Kloibhofer and Lugmair, 2012)
Long-eared owl	36° N	70° N	200	2000	400–600	Switzerland (Schmid et al., 1998)
			100	600		Germany (Gedeon et al., 2014)
				800		Slovakia (Danko et al., 2002)
			500	1200		Italy (Sergio et al., 2008)
Tawny owl	36° N	66° N	200	2000	400–600	Switzerland (Schmid et al., 1998)
			200	600		Austria (Dvorak et al., 1993)
			300	900		Slovenia (Vrezec, 2003)
				1000		Germany (Gedeon et al., 2014)
				1200		Poland (Sikora et al., 2007)
				1800		Slovakia (Danko et al., 2002)
Eurasian eagle owl	36° N	69° N	200	2600	400–600	Switzerland (Schmid et al., 1998)
			120	1000		Slovakia (Danko et al., 2002)
			900	1200		Poland (Sikora et al., 2007)
				1500		Germany (Gedeon et al., 2014)
				2000		Spain (Hagemeijer and Blair, 1997)
Eurasian pygmy owl	44° N	70° N	600	2400	1200–1400	Switzerland (Schmid et al., 1998)
			400	1600	600–1100	Slovakia (Danko et al., 2002; Pačenovský and Šotnár, 2010; Sikora et al., 2007)
					800–1000, 1200–1600	Austria (Dvorak et al., 1993)
			700	2100		Germany (Scherzinger, 1970)
					1400–1800	Bulgaria(Pačenovský and Shurulinkov, 2008)
Boreal owl	42° N	70° N	400	2200	1200–1400	Switzerland (Schmid et al., 1998)
			600	1000		Poland (Flousek et al., 2015)
			700	1000		Slovenia (Vrezec, 2003)
			800	1800		Austria (Dvorak et al., 1993)

limited quality of the diet available in these areas (accompanied by the higher proportion of *Sorex* shrews in the diet, Zárybnická et al., 2017a). The presence of other competitors, particularly tawny owl, can explain the limited occurrence of boreal owl at lower elevations (Hudec et al., 2011; Zárybnická et al., 2017a). The alternating distribution of boreal owl and tawny owl has also been documented in Slovakia and Poland (Flousek et al., 2015), Austria (Dvorak et al., 1993), Slovenia (Vrezec, 2003), and Switzerland (Knaus et al., 2018; Schmid et al., 1998). Clear evidence of competitive exclusion between these two species also reported Vrezec and Tome (2004a). Similar exclusion behaviour of boreal and tawny owl populations has been observed in the Ore Mountains in the Czech Republic (R. Ševčík and M. Zárybnická, unpubl. data). Therefore, we suggest that boreal owl can benefit from inhabiting coniferous forests at high elevations by reducing interspecific competition with other owl species, especially tawny owl. This narrowed habitat selectivity is in accordance with the high level of specialization of boreal owl reported by Morelli et al. (2019), indicating the potential risk for this species in the face of land-use changes and climate such as global warming (Julliard et al., 2006).

4.2. Pygmy owl

Pygmy owl showed a preference for cold quadrates in middle and low elevations. This owl species exhibits a Palearctic distribution and prefers to occupy boreal coniferous forests in the cold montane zone, while its distribution in southern Europe is limited (Hagemeijer and Blair, 1997). Like the boreal owl, the central and south European pygmy owl populations are suggested to be a relict of colder ages (Brambilla et al., 2015). Simultaneously, pygmy owl also prefers to inhabit high latitudes of taiga, where most of the other predators or competitors do not find suitable conditions for breeding and hunting (Pačenovský and Shurulinkov, 2008; Strøm and Sonerud, 2001). Based on atlas maps and local studies, pygmy owl inhabits old coniferous forests from lowlands to mountains in the Czech Republic (Hlásek, 1981; Hudec and Šťastný, 2005; Kloubec et al., 2015). However, our multivariate analysis discovered that this species preferred to occupy cold regions at middle and low elevation and avoided the highest elevation. An example of cold habitats in lowlands can be deep valleys with a temperature inversion; additional studies would be helpful to understand the distribution pattern of this owl in central Europe.

4.3. Tawny and eagle owls

Tawny and eagle owls preferred to occupy middle and low elevations of moderate temperatures. Both species exhibit a Palearctic distribution, reaching up to the highest latitudes in Europe (Hagemeijer and Blair, 1997; Hudec and Šťastný, 2005). They settle the temperate forest zone from boreal to Mediterranean habitats, where they occupy various forests from lowlands to mountains (Hagemeijer and Blair, 1997; Marchesi et al., 2002; Sasvári and Hegyi, 2011a, 2011b). In the Czech Republic, these two species inhabit mainly mixed and deciduous forests located in middle elevation (Hudec and Šťastný, 2005; Šťastný et al., 2006). Similar to the findings of our study, these species often occupy moderate elevations in most European countries (for details, see Table 3). Based on previous studies, both species inhabit a wide elevation band and adjust their distribution according to environmental conditions, such as, for example, food availability and intraspecific competition (Penteriani and Delgado, 2019; Sasvári and Hegyi, 2011a, 2011b).

4.4. Barn and long-eared owls

Barn owl and long-eared owl preferred to occupy the warmest quadrates within low elevations. The barn owl exhibits a cosmopolitan distribution, and it often inhabits lower latitudes and frequently occurs in Ethiopic areas (König and Weick, 2008; Riegert et al., 2021). In Europe, the northern distributional limit of this species reaches only 56°

N (Hagemeijer and Blair, 1997). Compared to the barn owl, the long-eared owl shows a Holarctic distribution and frequently occupies high latitudes reaching up to 70° (Hagemeijer and Blair, 1997). In temperate areas of Europe, both these species most often inhabit low and middle elevation (for details, see Table 3), probably due to optimal environmental conditions. It has been documented that cold temperatures can limit the occurrence and reproductive success of these owls. More specifically, continuous deep snow cover and harsh winters in the mountains can limit their occurrence due to limited access to small mammal prey (e.g., Altwegg et al., 2003; Altwegg et al., 2006; Sonerud, 1986). Low temperatures and severe weather can also limit barn owls' thermoregulation (resulting in increased body heat losses) and reduce the survival rate of this species (Altwegg et al., 2003; Massemin and Handrich, 1997). In Mediterranean areas, long-eared owl prefers to inhabit lower elevations due to the absence of open habitats and limited food availability at higher elevations (Bartolommei et al., 2013; Emin et al., 2018). The findings of our study confirm that barn and long-eared owls readily inhabit low-elevated and warm localities also in the Czech Republic.

4.5. Little owl

We found that the little owl preferred to inhabit the quadrates with intermediate temperatures in lowlands. The preference of this species for low elevation has been documented in other European regions (for details, see Table 3). Previous studies have also found that little owl readily occupies warm areas with low rainfall and snow cover (Andersen et al., 2017; Van Nieuwenhuyse et al., 2008), and cold winters limit the survival of this species due to increased winter mortality (Gouar et al., 2010; Van Nieuwenhuyse et al., 2008). From all the owl species included in our analysis, only the little owl exhibits the Turkey-Mediterranean distribution with the highest European range reaching 55° N (Hagemeijer and Blair, 1997; Hudec and Šťastný, 2005). The populations occurring in cold northern areas are more likely to decline and disappear compared to the southern populations (Andersen et al., 2017).

Landscape structure, represented by the presence of open areas, can affect the distribution of little owl (Hudec and Šťastný, 2005; Šálek and Schröpfer, 2008). Mainly, the occurrence of little owl depends on the presence of the agricultural landscape, including grassland, arable land, crops, orchards, and meadows (Šálek and Lövy, 2012; Šálek and Schröpfer, 2008; Van Nieuwenhuyse et al., 2008; Zabala-Albizua et al., 2006). The unsuitable agricultural management of these areas was a reason for the rapid drop of little owl populations documented during the last 60 years in central Europe (Šálek and Schröpfer, 2008). We found that the proportion of open areas significantly increased with decreasing elevation in the Czech Republic. Our findings suggest that little owl does not avoid to occupy colder areas in low elevations that can be represented, for example, by deep valleys with a temperature inversion. However, the low-elevated and warm regions with open habitats seem to be the most optimal for this species.

5. Conclusion

We found that elevation and temperature, controlled for habitat types, significantly influenced the owl distribution in the Czech Republic, but particular species showed different responses. Boreal and little owls were the most limited by elevation. While boreal owl preferred to occupy the highest elevations, little owl favored settling the lowest elevations. Boreal owl, pygmy owl, barn owl, and long-eared owl were the most limited by temperatures. While boreal and pygmy owls preferred to occupy the coldest quadrates, barn and long-eared owls inhabited the warmest quadrates. From a view of species protection of forest-dwelling animals, the boreal owl can be especially susceptible to global warming and intensive logging at high elevations.

Declaration of Competing Interest

None.

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3.2 Study II.

Forest structure determines nest box use by Central European boreal owls

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Authors contribution:

M. Zárybnická and B. Kloubec conceived and designed the research topic and field experiment.

M. Zárybnická and **R. Ševčík** wrote and revised the manuscript.

J. Riegert, M. Zárybnická and **R. Ševčík** analyzed and visualized data.

R. Ševčík analyzed audio recordings.

R. Ševčík, B. Kloubec, J. Šindelář, M. Kouba and M. Zárybnická collected field data.

R. Ševčík, M. Zárybnická, B. Kloubec, J. Riegert, J. Šindelář, and M. Kouba edited the manuscript.

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Forest structure determines nest box use by Central European boreal owls

Richard Ševčík[1], Bohuslav Kloubec[1], Jan Riegert[2], Jiří Šindelář[1], Marek Kouba[3] & Markéta Zárybnická[1✉]

Nest boxes represent a popular tool to support secondary cavity-nesting species. Surprisingly, the benefits and limitations of nest boxes for target species in different environments are poorly understood. We performed a 3-years experimental study in two different Central European forests to evaluate nest box use and breeding performance of boreal owl (*Aegolius funereus*) — a species well known for its readiness to occupy nest boxes. Based on territorial vocalisation, two boreal owl populations 200 km apart were similarly abundant in their environments. However, only the boreal owl population in young restored Norway (*Picea abies*) and blue (*Picea pungens*) spruce-dominated forests on mountain plateaus readily occupied nest boxes with the occupancy reaching 8–15%. Nest boxes lost their supporting function for the boreal owl in mature Scots pine (*Pinus sylvestris*)-dominated forests in the lowland, where the nest box occupancy reached 0–1%. As a result, the population of boreal owls that used nest boxes in the young restored forests produced 10 times more fledglings than the population inhabiting mature Scots pine forests. We explain the differences by the contrasting availability of natural tree cavities between the two study areas being much higher in mature Scots pine forests. For the first time, this study documents differences in nest box use despite similar food availability and population size of the target species. The study provides the findings-related recommendations for deploying nest boxes for boreal owls and points out a general lack of practical guides.

The availability of natural tree cavities is crucial for survival of secondary cavity-nesting species, including owls[1,2]. For example, the boreal owl, *Aegolius funereus,* depends on the availability of cavities excavated by the black woodpecker, *Dryocopus martius*[3,4]. Such cavities occur more frequently in management-free, old deciduous, and pine forests than in spruce monocultures[5–7]. When natural cavities are rare or lacking, artificial opportunities may play a key role for secondary-cavity nesters. Nest boxes are a case of a worldwide popular tool to enhance the availability of nest sites[2,8,9]. They also allow studying the breeding and trophic ecology of species, their life-history strategies, interspecific interactions, and provide conditions for camera nest monitoring that would be hard to do in natural cavities (e.g.,[3,9–11]). However, the readiness to use nest boxes differs among species (e.g., boreal owl vs. pygmy owl *Glaucidium passerinum*[4]), and it can even vary within one species under variable environments (e.g., great tit *Parus major*[12]). Despite the high popularity of nest boxes among amateur and professional ecologists, studies comparing the effectiveness of nest boxes in different environments and providing practical guides for deploying nest boxes for specific species are often entirely lacking.

The boreal owl is a secondary cavity nester with a Holarctic distribution, spreading across the boreal forest of northern North America, Europe, and Asia[13]. In Europe, this threatened species (European directive 2009/147/EC, Annex I) exhibits foraging, habitat, and nest-site specialization[14]. It predominantly inhabits coniferous forests in the northern latitudes and coniferous or mixed forests in high altitudes in Central and Southern Europe[4,15]. This species is limited by the availability of natural tree cavities excavated by black woodpeckers; however, it also readily breeds in artificial wooden boxes (e.g.,[3,16]). The readiness of this species to occupy nest boxes makes this owl a 'textbook example' of a species whose breeding biology and trophic ecology have been primarily discovered based on nest box populations (e.g.,[3,17,18]). However, the nest box occupancy by this species varies hugely over regions, countries, and continents, reaching from units to tens of percentages (Table 1). Surprisingly, we still

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State	Locality	Elevation	Period	No. of boxes/ year	No. of box-years	No. of nests			Nest box occupancy (%)				References
						Total	Min	Max	Total	Mean	Min	Max	
Canada	Southern Yukon		1984–96	13–105	573	6			1				[20]
Canada	Alberta region	470–920	2016	169	169	4			2				[21]
USA	Alaska	90–150	1995–97	36	108	29			27				[22]
USA	Alaska	200–650	2005–06	91, 108	199	23			12				[23]
USA	Alaska	110–690	2015	200	200	27			14				[24]
USA	Rocky Mts.	1700	1985–88	45	180	3			2				[17]
USA	Idaho	1520–2140	1988–90	283–450	1016					4			[25]
USA	Rocky Mts.		1995–01	250–450						1			[26]
China	Lianhuashan Mts.		2003–07	67	335		4	7			6	10	[27]
Sweden	Västerbotten		1980–84	500	2500	525	4	201	21		1	40	[28]
Sweden	Västerbotten		1981–82, 1984–85	44–149		330	5	99		30	6	66	[29]
Sweden	Västerbotten		1998–99	300	600	84					15	22	[30]
Sweden	Västerbotten		2006–07	273, 275	548	47			9		2	15	[31]
Finland	Kauhava region	30–120	1966–85	35–450	4577	352	2	63	8		2	22	[32]
Finland	Kauhava region	30–120	1966–08	hundreds	677	104			15				[3]
Czech Rep.	Ore Mountains	730–960	2000–03	100	400	72	10	26	18		10	26	[33]
Czech Rep.	Šumava Mts.	500–1300	1984–05	211	4448	316			7				[34]
Czech Rep.	Šumava Mts.	500–1100	1992–02	395		250				6	4	8	[35]
Czech Rep.	Šumava Mts.	400–1378	1978–02		5006	299				6			[36]
Czech Rep.	Krkonoše Mts.		1985–86	40, 60	100	1			1		0	2.5	[37]
Switzerland, France	Jura Mts.	1000–1600	1985–14	64–116	2550	425	2	39	17		3	55	[38]
Germany	Kaufunger Wald	250–580	1965–84	60	1200	76			6				[39]
Germany	Harz Mts.	450–850	1979–91	250	3250	390			12				[40]
Germany	Olpe	430–580	1981–10	4–64	1034	187	0	20	18		0	56	[41]
Italy	Cansiglio Highland		1989–20	80–100	2400	93			4				[42]
Serbia	Kopaonik National Park	800–2017	2011–13	63	189	9			5				[43]

Table 1. Nest box use by the boreal owl in Europe, North America, and Asia; the state, locality, elevation, period, the number of boxes, nests, box-years, and the nest box occupancy (expressed as the proportion of occupied nest boxes of checked boxes). The way how authors described their results varied hugely. Therefore, we present the information on the number of boxes, nests, and nest box occupancy from long-term studies either as a sum counted for the entire study period (marked as 'Total') or a yearly mean (marked as 'Mean') with minimum ('Min') and maximum ('Max') values.

poorly understand the general pattern of the nest box occupancy by boreal owls and the breeding performance of this species under various environments (for rare study, see[19]).

We performed nest box and territorial vocal experiments in two contrasting environments in Central Europe (Czech Republic) to examine the use of nest boxes and their benefits for target species, using boreal owl as a case species. We expected i) to find a higher nest box occupancy by boreal owls in young restored Norway (*Picea abies*) and blue (*Picea pungens*) spruce-dominated forests than in Scots pine (*Pinus sylvestris*) forests due to the substantially increased availability of natural cavities in the second area. As a result, ii) the fledgling productivity of the boreal owl population using nest boxes would be higher in young restored forests than in mature forests. We also expected to find iii) a higher nest box occupancy by other secondary cavity-nesting birds (i.e., passerines) in young restored Norway and blue spruce-dominated forests than in Scots pine forests and iv) no evidence for an interspecific competition limiting nest box use by boreal owls in any study area. Finally, we aimed to use our findings to create specific recommendations for deploying nest boxes for the boreal owl.

Materials and methods
Study areas.
In 2015–2017, we conducted the experimental study in two environments, in the northwest and the southern Czech Republic (200 km apart; Fig. 1), which differed in forest structure, elevation, and climate conditions (Table 2). We located the first study area in a historically air-polluted area on the Ore Mountains plateau, neighbouring Saxony, Germany. We have been using this study area for the boreal owl nest box research since 1999[33,44]. We gradually erected the second study area in 2012–2014 in the lowland Protected Landscape Area of the Trebon Basin close to the border to Austria.

The two study areas differed in the history of human activities. The Ore Mts. were exposed to extreme SO_2 and NO_x pollution emitted in the 1970–80s from factories located in the foothills, followed by extensive forest
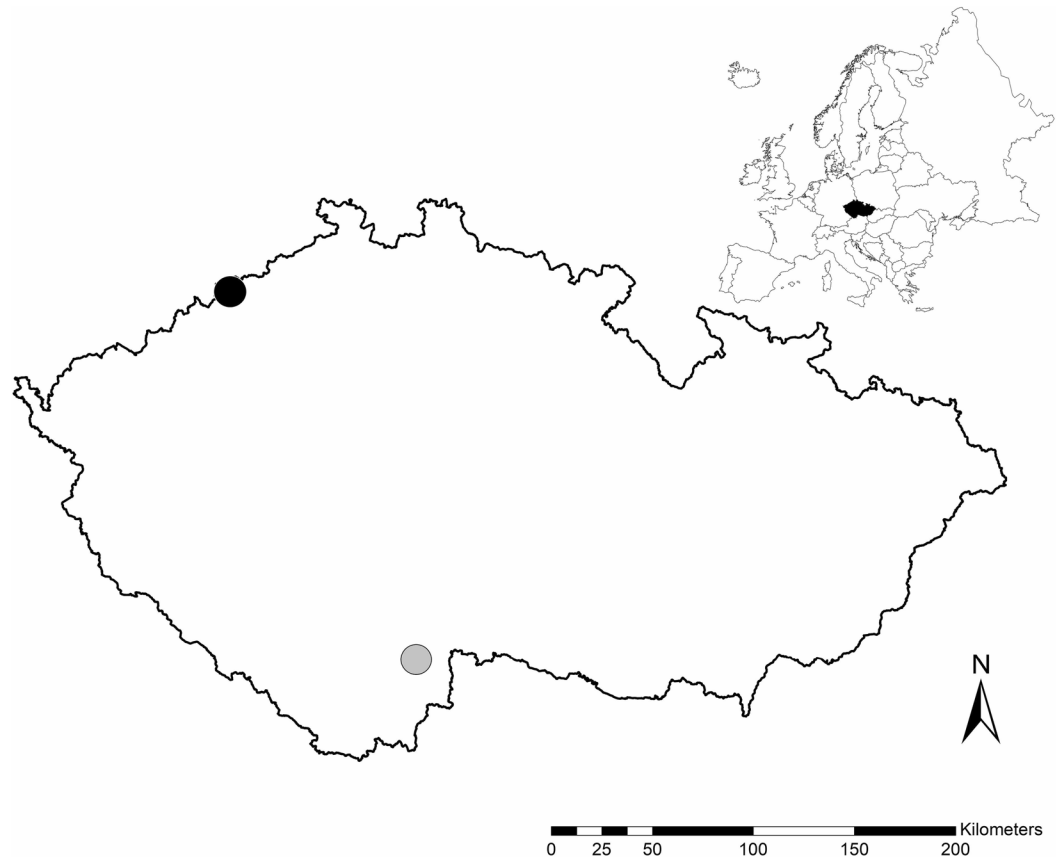
Figure 1. Two study areas in the Czech Republic: a historically air-polluted area in the Ore Mts. (51°N, 14°E, black point) and a protected landscape area in the Trebon Basin (49°N, 15°E; grey point).

	Ore Mts.			Trebon Basin		
		%	Mean ± SD		%	Mean ± SD
Latitude, longitude	51°N, 14°E			49°N, 15°E		
Area (km²)	150			400		
Elevation (m a. s. l.)	700–920		791.8 ± 69.8	420–500		456.9 ± 19.6
Daily temperature (°C)			7.0 ± 0.3			9.2 ± 0.6
Daily rainfall (mm)			2.5 ± 0.3			1.5 ± 0.2
Snow cover (days)			80.3 ± 17.6			31.7 ± 20.4
Forest habitat		87.0			47.0	
Pasture and grasslands		9.6			15.0	
Agriculture area		1.9			13.0	
Water area		1.0			10.0	
Urban area		0.5			15.0	
No. of territories	0.5–1			1–10		
No. of tree cavities	0–1			1–5		

Table 2. Basic information about the study areas. Geographical position, the size of the area, elevation, climate conditions (mean daily temperature, mean daily rainfall, and the yearly mean number of days with continual snow cover), habitat composition (based on CORINE Land Cover 2018), and estimates of the number of black woodpecker's territories (per 1 km²) and tree cavities (per 1 ha) excavated by black woodpeckers are shown.
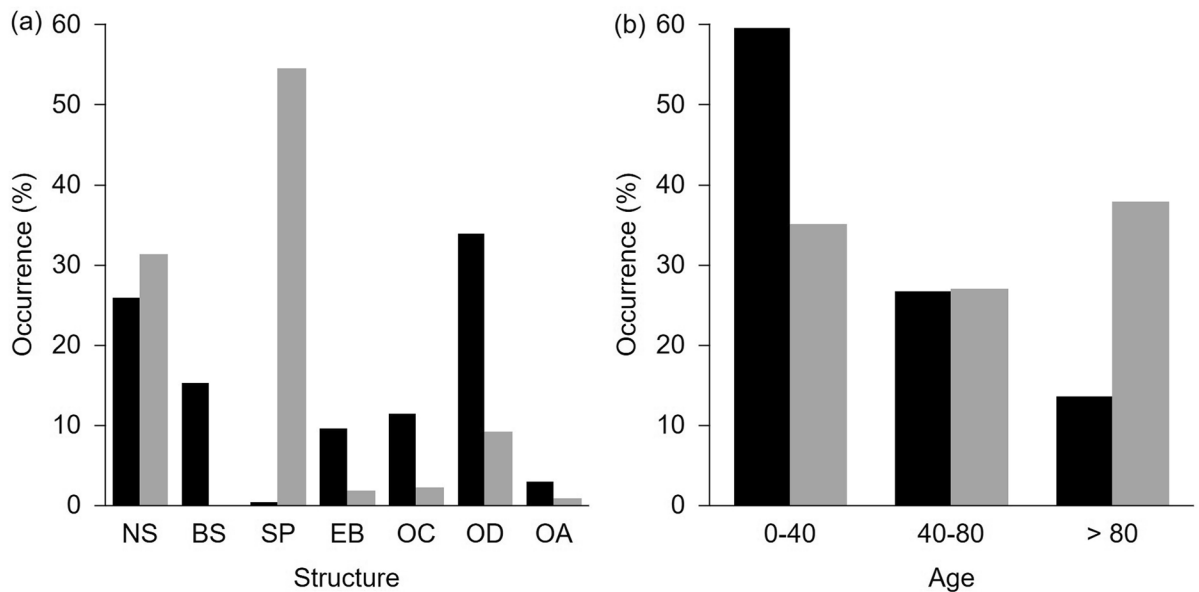
Figure 2. The structure (**a**) and age (**b**) of forest stands (in proportions) in the Ore Mts. (black bars) and the Trebon Basin (grey bars). NS – Norway spruce, BS – blue spruce, SP – Scots pine, EB – European beech, OC – other coniferous species, OD – other deciduous species, OA – open areas. Data are evaluated based on the vegetation maps of the Czech Forestry Institute.

losses, dramatic changes in animal communities, and massive restoration processes hindered by acid soil, harsh mountain climate, and extensive damage to young plantations caused by cervids[45]. Nowadays, the habitat of the Ore Mts. is formed by a mosaic of large areas of young coniferous (mainly native Norway spruce and non-native blue spruce) and deciduous stands, small patches (usually 0.5–2.0 ha) of mature Norway spruce, and old solitary European beech (*Fagus sylvatica*) trees. The Trebon Basin has been a protected landscape area since 1979, accompanied by forest, water, and agriculture management. The habitat consists of mature Scots pine and Norway spruce coniferous forests formed as monocultures with numbers of small (usually less 1-ha) clear-cuts.

Forest structure comparison. Forest habitats dominated both study areas, covering 87% and 47% of the Ore Mts. and Trebon Basin study area, respectively. The area of any of the other habitat types (pasture and grasslands, agriculture, water, and urban areas) did not exceed 15% (for details, see Table 2; data based on CORINE Land Cover 2018). We used vegetation maps of forest stands (the Czech Forestry Institute, 2015–2017) to compare species and age forest structures between the study areas. First, we grouped forest stands into seven categories according to the dominant tree species (i.e., Norway spruce, blue spruce, Scots pine, European beech, other coniferous stands, other deciduous stands, and clear-cuts). We counted the proportion of each species category within each study area. We found that the structure of forest stands differed significantly between the areas (Chi-squared test: Chi = 722.59, $P < 0.001$, df = 6). Norway (26.0%) and blue (15.4%) spruces were dominant tree species in the Ore Mountains, while Scots pine (54.5%) and Norway spruce (31.3%) were dominant tree species in the Trebon Basin (Fig. 2a). Second, we grouped forest stands into three categories according to age (0–40 years, 40–80 years, > 80 years). We counted the proportion of each age category within each study area. We found the age of forest stands significantly differed between the areas (Chi-squared test: Chi = 32.67, $P < 0.001$, df = 2). The less-than-40 years habitats dominated in the Ore Mts. On the contrary, all age categories of forest stands in the Trebon Basin occurred evenly (Fig. 2b).

Black woodpecker populations. We recorded a substantially more abundant population of black woodpeckers (assessed based on territorial calls[46]) and number of cavities excavated by this species in the Trebon Basin than the Ore Mts. (Table 2).

Nest box occupancy. To evaluate nest box occupancy, we used an existing nest box system in the Ore Mts. (for details, see the chapter Study areas) in which 246 nest boxes were evenly distributed in forest habitats over an area of 150 km² with a density (mean ± SD) 1.65 ± 0.05 nest boxes/km². In 2012–2014, we erected a similar nest-box distribution scheme in the Trebon Basin. Forest habitats of this area were separated by other habitat types (i.e., pastures, agriculture, water, and urban areas) to a greater extent than in the Ore Mts., covering a total of 400 km². In the Trebon Basin, we evenly distributed 245 nest boxes with a density (mean ± SD) of 0.60 ± 0.01 nest boxes/km².

We provided the same type of nest boxes in both study areas. The nest boxes were made of 2-cm thick wooden planks. The bottom area dimensions counted for 20–25 × 20–25 cm, the height of the walls was 40 cm, and the roof exceeded the front wall by 5 cm. The entrance had a diameter of 8 cm. All nest boxes were painted with dark brown colour and filled with a 3–5 cm layer of sawdust, resulting in an effective distance of 20–22 cm from the

bottom (i.e., top of the sawdust) to the lowest part of the entrance. We positioned nest boxes 3–5 m above the ground and kept them in good conditions, i.e., they were repaired, cleaned, and filled with new sawdust after each breeding season. The surrounding of all nest box entrances was kept free of vegetation. The mean age of nest boxes (i.e., the number of years since the nest box installation or reinstallation counted for all nest boxes in all study years) was (mean ± SD) 4.9 ± 4.4 years in the Ore Mts. (n = 722 boxes) and 3.2 ± 1.1 years in the Trebon Basin (n = 724 boxes).

We identified nest box use by boreal owls and other animals based on present animals and their active nests or reliable traces of animal activities (e.g., an abandoned nest or nest material) inside the boxes. Each year, we checked 230–246 boxes in the Ore Mts. and 237–245 boxes in the Trebon Basin to identify the number of boreal owl nests. We included nest boxes with the presence or absence (0/1) of boreal owl nests in the GLMM analysis (see below). We further conducted synchronized spring (i.e., in April 2015 and May 2016–2017) and autumn (in September 2016 and October 2017) nest box inspections in both study areas to identify nest box use by boreal owls and other animal taxa. We synchronously checked 230–246 nest boxes (i.e., 230, 246, and 246 boxes in both spring and autumn) and 56–245 nest boxes (i.e., 245, 242, and 237 boxes in spring and 0, 56, and 200 boxes in autumn) during spring and autumn nest box inspections in 2015–2017 in the Ore Mts. and Trebon Basin, respectively. We included nest boxes with the presence or absence (0/1) of other taxa in the CCA analysis (see below). We also calculated the nest box occupancy rate as the number of boxes with present animal taxa or their traces per all checked nest boxes within a specific period and year. Alternatively, we presented the nest box occupancy as the proportion of occupied nest boxes of all erected nest boxes.

Boreal owl nests. We accomplished additional inspections in the boxes where boreal owl nests occurred to determine the number of eggs, fledglings, nests depredated by martens (*Martes* sp.), and nests abandoned by boreal owl females with no fledgling produced (according to[19]). We counted boreal owl breeding productivity based on these data; however, we did not include additional inspections in statistical analyses.

Owls' vocalisation. At the beginning of April and May in 2015–2017 (a total of six recording events), we distributed audio recordings across both study areas to monitor the presence and absence of all owl species based on territorial vocal activity. In the Ore Mts., we placed 36 audio recorders during each recording event on sampling points within a regular grid with a span of (mean ± SD) 2.0 ± 0.3 km (min–max: 1.6–2.6 km, 25–75% range: 1.8–2.1 km, see also[47]). In Trebon Basin, we placed 32 audio recorders within a span of 2.5 ± 0.6 km (min–max: 1.7–3.4 km, 25–75% range: 1.9–2.7 km). We installed audio recorders (Olympus DM650, Olympus Corporation, Japan) with automatic time-recording settings during suitable weather conditions (i.e., without strong wind and precipitations) on tree trunks at the height of 1.5 m above the ground. We left audio recorders exposed for one night during each recording event (April, May 2015–2017). We set the recording time of each audio recorder (at least) from 8 PM to 6 AM, allowing us to evaluate owl vocalisation during continuous 10-h recording at each sampling point (recorder) and recording event. We collected a total of 216 and 192 recordings (sampling points) in the Ore Mts. and Trebon Basin, respectively, out of which we excluded 13 and 14 recordings due to technical failures. As a result, we used a total of 2030 h (i.e., 203 sampling points) in the Ore Mts. and 1780 h (i.e., 178 sampling points) in the Trebon Basin to evaluate territorial owl calls.

We transformed particular audio recordings into spectrograms and analysed them using AMSrv software[48], setting the spectrum at 1 min with FFT length, the window size of 4096 × 1366. We used no filters to remove background noise. We recognized the vocal activities of owls based on territorial calls of particular species[46]. We included sampling points with vocal presence or absence (0/1) of each owl species into subsequent analyses. Simultaneously, we calculated the vocal occupancy rate as the number of sampling points with the vocal presence of owl species per all sampling points, sorted according to the sampling period and year. Based on vocal activity, we also estimated the density for each owl species per 10 km^2, considering the area of 3.14 km^2 (radius 1 km) per one sampling point.

Small mammal abundances. The boreal owl primarily feeds on small mammals, mainly *Microtus* and *Myodes* voles, *Apodemus* mice, and *Sorex* shrews[18,49]. The abundance of voles and mice affects breeding characteristics, including territorial vocal activity[47], breeding performance[19], home range size[50], and parental investment[51]. Therefore, we assessed the abundance of small mammals using snap trapping carried out every year at the beginning of June by setting up snap traps at six blocks (30 × 90 m, 4 × 10 traps, 10-m span) within representative habitats of each study area. The traps were left for three days in the field and checked every morning. We determined all captured small mammals (n = 102 individuals) to species and grouped them into four categories: *Apodemus* mice, *Microtus* voles, *Myodes* voles, and *Sorex* shrews. We also calculated the abundance index as the number of captured individuals of each category per 100 trap nights for each trapping site (for details, see[18]).

Statistical analyses. We used generalized linear mixed models (GLMM) in R 4.0.2 software[52] to assess the effect of the study area and year on the abundance of small mammals. Using *lmer* function (package Lme4), we created four models with *Apodemus* mouse, *Myodes*, and *Microtus* vole, and *Sorex* shrew abundances as dependent variables. We calculated the number of trapped individuals per 100 trap nights for each trapping site, study area, and year (trapping index) for each dependent variable. The study area, year, and the interaction of the study area and year were used as independent variables and the trapping site as a random effect. We also calculated partial relationships between the study areas and years using a post-hoc test (function *lsmeans* in lsmeans package).

Response variable	Explanatory variable	% of explained variability	F	P
Vocal occupancy rate	Study area	56.53	8.2	0.002
	Year	26.37	3.8	0.002
	Sampling period	8.28	1.2	0.306
Nest box occupancy rate	Study area	36.87	30.0	0.002
	Sampling period	50.31	40.4	0.002
	Year	8.05	6.6	0.002

Table 3. The results of CCA analyses. First analysis: the effect of the study area (Ore Mts., Trebon Basin), year (2015–2017), and sampling period (April, May) on the vocal occurrence (0/1) of each owl species. Second analysis: the effect of the study area, year, and sampling period (spring, autumn) on nest box occupancy (0/1) by animal taxa (boreal owl, goldeneye, pine marten, passerines, bats, and insects).

To compare the nest box occupancy by boreal owls between the study areas, we used GLMM analysis (*lmer* function) with a binomial distribution of the dependent variable. We examined the effect of the study area on the occurrence of boreal owl nests (0/1). We included the density of nest boxes (i.e., the number of nest boxes within a buffer of 1000 m of each nest box) as a covariate and ID box and year as random effects.

We performed a multivariate canonical correspondence analysis (CCA) in Canoco 5 software[53] to examine the effect of primary predictors, i.e., the study area, year (2015–2017), and period (April, May) on the vocal occurrence (0/1) of each owl species. We used the sampling point of each audio recording as a categorical covariate. Further, we computed another CCA analysis to examine the effect of primary predictors, i.e., the study area, year (2015–2017), and period (spring, autumn) on nest box occupancy (0/1) by boreal owls and other animal taxa (i.e., pine marten *Martes martes*, passerines, common goldeneye *Bucephala clangula*, insects, bats). We used the number of boxes in a buffer of 1000 m around each box (continuous variable) and ID box (categorical variable) as covariates.

Ethical statement.   We conducted our research in conformance with all applicable laws; we worked under the permissions of SR/0006/TR/2015 and 173/049/ZPZ/2015/ZD-838 issued by the Nature Conservation Agency of the Czech Republic.

Results

Small mammal abundances.   *Apodemus* mice and *Myodes* voles were the most abundant species in both study areas, counting 54.0% (n = 41) and 40.8% (n = 31) of all trapped individuals in the Ore Mts. and 53.9% (n = 14) and 38.5% (n = 10) of all trapped individuals in the Trebon Basin. *Microtus* voles and *Sorex* shrew were rare species (< 4%) in both study areas (Supplementary Information, Table S1). The abundance of *Myodes* voles, *Microtus* voles, and *Sorex* shrews did not differ between study areas and years (Supplementary Information, Table S2). However, the abundance of *Apodemus* mice was significantly affected by the interaction of the study area and year (GLMM; Chi = 13.45, df = 32, $P = 0.004$, Supplementary Information, Table S2). A post-hoc test showed that *Apodemus* mice were significantly more abundant in 2017 in the Ore Mts. compared to the Trebon Basin (post-hoc test; t = 3.58, $P = 0.011$, Supplementary Information, Table S3. In the Ore Mts., the abundance of *Apodemus* mice also differed significantly between 2016 and 2017 (post-hoc test; t = − 4.21, $P = 0.004$, Supplementary Information, Table S3).

Owls' vocalisation.   Based on territorial vocal activity, we identified the same five owl species — boreal owl, tawny owl *Strix aluco*, long-eared owl *Asio otus*, Eurasian pygmy owl, and Eurasian eagle owl *Bubo bubo* — within each study area. The vocal occurrence rate of owl species (all owl species included) varied from 0 to 0.59 and 0 to 0.58 per sampling point in the Ore Mts. and Trebon Basin, respectively (Supplementary Information, Table S4). Using CCA, we found a significant effect of the study area and year on the vocal occurrence of owl species, but the sampling period (April, May) had no effect (Table 3). The first and second ordination axes explained together 94.7% of the variability. Boreal and tawny owls were the most frequently recorded owl species in both study areas and all years (Supplementary Information, Table S4). Comparing the study areas showed that the boreal owl vocal occupancy rate was similar and simultaneously the highest in 2015 in both study areas (Fig. 3, Supplementary Information, Table S4). However, it was slightly higher in 2016 and 2017 in the Ore Mts. compared to the Trebon Basin (Fig. 3, Supplementary Information, Table S4). Contrary, the vocal occupancy rate of the tawny owls was similar in 2016 in both study areas, but it was higher in 2015 and 2017 in the Trebon Basin compared to the Ore Mts. (Supplementary Information, Table S4). Pygmy owls occurred more frequently in the Trebon Basin than in the Ore Mts.; however, long-eared owls showed an opposite trend (Fig. 3, Supplementary Information, Table S4). Eagle owl was a rare species in both study areas; it was absent in 2015 and 2017 in the Ore Mts. and 2016 in the Trebon Basin (Fig. 3, Supplementary Information, Table S4).

The density of vocalising owl populations reached yearly 0–1.87 and 0–1.85 individuals per 10 km^2 in the Ore Mts. and Trebon Basin, respectively (for details, see Supplementary Information, Table S4). Boreal and tawny owls were the most abundant species in the Ore Mts., followed by long-eared owls, pygmy owls, and eagle owls. Tawny and boreal owl were the most abundant species in the Trebon Basin, followed by pygmy owl, long-eared owl, and eagle owl (Supplementary Information, Table S4).
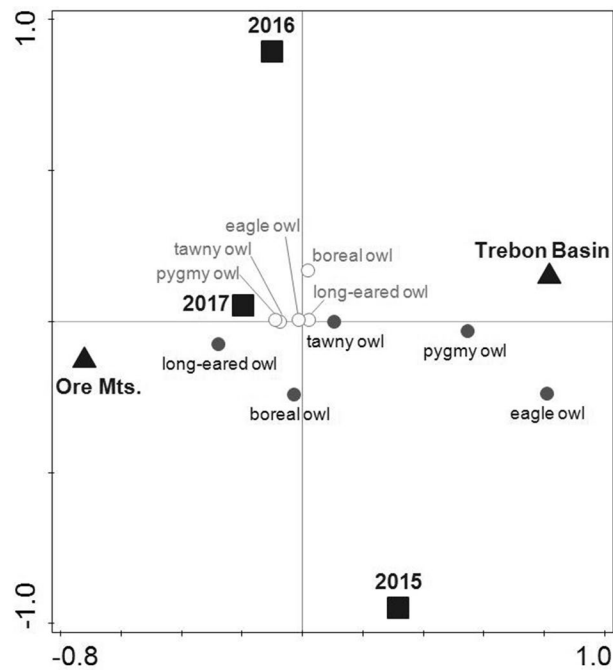
Figure 3. The effect of the study area (Ore Mts. and Trebon Basin, black triangle) and year (2015–2017, black square) on the distribution of owl species (boreal, tawny, pygmy, long-eared, and eagle owls) based on the vocal activity of owls. The presence (grey circle, black front) and the absence (white circle, grey front) of individual owl species are shown. The canonical correspondence analysis (CCA) was used. The first and second ordination axes together explained 94.7% of the variability.

Model	AIC	df	Chi	% of explained variability	P
Null model	591.88	1442			
Null model + area	550.61	1441	43.27	7.41	< 0.001

Table 4. The results of GLMM analysis (*lmer* function). The effect of the study area on nest box occupancy (0/1) by boreal owls.

Boreal owl populations. Boreal owls readily used nest boxes in the Ore Mts., but not in the Trebon Basin. We identified six main differences. First, boreal owls nested in boxes (pooled spring and autumn inspections) more often in the Ore Mts. than the Trebon Basin (GLMM; Chi = 43.27, df = 1441, $P < 0.001$, Table 4). Second, during the spring inspections, the nest box occupancy reached 7–10% in the Ore Mts., but only 0–1% in the Trebon Basin (Supplementary Information, Table S5). Third, the total number of boreal owl nests (both active and abandoned) found during spring and autumn nest box inspections was more than 10 times higher in the Ore Mts. (76 nests) than in the Trebon Basin (5 nests, Table 5). Thus, the total nest box occupancy reached 8–15% in the Ore Mts. and only 0–1% in the Trebon Basin. Fourth, the boreal owl females breeding in nest boxes produced yearly 128.3 ± 49.4 eggs and 63.3 ± 52.1 fledglings (mean ± SD, n = 76 nests) in the Ore Mts., but only 6.0 ± 5.6 eggs and 5.3 ± 4.7 fledglings (n = 5 nests) in the Trebon Basin (Table 5). Fifth, pine martens predated six boreal owl nests in the Ore Mts. and one nest in the Trebon Basin (Table 5). Finally, the boreal owl females abandoned 24 nests in the Ore Mts., and no in the Trebon Basin (Table 5).

Nest box occupancy by other animals. We identified a total of 487 animal activities during synchronized 2,194 spring (April–May) and autumn (September–October) nest box inspections in the two study areas (Supplementary Information, Table S5). Using CCA, we found a significant effect of the study area, year, and sampling period on the occurrence of animal species in nest boxes (Table 3). The first and second ordination axes of the model explained 98.7% of the variability together. Boreal owls, passerine birds, and pine martens were more frequent users in the Ore Mts., while bats, insects, and common goldeneyes occurred more often in the Trebon Basin (Fig. 4).

During the spring (April–May) nest box inspections, passerine birds (Paridae > 90%) and boreal owls were the most frequent dwellers of nest boxes in the Ore Mts. (Fig. 4). Their nest box occupancy reached 5–30% and 7–10%, respectively (for details, see Supplementary Information, Table S5). Pine martens rarely occupied nest boxes in the Ore Mts. during spring (nest box occupancy was ≤ 1%; Supplementary Information, Table S5. The

	Ore Mts.					Trebon Basin				
	2015	2016	2017	Mean ± SD	Mean % ± SD	2015	2016	2017	Mean ± SD	Mean % ± SD
Vocal occupancy rate										
April	0.59	0.47	0.50	0.52 ± 0.06		0.52	0.23	0.34	0.36 ± 0.15	
May	0.50	0.17	0.39	0.35 ± 0.17		0.58	0.19	0.34	0.37 ± 0.20	
Vocal density per 10 km²										
April	1.87	1.50	1.59	1.65 ± 0.19		1.64	0.72	1.09	1.15 ± 0.46	
May	1.59	0.55	1.24	1.13 ± 0.53		1.85	0.61	1.09	1.18 ± 0.63	
Spring nest box occupancy (%)	10	9	7	8.7 ± 1.5		1	< 1	0	0.7 ± 0.6	
Total nest box occupancy (%)	15	9	8	10.7 ± 3.8		1	< 1	0	0.7 ± 0.6	
Nest box occupancy rate	0.15	0.09	0.08	0.10 ± 0.04		0.01	< 0.01	0	0.007 ± 0.006	
No. of boxes	230	246	246	240.7 ± 9.2		245	242	237	241.3 ± 4.0	
No. of all nests	34	23	19	25.3 ± 7.7		3	2	0	1.7 ± 1.5	
No. of active nests (spring)	23	23	18	21.3 ± 2.9		3	2	0	1.7 ± 1.5	
No. of additional nests (autumn)	11	0	1	4.0 ± 6.1		0	0	0	0.0	
No. of successful nests	27	6	13	15.3 ± 10.7	58.0 ± 28.2	2	2	0	1.3 ± 1.2	83.3 ± 23.6
No. of predated nests	0	5	1	2.0 ± 2.6	9.0 ± 11.3	1	0	0	0.3 ± 0.6	16.7 ± 23.6
No. of abandoned nests	7	12	5	8.0 ± 3.6	33.0 ± 16.8	0	0	0	0.0	
No. of eggs	181	83	121	128.3 ± 49.4		11	7	0	6.0 ± 5.6	
No. of fledglings	114	10	66	63.3 ± 52.1		9	7	0	5.3 ± 4.7	

Table 5. Boreal owls nesting in 2015–2017 in the Ore Mts. and Trebon Basin: the vocal occupancy rate, the density of vocalising individuals, the proportion of spring (i.e., only nests during spring inspections) and total (i.e., all nests) nest box occupancy, the number of boxes, all nests, active nests (i.e., during spring nest box inspections), additional nests (i.e., during autumn nest box inspections), successful nests, nests predated by martens, nests abandoned by boreal owl females (including the proportion of all nests), and the total number of eggs and fledglings.
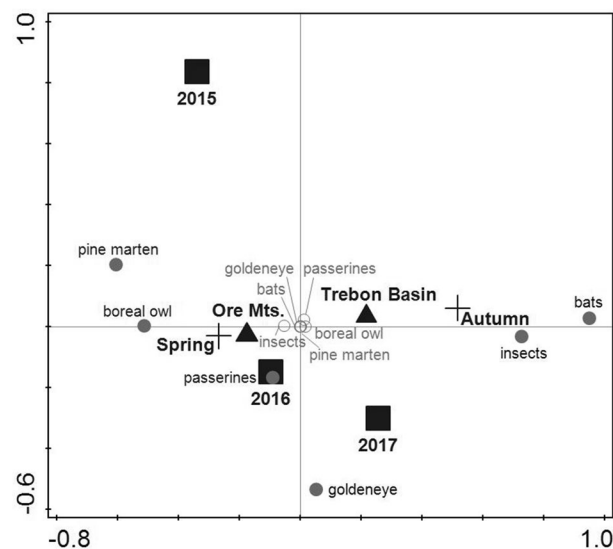

Figure 4. The effect of the study area (Ore Mts. and Trebon Basin, black triangle), year (2015–2017, black square), period (spring and autumn nest box inspections, black cross) on nest box use by different taxa (boreal owl, pine marten, goldeneye, passerines, bats, and insects). The presence (grey circle, black front) and the absence (white circle, grey front) of different taxa are shown. The canonical correspondence analysis (CCA) was used. The first and second ordination axes together explained 98.7% of the variability.

only passerine birds (Paridae > 90%) were occasional spring nesters in the Trebon Basin, reaching 7–8% occupancy. Boreal owls, common goldeneyes, and pine martens were rare spring nesters in the Trebon Basin (nest box occupancy was ≤ 1%; Supplementary Information, Table S5).

During the autumn nest box inspections, no animals inhabited nest boxes in the Ore Mts. Only additional abandoned nests of passerine birds (nest box occupancy reached 6–8%) and one boreal owl nest (< 1%) were

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built after completing our spring nest box inspections (Supplementary Information, Table S5). Insects (Vespidae) appeared in only one nest box in the Ore Mts. (Supplementary Information, Table S5). On the contrary, insects (Vespidae and Apidae > 90%) were most often dwellers of the nest boxes during autumn inspections in the Trebon Basin (Fig. 4); their occupancy reached 44–52% (Supplementary Information, Table S5). Additional abandoned passerine nests also occurred during the autumn inspections in the Trebon Basin, reaching the occupancy of 0–19% (Supplementary Information, Table S5). Finally, bats occupied nest boxes in this study area (Fig. 4), with less than 2% (Supplementary Information, Table S5).

Discussion

Population size and nest box use.   Based on territorial vocal activity, we found that the two boreal owl populations in the Ore Mts. and Trebon Basin were of similar size in 2015, and that the one in the Ore Mountains was more abundant in 2016 and 2017 than in the Třeboň Basin. However, the Ore Mts.' boreal owls used nest boxes much more frequently than their counterparts in the Trebon Basin in all study years; the yearly nest box occupancy reached 8–15% and 0–1%, respectively. As a result, the boreal owl population using nest boxes in the Ore Mts. produced 10 times more fledglings than the same population in the Trebon Basin.

In general, the readiness of boreal owls to use nest boxes is inconsistent over the Holarctic region, reaching the nest box occupancy of 0–66% (for details, see Table 1). Some studies have shown that boreal owls preferred using nest boxes to natural cavities; however, other studies have documented that they did not use nest boxes at all or only rarely. The authors have suggested various reasons for the variability in nest box occupancy rate, including the availability of natural cavities, different breeding success in nest boxes and tree cavities, food availability, and nest box age. Our experimental study has documented that the occupancy rate differed significantly between the two study habitats, even though food abundances and the boreal owl population sizes were comparable. We suggest that the main reason for this contrast lies in the different availability of natural cavities that resulted from different forest structures between the two study areas (the first hypothesis). The explanations are following:

1. Availability of natural cavities

Natural nest-site opportunities for boreal owls are represented almost solely by the cavities excavated by black woodpeckers[3,16]. Their availability increases with increasing age of the forests, and simultaneously, it is higher in deciduous and pine forests than spruce forests[7,54,55]. In our study areas, the species and age forest structure differed substantially. It influenced the abundance of black woodpecker populations and the availability of tree cavities excavated by this species being much higher in mature Scots pine-dominated forests of the Trebon Basin than young restored forests of the Ore Mts. During our long-term study in the Ore Mts. (since 1999; Zárybnická, unpublished data), we recorded even a higher nest box occupancy rate by boreal owls, up to 26% (2001–2006), than in the current study (2015–2017). Over the years, this decrease in a nest box occupancy rate probably resulted from gradual vegetation succession accompanied by the increasing availability of tree cavities excavated by black woodpeckers (Zárybnická and Kilb, unpublished data). However, the abundance of the black woodpecker population and the availability of natural cavities are still much lower in the Ore Mts. than in the Trebon Basin nowadays. Therefore, we suggest that the lack of natural tree cavities was the main reason for a substantially higher readiness of boreal owls to occupy nest boxes in the Ore Mts. Following our third hypothesis, we also found a lower nest box occupancy rate by other secondary cavity-nesting birds, i.e., passerine birds, in the Trebon Basin compared to the Ore Mts. (0–19% vs. 5–30%). Additionally, pygmy owls — which almost solely use natural tree cavities for their breeding and avoid nest boxes in Central European conditions[4] — were substantially higher in their population size in the Trebon Basin than the Ore Mts. Riegert and Kloubec (unpublished data) have confirmed that pygmy owls frequently nest in natural cavities while avoiding nest boxes in the Trebon Basin.

2. Age of nest boxes

The occupancy rate of nest boxes by boreal owls significantly decreases with their age[3,56]. The increased risk of nest predation by martens in older boxes[57,58] or food depletion in the vicinity of old nest boxes[59] have been suggested to explain this effect in boreal owls. However, we found a significantly higher nest box occupancy rate in the Ore Mts. than in the Trebon Basin, even though the mean age of nest boxes (all boxes in all study years) was about 1.7 years higher in the Ore Mts. than in the Trebon Basin. Therefore, the age of nest boxes was not a reason for differences in the nest box occupancy rate between the study areas.

3. Maintaining nest boxes

The quality of nest boxes and their maintenance can affect nest box use by boreal owls. For example, it is essential to install nest boxes high enough above the ground, regularly relocate and maintain nest boxes, keep nest box content dry and clean, and keep the surrounding of the nest box entrance free of branches (Zárybnická, unpublished data). Still, experimental studies are lacking. We used the same quality, maintenance, and installation of nest boxes in both study areas, preventing these factors from consideration as relevant reasons for differences in boreal owls' nest box occupancy between the study areas.

4. Competition with other animals

Other animals can compete for nest boxes with boreal owls. For example, Hruška[60] documented two boreal owl nests in natural cavities that failed after wild bees occupied them. Similarly, hornets, wasps, bumblebees[61,62], or ants (Riegert, unpublished data) can compete with passerine birds for nest boxes. However, relationships between hornets' and birds' occupancy rates may not be found[63]. In the Ore Mts., hornets were absent in nest boxes, and only wasps occupied one nest box during the autumn inspections. Thus, insects did not limit the boreal owl population in the Ore Mts. In the Trebon Basin, hornets only occupied 0–11% of our erected nest boxes during the spring inspections but up to 44–52% during autumn inspections. The period of nest box occupancy by insects did not overlap with that of the boreal owl in the Trebon Basin, avoiding interspecific competitions. Further, martens can raise their young in nest boxes and thus potentially compete for nesting sites with boreal owls. However, we discovered only three boxes with pine marten adults providing their young during spring inspections in the Ore Mts., and one such case was recorded in the Trebon Basin. These rare cases document that pine martens did not compete for nest boxes with boreal owls. Finally, passerine birds occupied up to 30% and 8% of erected boxes during spring inspections in the Ore Mts. and Trebon Basin, respectively. Since passerines are alternative prey for the boreal owl[3,18], we are convinced that these birds would rather avoid the competition for nest boxes with the boreal owl. Overall, it seems clear that the competition with other animals was not a reason for the differences in nest box use between the study areas (the fourth hypothesis).

Breeding performance in nest boxes. Martens depredated only 8% of nests in the Ore Mts., and one nest failed for the same reason in the Trebon Basin. The rate of nest predation by martens in nest boxes and natural cavities varies across regions. For example, in Germany, martens depredated 59% of owl nests placed in boxes, but only 24% in natural tree cavities[64]. In the Spain Pyrenees, the trend was the opposite; martens destroyed 50% of nests in tree cavities, but only 15% in nest boxes[65]. During the long-term study in the Ore Mts., we found out that the predation rate of boreal owl nests by martens varied hugely among years, reaching 0–50%; and the availability of *Apodemus* mice was its main drive[66]. In addition to nest failure due to predation, we also recorded that females abandoned 20–52% of nests in the Ore Mts., probably due to insufficient providing of females and nestlings by males[67]. Our study did not compare owl breeding success in nest boxes and tree cavities. However, Hruška[60] performed long-term research (2006–2020, 123 nests) on a boreal owl population nesting in natural tree cavities in the Vysočina Hills in the central Czech Republic. Hruška[60] found that 33–63% of boreal owl nests were successful each year, martens depredated 6–50% of nests, and up to 25% failed due to water flooding, including one nest where nestlings drowned (see also[68]). Water flooding does not happen in maintained nest boxes and has never been identified as a reason for nest failure in our study areas (Zárybnická, unpublished data). These findings indicate that breeding success of boreal owls nesting in wooden boxes and natural cavities is similar. Alternatively, maintaining and preventing nest boxes from undesirable environmental processes can increase owl breeding success in nest boxes compared to natural cavities.

Recommendations for nest box deploying. We have documented that nest boxes can effectively support boreal owl populations and be a suitable tool for collecting biological information and material. At the same time, nest boxes can lose their supporting function for the target species under specific environmental conditions. Based on our findings, we provide the following specific recommendations for nest box deploying in Central European conditions to support boreal owl populations.

First, nest boxes should be distributed preferably in forest habitats that suffer from short-term or long-term lack of natural tree cavities. Examples of such habitats are young forest stands, intensively managed forest plantations, and forest stands exposed to other anthropogenic (e.g., atmospheric pollution), climatic (e.g., windthrow calamity, heavy snowfall), and biotic (e.g., an outbreak of insects or fungi) process followed by extensive forest losses. Such habitats suffer from the lack of black woodpeckers and other woodpeckers as well[3,4]. The size of the black woodpecker population can be a bioindicator of the availability of natural cavities for nocturnal boreal owls and a signal to provide additional nesting opportunities.

Second, nest boxes should be distributed preferably in coniferous forest habitats at high and middle elevations (above 600 m a. s. l.), providing optimal climate conditions for the study species[15,34,69]. Among owls in the Czech Republic, only the boreal owl prefers inhabiting the highest elevations[15,34]. Our findings support the elevational preference because the boreal owl was the most abundant owl species in all years on the Ore Mts. plateau. At the same time, the situation differed in the Trebon Basin lowlands, in which tawny owls dominated during two of three study years. Therefore, elevational optimum should be considered when practical support for the boreal owl is developed.

In general, during our study, we have identified a lack of specific recommendations for deploying nest boxes for the boreal owl. For example, it would be helpful to guide which habitats and environmental conditions to prefer for nest box deployment, which microhabitats to prefer for nest box installation, how nest boxes to maintain, when nest boxes to relocate, and which nest box dimensions and protection against predators to use. We conclude the comprehensive practical guides should be a topic for further review.

Conclusions

The abundances and community structures of small mammals were similar in the Ore Mts. and Trebon Basin during the whole study, apart from one year (2017) when *Apodemus* mice peaked in the Ore Mts. Boreal owl populations were comparable in size based on territorial vocalisation in both study areas, but their readiness to occupy nest boxes differed substantially. Nest boxes were an efficient tool to support the availability of nesting opportunities for the study species in young restored forests in the historically air-polluted Ore Mts. However,

nest boxes lost their supporting function for the boreal owl in mature Scots pine forests in the Trebon Basin. Therefore, deploying nest boxes should be considered carefully under local environmental conditions.

Data availability
All data produced from this study are available in the manuscript (Tables 1, 2, 3, 4, 5 and Figs. 1, 2, 3, 4) and the Supplementary Information file (Tables S1–S5).

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Author contributions

M.Z. and B.K. conceived and designed the research topic and field experiment. M.Z. and R.S. wrote and revised the manuscript. J.R., M.Z., and R.S. analysed and visualised data. R.S. analysed audio recordings. R.S., B.K., J.S., M.K., and M.Z. collected field data. All authors edited the manuscript.

Competing interests

The authors declare no competing interests.

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3.3 Study III.

Vocal activity of the Central European Boreal Owl population in relation to varying environmental conditions

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Authors contribution:

M. Zárybnická, **R. Ševčík**, and J. Šindelář conceived and designed the research topic and field experiment.

R. Ševčík and M. Zárybnická wrote original draft and revised the manuscript.

R. Ševčík and J. Šindelář collected field data.

R. Ševčík analyzed audio recordings.

J. Riegert, M. Zárybnická and **R. Ševčík** analyzed and visualized data.

R. Ševčík, M. Zárybnická, J. Riegert, and J. Šindelář edited the manuscript.

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Vocal activity of the Central European Boreal Owl population in relation to varying environmental conditions

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Vocal activity is one of the main attributes that enables assessment of the presence and abundance of animal populations. However, analyses of the factors affecting vocal activity are rarely studied, especially in owls. We studied the vocal activity of Boreal Owl (*Aegolius funereus*) using acoustic monitoring in relation to environmental factors in Central Europe (Czech Republic), over an area of 100 km². We analysed a total of 1,310 hours of sound recordings collected over two years (2015 and 2016) at the turn of March/April and April/May. The frequency of sampling points in which we recorded Boreal Owl vocalizations varied from 0.17 to 0.59 and was higher in the year of increased prey abundance (2015) and higher earlier in the breeding season (March/April). The duration of Boreal Owl vocal activity varied from 1 to 60 minutes per hour and was related to temporal factors. In particular, the duration of Boreal Owl vocalization increased late in the breeding season (April/May) and in the year of higher prey abundance (2015), and it showed two peaks of vocal activity during the night. Weather conditions, the occurrence of nesting Boreal Owl pairs, and the vocalization of other owl species had no effect on Boreal Owl vocalization. These findings highlight the importance of between-year, seasonal, and within-night variability in the Boreal Owl vocal activity and document that acoustic monitoring based on sound recorders works well for monitoring of nocturnal bird species.

1. Introduction

Vocal communication represents an effective way for animals to transmit information between each other. They use a wide range of sounds for defending territory, attracting mates, deterring predators, navigating, finding food, and staying in touch with members of their social group (Marler & Slabbekoorn 2004, Catchpole & Slater 2008, Bradbury & Vehrencamp 2011). Acoustic monitoring using modern technologies, including sound recordings (Blumstein *et al.* 2011), enables us to detect vocal activities over a wide range of wavelengths, from ultrasound to infrasound (Whytock & Christie 2017), for long time intervals (Frommolt 2017, Whytock & Christie 2017), and under different temporal (Tremain *et al.* 2008, Odom & Mennill 2010) and spatial conditions (Blumstein *et al.* 2011, Hodge *et al.* 2013, Deichmann *et al.* 2017). Using acoustic methods

we can also reveal the presence/absence of a species and their abundance (Fischer *et al.* 1997, Haselmayer & Quinn 2000, MacSwiney *et al.* 2008), and identify individuals, their age, gender (Blumstein *et al.* 2011), and variations in vocal spectrum and singing style (Forstmeier & Balsby 2002, Brunner & Pasinelli 2010, Halfwerk *et al.* 2011). However, despite the availability of various information, studies describing vocal patterns in birds, particularly in owls, are still needed (Kloubec 2007, Kloubec & Čapek 2012, Rasmussen *et al.* 2012).

Nocturnal bird species use vocalizations to defend their territories, attract mates, or to maintain communication within pairs (e.g., Ganey 1990, Penteriani 2002, Odom & Mennill 2010). The vocal activity of nocturnal birds can vary with biotic and abiotic factors. One factor is the time of year, with the calling peak occurring during reproduction (Slagsvold 1977, Clark & Anderson 1997, Amrhein *et al.* 2002, Kloubec & Čapek 2012), and another is the time of day, with the highest calling frequency around dusk and dawn (Kloubec & Pačenovský 1996, Clark & Anderson 1997, Mougeot & Bretagnolle 2000, Kloubec 2007).

'The vocal activity of nocturnal birds can be also related to prey abundance (Lundberg 1980, Swengel & Swengel 1995), weather conditions (Slagsvold 1977, Lengagne & Slater 2002), the occurrence of second or replacement clutches and the presence of unpaired mates (Galeotti & Pavan 1993, Amrhein *et al.* 2002, Kloubec 2007), or inter-specific competition (Crozier *et al.* 2006, Zuberogoitia *et al.* 2008, Lourenco *et al.* 2013). However, comprehensive analyses of factors affecting vocal activity, including food and weather conditions, circadian and circannual patterns, and intra- and inter-specific competition are especially rare in owls (Kloubec & Čapek 2012, La 2012).

The Boreal Owl (*Aegolius funereus*) is a small, nocturnal, "sit and wait" avian predator with a Holarctic breeding range. It feeds on voles in Northern Europe (Korpimäki & Hakkarainen 2012) and voles and mice in Central Europe (Zárybnická *et al.* 2011,2013). This owl inhabits predominantly old-growth coniferous forests (Šťastný *et al.* 2006, Korpimäki & Hakkarainen 2012, Zárybnická *et al.* 2017) and places its nests in natural tree cavities and nest boxes (Korpimäki & Hakkarainen 2012, Zárybnická *et al.* 2015a).

Timing of breeding, clutch size, reproductive success, home range size, and parental care are influenced by food abundance (*Apodemus* mice and *Microtus* voles in Central Europe) which changes greatly between years and during the breeding season (Zárybnická *et al.* 2013, Zárybnická & Vojar 2013, Zárybnická *et al.* 2015a, b, Kouba *et al.* 2017). Boreal Owls usually breed between March and July (Korpimäki & Hakkarainen 2012, Zárybnická *et al.* 2012) using their calls to defend their territories and to attract mates (Mikkola 1983).

Vocalizations of Czech Boreal Owls are performed from February to May, with the peak in early season, that is in March and April (Vacík 1991, Kloubec 2007). Their vocalizations are usually detectable up to a distance of 0.5–1 km, or 1–3 km during more suitable weather conditions (Vacík 1991, Kloubec & Pačenovský 1996). Vocal activity usually varies according to food supply (Palmer 1987, Kloubec & Pačenovský 1996), during the course of the night (Kloubec & Pačenovský 1996), and it can be reduced during inclement weather (Mikkola 1983, Palmer 1987, Kloubec & Pačenovský 1996, Kloubec 2007). It may also be affected by con- and heterospecifics. In particular, vocal activity may be increased with increasing density of Boreal Owl individuals (Kloubec 1986, König *et al.* 1999).

Moreover, Boreal Owls avoid territories of their competitors and predators, for example Tawny Owl (*Strix aluco*) (Vrezec & Tome 2004) or Ural Owl (*Strix uralensis*) (Hakkarainen & Korpimäki 1996), suggesting that vocalizations of Boreal Owls may also be influenced by the presence of other owl species. However, individual studies have usually focused separately on particular effects, without a comprehensive approach allowing us to understand the relative significance of individual factors to Boreal Owl vocalization. Moreover, most studies have been performed based on a standard method of vocal registration by individual observers during selected parts of the night and they often used voice provocation, which can alter the results.

Here we studied variability in the vocal activity of Boreal Owl based on acoustic monitoring using sound recorders. We predicted that the vocal activity of the Central European Boreal Owl would vary under a temporally variable environment (the year, the breeding season, and the hour of the
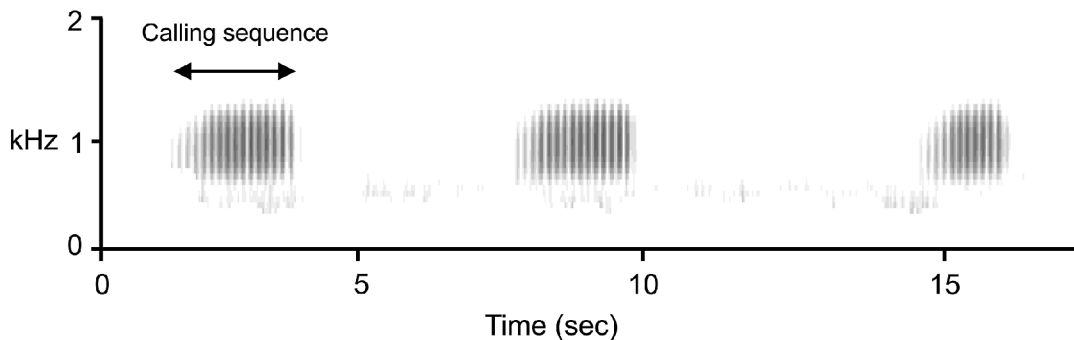
Fig. 1. The example of a spectrogram of Boreal Owl vocalization recorded in the Ore Mountains with one calling sequence indicated.

night), weather conditions (wind speed and rain), and inter and intra specific competition (the occurrence of Boreal Owl breeding pairs and the presence of other vocalizing owls). We also evaluated the vocal activity of other owl species to show its between-year and within-breeding season variability.

2. Methods

2.1. Study area and species

The study was conducted in the northern part of the Czech Republic (50° N, 13° E), on the Ore Mountain plateau (730–960 m a. s. l.; area 100 km²) during the years 2015 and 2016. The study site was characterized by a heterogeneous mosaic of old forests of Norway Spruce (*Picea abies*), fragments of young secondary forests dominated by non-native Blue Spruce (*Picea pungens*), native deciduous trees (mainly European Beech *Fagus sylvatica*, European Larch *Larix decidua*, Rowan *Sorbus aucuparia*, European Hornbeam *Carpinus betulus*, alders *Alnus* spp., and birches *Betula* spp.), and open areas with solitary beech trees (Zrybnická *et al.* 2015c). Within the study site, Boreal Owls breed primarily in nest boxes (> 90% of nests) because the abundance of natural cavities is low, and breeding density used to reach to 10–30 pairs each year, depending on prey abundance (for details, see Zárybnická *et al.* 2015c).

2.2. Vocal activity of owls

Sound recorders (Olympus DM650) were installed within the study area during two periods. The first period took place between March 23 and April 1 and the second period between April 27 and May 4. All recorders were placed on 'sampling points' located in a regular grid, 2 km from each other (radius 1 km) throughout the whole study area. Each recorder was placed on a tree trunk at a height of 1.5 m above the ground and left there for one night from 20:00 to 6:00 (i.e., 10 hours). During the period 2015–2016, we performed 144 recordings at 36 different sampling points, of which 13 recordings were not included in the analyses due to technical failures. For the first period (March 23–April 1), we analysed data from 34 and 36 sampling points in 2015 and 2016, respectively. For the second period (April 27–May 4), we used data from 26 and 35 sampling points in 2015 and 2016, respectively. Sound recordings were transformed to spectrograms (Fig. 1) and analysed using AMSrv software (Savický 2009). The spectrum was set at 1 min with FFT length and with a resolution of 4,096 and 1,366 window size. We used no filters to remove background noise.

We assessed the frequency of sampling points in which we recorded vocalizations of Boreal Owl and other owls (including Tawny Owl, Long-eared Owl *Asio otus*, Pygmy Owl *Glaucidium passerinum*, Eagle Owl *Bubo bubo*, and Little Owl *Athene noctua*) in relation to the year (2015, 2016) and recording period (March/April, April/May). The vocalization of each owl species was considered to be present when a specific territory call (based on bird voices in Kloubec *et al.* 2015) was detected at least once during the sampling period. We also analysed the duration of Boreal Owl vocal activity with associated variables being: year; re-

cording period; the hour of the night (20:00–6:00); wind speed (0–8.6 m/s); the presence/absence of rain; the presence/absence of other owl vocalizations; and the presence/absence of occupied Boreal Owl nest sites.

We defined the duration of Boreal Owl vocal activity as a sequence of continuous calling without a break (Fig. 1) and measured it as a total number of minutes of vocal activity per hour of recording. In total, 1,310 hours during 131 recordings at 36 sampling points were collected. For the purposes of the analyses, we excluded data with no Boreal Owl vocalization, meaning that we used 228 hours with Boreal Owl vocalization. We also used the presence/absence of vocalizations of other owl species during Boreal Owl vocalization. In particular, we included Tawny Owl and Long-eared Owl, which were detected during a total 35 and 11 hours of Boreal Owl vocalizations, respectively. Other species (including Pygmy Owl, Eagle Owl and Little Owl) were not commonly detected during Boreal Owl vocalizations and thus they were not included in the analyses. We further used a presence/absence of occupied Boreal Owl nest sites (pairs) located in nest boxes within a radius of 1 km around each sampling point. We chose a 1 km radius because Boreal Owl vocal calling is usually detectable up to a distance of 1 km (Vacík 1991, Kloubec & Pačenovský 1996).

2.3. Prey abundance

Small mammal abundance is the main predictor of reproductive success of Boreal Owl in our study area (Zárybnická 2009a, Šindelář *et al.* 2015, Zárybnická *et al.* 2015a, d). We assessed the abundance of small mammals using snap-traps each year. Trapping was carried out each year at the beginning of June by setting up snap-traps in six areas (4 × 10 trap grid, span 10 m, 40 traps in total for each grid). The trapping points were evenly distributed throughout the study area (i.e., there is no detailed information on prey abundance for each sampling point). The traps were left out for three days and checked every morning. We calculated the abundance of small mammals as the number of captured individuals per 100 trap nights in each trapping area. All captured mammals ($n = 19$) were determined to species level.

2.4. Weather conditions

We used data from the Czech Hydrometeorological Institute on outdoor temperature (actual temperature in °C at each hour), rain (mm per hour), and wind speed (actual wind speed in m/s at each hour). As the precipitation showed low variability (median = 0, SD = 0.16, min = 0, max = 1.9 mm/hour, $n = 1310$ hours), we used a binomial distribution for the presence/absence of rain (0/1) for the purposes of the statistical analyses. Mean wind speed and temperature reached 2.4 m/s (median = 1.9, min = 0, max = 8.6, $n = 1310$ hours) and 4.6 °C (median = 4.7, SD = 2.6, min = –0.8, max = 11.5, $n = 1310$ hours), respectively, and both factors negatively correlated to each other (Spearman Rank Correlations; $r_s = –0.335$, $P < 0.001$, 95% confidence intervals: lower –0.396, upper –0.271, $n = 1310$ hours). As wind speed is known as a limiting factor of Boreal Owl vocalization and its influence is more pronounced than that of temperature (Bondrup-Nielsen 1978, Mikkola 1983, Palmer 1987), we used the wind speed and we did not include the temperature in the analyses.

2.5. Statistical analyses

The between-year differences in the abundance of small mammals were calculated using non-parametric Wilcoxon Matched Pairs Test (StatSoft 2013). The comparisons of the frequencies of sampling points between years (2015 *vs.* 2016) and the recording periods (March/April *vs.* April/May) were analysed using Chi-square tests (StatSoft 2013). We applied Bonferroni correction for dependent tests within each species. The level of significance after Bonferroni correction was set to 0.025.

The effect of factors related to duration of Boreal Owl vocalization (dependent variable) was tested in R 3.4.4. software (R Development Core Team 2011) using multi-model inference approach (model.avg function in MuMIn package) (Anderson & Burnham 2002, Whittingham *et al.* 2006, Burnham *et al.* 2011) based on AIC differences. We used the following factors for building candidate GLMM models (glmer function in lme4 package): the year (2015, 2016), the recording period (March/April, April/May), the hour of the night (20:00–06:00 as a categorical variable), the

Table 1. The total number of sampling points, the number of sampling points with the occurrence of owl vocalizations, and the frequency of sampling points at which owl vocalization occurred. Owl vocalizations were documented using sound recorders in the Ore Mountains at the turn of March/April and April/May in 2015 and 2016.

1 = No. of points, 2 = No. of points with vocal, 3 = Frequency of vocal./point.

Owl species	2015						2016					
	March/April			April/May			March/April			April/May		
	1	2	3	1	2	3	1	2	3	1	2	3
Aegolius funereus	34	20	0.59	26	13	0.50	36	17	0.47	35	6	0.17
Strix aluco	34	14	0.41	26	10	0.38	36	17	0.47	35	14	0.40
Bubo bubo	34	0	0	26	0	0	36	1	0.03	35	0	0
Glaucidium passerinum	34	3	0.09	26	2	0.08	36	2	0.06	35	2	0.06
Asio otus	34	3	0.09	26	3	0.12	36	3	0.08	35	3	0.09
Athene noctua	34	0	0	26	0	0	36	1	0.03	35	0	0

absence/presence of rain (0–1), wind speed (m/s), the absence/presence of Tawny Owl (0–1) and Long-eared Owl vocalization (0–1), and the absence/presence of other breeding Boreal Owl pairs (0–1).

We built null and 32 alternative models with Gamma distribution of dependent variable and sampling point as a random intercept. We created these models with each individual factor, and we consequently added temporal factors (the year, the recording period, and the hour of the night), weather factors (wind, rain), and inter-specific (occurrence of Tawny and Long-eared Owl vocalization) and intra-specific (occurrence of Boreal Owl breeding pairs) competition factors. We also tested interactions between temporal variables (year, recording period and hour). To validate our models, we checked for the pattern of residuals.

3. Results

The abundance of small mammals was significantly higher in 2015 (mean ± SD, 2.50 ± 1.18 ind./100 trap nights) than in 2016 (0.14 ± 0.34 ind./100 trap nights) (Z = 2.2, P = 0.02, n = 6). In 2015, we caught 18 small mammals: 11 Yellow-necked Mice (*Apodemus flavicollis*), 4 Bank Voles (*Myodes glareolus*), 2 Common Shrews (*Sorex araneus*) and 1 Common Vole (*Microtus arvalis*). In 2016, only one bank vole individual was caught.

The frequency of sampling points detecting vocalizations of Boreal Owls varied from 0.17 to 0.59, being higher at the turn of March/April compared to April/May (Chi = 5.0, P = 0.025) and being higher in 2015 compared to 2016 (Chi = 5.7, P = 0.020) (Table 1). The frequency of sampling points detecting vocalizations of Tawny Owl (min 0.38, max 0.47 per sampling point) was similar to Boreal Owl and stable between years (Chi = 0.2, P = 0.700), and it was higher at the turn of March/April compared to the turn of April/May (Chi = 5.7, P = 0.021) (Table 1). The frequency of sampling points detecting vocalizations of Long-eared Owl and Pygmy Owl was also stable between years (Chi = 0.130, P = 0.718; Chi = 0.528, P = 0.467) and during the breeding season (Chi = 0.087, P = 0.768; Chi = 0,528, P = 0.467), but it reached substantially lower values than Boreal and Tawny Owl (Table 1). At the turn of March/April in 2016, vocalizations of Eagle Owl and Little Owl were also recorded (Table 1).

The duration of vocal activity of Boreal Owl varied from 1 to 60 min per hour and from 1 to 230 min per night. Results of multi-model inference revealed that the interaction between years, recording periods and the hour of the night had the strongest effect on vocalization of Boreal Owl (Table 2, 3). The duration of vocal activity was higher late in the breeding season (April/May) compared to the early breeding season (March/April) in 2015, but this trend was not documented in 2016 (Fig. 2a–b). Further, an indicative effect of the hour of the night

Table 2. Set of candidate models used for multi-model inference. AIC values (AICc), changes of AIC (ΔAIC), and AIC weight (wi(AIC)) are shown. Abbreviations of factors: year (Y), recording period (P), hour (H), wind speed (WS), the occurrence of Long-eared Owl vocalization (OLV), Tawny Owl vocalization (OTV), Boreal Owl nesting pairs (OBN), and rain (R). Asterisks indicate the interaction of variables.

Model	df	AICc	ΔAIC	wi(AIC)
P*Y	6	1468.27	0.00	0.70
H+OLV+P+WS+Y	8	1473.61	5.34	0.05
H+OBN+P+WS+Y	8	1473.73	5.46	0.05
OLV+OBN+P+Y	7	1473.77	5.50	0.04
P	4	1474.24	5.97	0.04
OLV+OBN+P+WS+Y	8	1474.68	6.41	0.03
H+R+OTV+P+WS+Y	9	1475.83	7.56	0.02
OLV+OBN+OTV+P+WS+Y	9	1476.60	8.33	0.01
H*P	6	1476.87	8.60	0.01
H+OBN+OTV+P+WS	8	1476.93	8.66	0.01
Y	4	1477.11	8.84	0.01
H+OLV+R+OTV+P+WS+Y	10	1477.35	9.08	0.01
OLV+OBN+R+OTV+P+WS+Y	10	1477.73	9.46	0.01
H*Y	6	1477.99	9.72	0.01
H+OLV+OBN+R+OTV+P+WS+Y	11	1478.46	10.19	0.00
H+WS+Y	6	1479.04	10.77	0.00
H+OBN+Y	6	1479.12	10.85	0.00
OLV+OBN	5	1479.63	11.35	0.00
OLV+OBN+Y	6	1479.80	11.53	0.00
OBN	4	1479.81	11.53	0.00
H+OBN	5	1480.29	12.02	0.00
H+R+OTV+P+WS	8	1480.31	12.04	0.00
H+R+WS+Y	7	1480.69	12.41	0.00
OLV	4	1480.71	12.44	0.00
Null model	3	1480.90	12.63	0.00
R	4	1480.91	12.63	0.00
H	4	1481.04	12.77	0.00
H+R	5	1482.02	13.74	0.00
H+OLV+R+WS+Y	8	1482.02	13.75	0.00
WS	4	1482.05	13.78	0.00
OTV	4	1482.60	14.32	0.00
H+R+OTV	6	1483.27	14.99	0.00
H+R+OTV+WS	7	1485.14	16.87	0.00

was found (Table 2, 3). Two peaks of vocal activity were recorded between 23:00–24:00 and 03:00–04:00 (Fig. 2c). The effect of other variables (i.e. rain occurrence, wind speed, the presence of other Boreal Owl nesting pairs, Long-eared Owl vocalization, and Tawny Owl vocalization) was not significant (Table 2, 3).

4. Discussion

We found Boreal Owl and Tawny Owl were the most abundant species in our study area, while Eagle Owl and Little Owl occurred rarely. The frequency of sampling points in which we recorded Boreal Owl vocal activity changed between years and within the breeding period. No such relationship was found in other owls, except for Tawny Owl in which the frequency of sampling points with vocalizations changed during the breeding period.

Boreal Owl vocalizations occurred at more sampling points at the turn of March/April compared to the turn of April/May. In Northern and Central Europe, a peak of vocal activity of Boreal Owl usually occurs during February/March and March/April, respectively (Mikkola 1983, Kloubec & Pačenovský 1996, Kloubec 2007, Korpimä-

ki & Hakkarainen 2012). In our study, females initiated egg laying on average on April 21 (*SD* = 23 days, *n* = 58 nesting attempts, M. Zárybnická unpubl. data). As the vocal activity of owls usually decreases during egg laying, when individuals communicate using contact voices only (Lundberg 1980, Korpimäki 1981, Vacík 1991), we suggest the vocal activity of our Boreal Owls was probably reduced in the late breeding season because egg laying was already initiated.

On the other hand, the duration of Boreal Owl vocal activity showed the opposite trend; it increased at the turn of April/May compared to the turn of March/April in the year of high food abundance, but this trend was not found in the year of food scarcity. It has been documented that unpaired (bachelor) males usually call throughout the night or even during daytime later in the breeding season (Vacík 1991, Mrlík 1994, Kloubec & Pačenovský 1996, Korpimäki & Hakkarainen 2012). We recorded a similar situation in our study area in 2003 where a Boreal Owl male, after an unsuccessful nesting attempt due to predation by Pine Marten (*Martes martes*), intensively called during night and midday to find a new mate (M. Zárybnická unpubl. data). Therefore, we suggest more intensive Boreal Owl vocalizations presented at fewer sampling points in late breeding season could probably have resulted from increased activity of unpaired individuals.

We found that year explained both the frequency and duration of Boreal Owl vocal activity. Boreal Owl vocalization occurred at more sampling points and for a longer time in 2015 compared to 2016. We further found different food conditions between two years; the peak of Yellow-necked Mouse was in 2015 while a scarcity of both voles and mice occurred in 2016. It has been documented that the vocal activity of Boreal Owl increased with a higher number of breeding owl pairs (Kloubec & Pačenovský 1996) while the breeding density of Boreal Owl usually depends on the availability of small mammals (Korpimäki & Hakkarainen 2012). In particular, young and in-
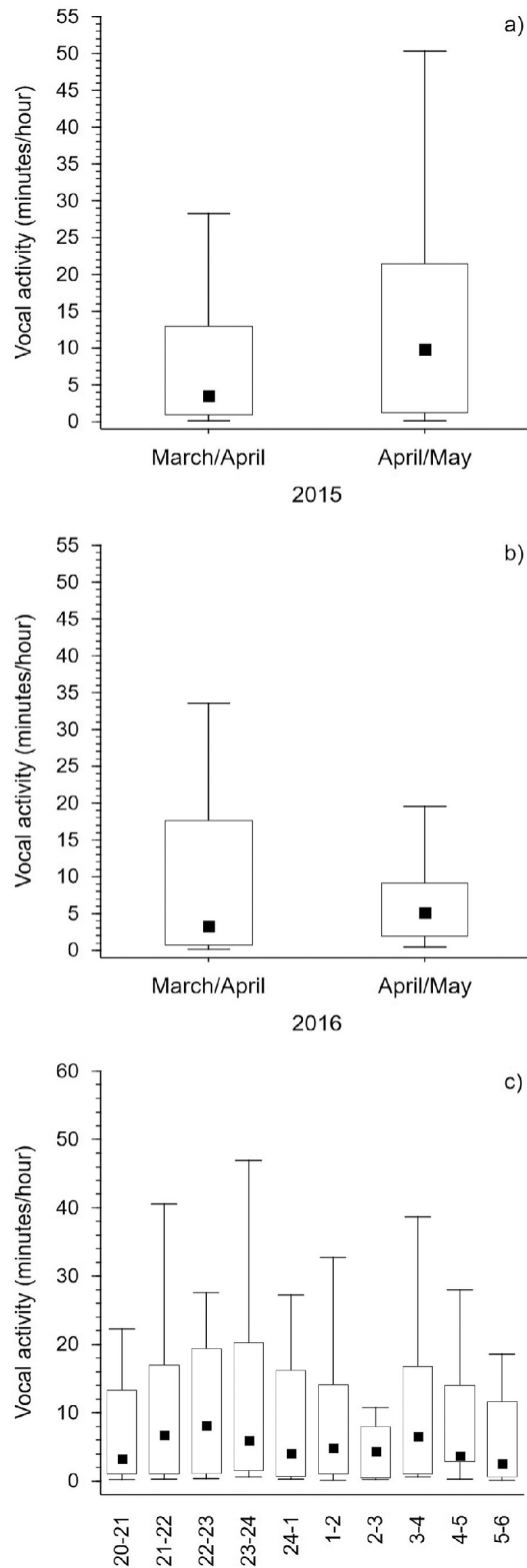

Fig. 2. The duration of Boreal Owl vocalization in relation to a) the year, b) the recording period (*P* < 0.001), and c) the hour of the night. Box plots: median, range 25–75% of data, non-outlier range.

Table 3. The effect of particular factors on the duration of Boreal Owl vocalization based on full-model Multi-model inference. RVI – relative variable importance. Asterisks indicate the interaction of variables. Significant ($P < 0.05$) or indicative ($P < 0.10$) results are in bold.

Independent variables	RVI	Estimate	z	P
Intercept		1.654	4.969	**< 0.001**
Recording period	0.96	0.807	3.033	**0.002**
Year	0.93	−0.196	0.699	0.485
Recording period*Year	0.70	−0.947	2.362	**0.018**
Hour	0.18	−0.042	1.361	**0.073**
Wind (m/s)	0.16	−0.093	1.161	0.246
Long-eared Owl vocalization (0/1)	0.16	0.400	0.976	0.329
Neighbouring nest of Boreal Owl (0/1)	0.16	0.345	1.074	0.283
Tawny Owl vocalization (0/1)	0.06	0.162	0.620	0.535
Rain (0/1)	0.04	−0.309	0.763	0.446
Hour*Recording period	0.01	0.002	0.035	0.972
Hour*Year	0.01	0.067	1.166	0.244

experienced males used to breed in good food years while they do not breed during years of food scarcity (Korpimäki 1988). In our study area, between-year breeding densities of owls do not vary significantly (Zárybnická *et al.* 2013, Zárybnická *et al.* 2015a, Zárybnická *et al.* 2016).

However, the number of Boreal Owl nesting pairs was higher in 2015 compared to 2016 (34 *vs.* 24 breeding pairs, M. Zárybnická unpubl. data) suggesting that the vocal activity of Boreal Owl may differ significantly in years of extremely different food abundance. Similarly, Kloubec & Pačenovský (1996) documented a positive relationship between the frequency of vocalization in Boreal Owl and the number of prey items in food material collected from owl nests, and Palmer (1987) found a relationship between Boreal Owl vocal activity and prey abundance in North America. Swengel & Swengel (1995) revealed these relationships in Saw-whet Owl (*Aegolius acadicus*), and Lundberg (1980) found a positive relationship between the frequency of vocal activity in Ural Owl and vole abundance. Finally, we suggest the increased vocal activity of Boreal Owls in our study area probably resulted from increased density of breeding pairs as a result of the increased availability of small mammals.

In our study, Boreal Owls showed two peaks of vocal activity during the night, between 23:00–24:00 and 03:00–04:00, while they reduced its vocal activity between 24:00–03:00. Similarly, the vocal activity of Central European Boreal Owls, measured by vocal registrations (with vocal prov-

ocation by owls), dropped during midnight, and it also changed during the season (from March to May) in line with changing sunset and sunrise (Kloubec & Pačenovský 1996). Biphasic circadian rhythms of Central European Boreal Owl males, with peaks during dusk and down were also documented based on the frequency of prey delivery to the nests (Klaus *et al.* 1975, Korpimäki 1981, Zárybnická *et al.* 2012). Similarly to males, Central European Boreal Owl females reduce their activities (measured as the frequency of departures from their nests during incubating and nestling period) between 23:00–03:00 (Drdáková-Zárybnická 2008).

However, owl males can show monophasic patterns of activity when they increase the frequency of prey delivery to their nests during the nestling and fledgling phase (Zárybnická 2009b, Zárybnická *et al.* 2012) and/or during short nights in northern areas (Klaus *et al.* 1975, Korpimäki 1981, Zárybnická *et al.* 2012). We suggest the biphasic pattern of vocal activity of Boreal Owl males resulted from resting phases that males took between 24:00–03:00 h during long nights (taking around ten hours in April in Central Europe) and low hunting effort of non-breeding males.

Variability in Boreal Owl vocalizations can also result from other factors and particularly an individual and territorial quality such has been documented in Tawny (Appleby & Redpath 1997) and Eagle Owls (Penteriani *et al.* 2002, Penteriani 2003). Although Kloubec (1986) showed that the vocal activity of Boreal Owl tended to increase at

localities with increased Boreal Owl densities, König *et al.* (1999) found that Boreal Owl can survive in a small area without the males being aggressive (10 breeding pairs/10 km^2). In our study, we were not able to identify individuals of calling Boreal Owls, but we found the duration of Boreal Owl vocalizations did not significantly differ between localities with the absence or presence of Boreal Owl breeding pairs.

Owls are also frequently preyed on by other owl species and particularly smaller and weaker species may be taken as prey (Mikkola 1976). As a result, smaller and weaker species adjust their behaviour during the presence of competitors or predators. For example, the Little Owl reduced vocalization in the presence of its predator, the Barn Owl (*Tyto alba*) (Zuberogoitia *et al.* 2008), and a similar relationship was found between Tawny Owl and Eagle Owl (Lourenco *et al.* 2013). In our study, the vocalization of other owl species, namely Long-eared Owl and Tawny Owl, had no effect on the duration of Boreal Owl vocal activity. In particular, no inter-specific competition was revealed despite both Tawny and Boreal Owls greatly competing with each other for nest cavities (Petty 1989, Sunde *et al.* 2001, Korpimäki & Hakkarainen 2012), similar prey (Balciauskas & Balciauskiene 2014, Solonen *et al.* 2017, Yatsiuk & Filatova 2017), and habitats (Vrezec 2003, Vrezec & Tome 2004, Jensen *et al.* 2012). Since territories of Boreal and Tawny Owls can be highly segregated within habitats (Vrezec & Tome 2004) and across altitudes (Hudec *et al.* 2011, Flousek *et al.* 2015, Zárybnická *et al.* 2017), we suggest the absence of inter-specific competition could resulted from different space use of owl populations in our study site.

Finally, the presence of rain or wind speed had no effect on the duration of vocal activity of our Boreal Owls. Some authors have documented that strong wind speed, heavy rain, snow, and cloudiness reduce the vocal activity of owls, including Boreal Owl (Vacík 1991, Mrlík 1994, Kloubec & Pačenovský 1996, Lengagne & Slater 2002, Kloubec 2007). As a result, most authors avoided acoustic monitoring during unsuitable weather conditions (Freeman 2000, Galeotti & Sacchi 2001, Tripp & Otter 2006, Kissling *et al.* 2010). We suggest that the absence of heavy rains (the precipitations varied between 0.0 and 1.9 mm per hour in our data) and strong winds (reaching up to 8.6 m/s) has probably given cause for the missing effect of weather conditions on the vocal activity of our Boreal Owl.

We conclude that we have performed a rare study documenting the utilization of acoustic monitoring based on sound recorders in birds of prey with nocturnal activity, providing the basic methodology for further studies. We found that Boreal Owl vocalizations varied significantly between years, within breeding season (depending on food abundance), and over the course of the night. However, we did not confirm the effect of weather conditions, or inter- and intra- specific competition on the duration of Boreal Owl vocalization.

Ympäristötekijöiden vaikutus helmipöllön ääntelyyn Keski-Euroopan populaatiossa.

Äänet mahdollistavat eläinpopulaatioiden paikallistamisen ja koon arvoinnin. Yksilöiden ääntelyaktiiviisuuteen vaikuttavia tekijöitä on tutkittu hyvin vähän, varsinkin pöllöillä. Selvitimme ympäristötekijöiden vaikutusta helmipöllön ääntelyyn akustisella seurannalla Tsekissä Keski-Euroopassa (100km2 tutkimusalue).

Analysoimme 1310 tuntia äänitteitä kahden kevään (2015 ja 2016, maalis–toukokuu) ajalta. Helmipöllöjä havaittiin 17–59 %:ssa havaintopisteistä. Havaintoja tehtiin enemmän vuosina, jolloin saaliseläimet olivat runsainpia (vuosi 2015), ja enemmän lisääntymiskauden alussa maalis–huhtikuussa. Ääntelyjakson kesto vaihteli 1–60 minuutin välillä: ääntelyjaksot olivat pidempiä lisääntymiskauden lopussa ja saaliiden huippuvuosina (2015). Yön aikana havaittiin kaksi korkeamman aktiiviisuuden jaksoa. Sääolosuhteilla, muiden helmipölöparien läheisyydellä tai muiden

pöllölajien ääntelyllä ei ollut vaikutusta helmipöllön ääntelyaktiivisuuteen.

Helmipöllön aktiivisuutta tutkittaessa on siis tärkeä ottaa huomioon sekä vuosien välinen, vuodenaikainen ja vuorokaudensisäinen vaihtelu. Tulostemme mukaan akustista seurantaa voidaan käyttää myös yöaktiivisten lintujen seurantaan.

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4. Discussion

4.1 Effect of elevation and temperature on the boreal owl population and future consequences

Study I, based on the data on the presence or absence taken from the breeding atlas obtained by Citizen Science, shows a significant effect of elevation and temperature on the distribution of breeding populations of the boreal owl in the Czech Republic. Using multivariate analysis, it was found that the boreal owl, is the only species compared to other studied owls breeding in the Czech Republic, that prefers high elevation and cold temperatures. Similar results were also obtained from studies of local populations in this area from the Ore Mts. and Šumava Mts. (Zárybnická et al. 2015d, Zárybnická et al. 2015e, Zárybnická et al. 2017b). The preference for higher elevation has also been documented in other European countries based on monitoring breeding populations. For example, Vrezec (2003) and Flousek et al. (2015) found that the boreal owl most often breeds between 600–1000 m a.s.l. in Slovenia and Poland, and the Alpine population primarily inhabits elevations between 800–2200 m a.s.l. (Dvorak et al. 1993, Schmid et al. 1998). Additionally, the abundance of breeding boreal owls increases with increasing elevation, which correlates with the occurrence of Norway spruce — a habitat that is supposed as a crucial factor for the species distribution, despite deteriorating food availability (Kolář et al. 2017, Zárybnická et al. 2017b). However, in *Study I*, it was found that the probability of occurrence of this species increases with increasing elevation, even after removing the effect of landscape cover, suggesting that other factors also influence populations of this boreal owl in the Czech Republic.

The preference for lower temperatures in the boreal owl has also been noted in other studies, which have been conducted mainly in Southern Europe (e.g., Brambilla et al. 2015, Cerman et al. 2022). However, rising temperatures associated with global warming can, in many cases, significantly affect the distribution, physiology, reproductive cycle, or local abundances of many boreal species, including the boreal owl (Korpimäki and Hakkarainen 2012, Reif and Flousek 2012, Cerman et al. 2022). Many studies, including *Study I*, support the idea that Central and Southern European populations of the boreal owl are a relic of the Ice Age (e.g., Korpimäki and

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Hakkarainen 2012, Brambilla et al. 2015, Brambilla et al. 2017, Cerman et al. 2022). Due to effective isolation, this species can inhabit sites with low ambient temperatures. However, at higher temperatures, it may instead suffer physiological stress (Hayward et al. 1993, Hohtola et al. 1994). For example, Hayward et al. (1993) observed a tendency for boreal owl individuals to lower their body temperature using gular fluttering at 18–23 °C. Furthermore, temperature and snow cover height were found to have a significant effect on reproductive success in this species. Clutch size, breeding densities, and body conditions of the adult boreal owl decrease with increasing temperature during winter and decreasing snow cover depth (Kouba et al. 2020, 2021), which is closely related to the influence of temperature and other climatic conditions on the survival and abundance of their prey (Aars and Ims 2002, Hörnfeldt 2004, Solonen 2004, Zárybnická et al. 2017a). Additionally, some modeling studies based on current data on the distribution of the boreal owl predict that southern populations of this owl will retreat further into the mountains in the future, and their populations will decline considerably or even disappear locally with climate change by the late 21st century on the southern edge of its Holarctic breeding range (Brambilla et al. 2015, Brambilla et al. 2017, Brambilla et al. 2020). Therefore, given the preference for higher elevations and cold temperatures by boreal owls in the Czech Republic, we can likely expect an effect of rising temperatures on the distribution and abundance of populations of this cold-adaptive owl species, even in this country, however only time will tell if these predictions are accurate.

 4.2 Species interaction and future distribution of the boreal owl

Interspecific dynamics play a significant role in driving the occurrence of boreal owls, the species most sensitive to interspecific interactions. For example, Brambilla et al. (2020) found that a combination of environmental factors such as habitat, climate, and interactions with other species are chief predictors of the occurrence of the boreal owl in Southern Europe. The tawny owl, as the main competitor and predator, is considered to be an important factor controlling the abundance and distribution of the boreal owl (Vrezec and Tome 2004b, Brambilla et al. 2020). Due to distinctive negative interactions, the boreal owl inhabits coniferous forests at higher elevations and strictly avoids the territories of the tawny owl, which occurs mainly in deciduous and mixed forests at lower elevations, despite the fact that these habitats may offer optimal

breeding conditions for the boreal owl (Vrezec 2003, Vrezec and Tome 2004b, Brambilla et al. 2015, Brambilla et al. 2020). Different ranges of the boreal owl and tawny owl distributions have been also documented in Slovakia, Poland (Flousek et al. 2015), Austria (Dvorak et al. 1993), Slovenia (Vrezec 2003), and Switzerland (Schmid et al. 1998). However, Brambilla et al. (2020) predict and observe a spatial increase in areas with negative interactions due to increasing temperatures, and these interspecific interactions with the tawny owl will likely harm Alpine populations of the boreal owls in the future. In addition, in Southern Europe, there is currently a 25% overlap of suitable habitat for boreal owl with areas of tawny owls, however, future predictions estimate an increase in this proportion of optimal habitat for both species to 54% (Brambilla et al. 2020). In the Czech Republic, the occurrence of the boreal owl in lower elevations also was suggested to be limited due to the presence of the tawny owl (*Study I*, Šťastný et al. 2006, Hudec et al. 2011, Flousek et al. 2015, Zárybnická et al. 2017b). In *Study I*, the preference for moderate temperatures was demonstrated in the tawny owl, so therefore, a positive relationship between its expansion to higher elevations and the global increase in temperatures in the Czech Republic can be expected for this species. In Slovakia, for example, it has been observed that the boreal owl has started to seek suitable nesting sites in old-growth mixed forests of lower elevations (below 500 m), while the tawny owl has spread to higher elevations in this area and occupied former boreal owl territories (Pačenovský and Kürthy 2022). The authors attribute the movement of these populations to climate change and the degradation of coniferous forests at higher elevations due to the rapid drying of forest stands and anthropogenic activity. Pepłowska-Marczak (2019) and Osojca (2004) report that Polish populations of the boreal owl prefer a different type of forest cover than Norway spruce reported by many studies. In this region at lower elevations, it inhabits pine forests that are more than 110 years old. Even in *Study II*, a population of boreal owls, comparable in size to that found at higher elevations, was recorded in low-elevation forest stands with a higher proportion of Scots pine and higher age diversity. Temperate mixed forests of lower elevation offer a higher quality of diet available (Zárybnická et al. 2017b) and thus may be crucial for the conservation of this boreal species, as in years with higher food supply, the boreal owl may use these stands even in the presence of larger competitors (Ratajc et al. 2022). Additionally, in Poland, the boreal owl has been recorded nesting in cavities within 200 m of tawny owls' nests (Pepłowska-Marczak 2019), however, investigations into the reproductive

success of these pairs have not been conducted, although it is understood that the presence of a predator and competitor in a territory can reduce the fitness of breeding owls (e.g., Morosinotto et al. 2017). It is clear that the effect of climate and habitat change can combine with interspecific interactions so it is expected that cold-adaptive boreal owls will move to a higher latitudes or elevations or might adapt to these changes. However, in temperate coniferous and mixed forests at higher and lower elevations suitable for the boreal owl, nest boxes may provide good colonization opportunities for this species, especially in forests subject to intensive management where the supply of nesting habitat for the boreal owl is temporarily limited.

4.3 Breeding opportunities in cavities and nest boxes

In *Study II*, the effect of forest structure on the utilization of nest boxes by boreal owls in two different habitats was determined using two similarly sized populations, monitored based on territorial calls. However, only boreal owl populations inhabiting young Norway and blue spruce forests at higher elevations used nest boxes more frequently (8–15%) than populations inhabiting old pine forests at lower elevations with higher black woodpecker densities (0–1%). In general, the readiness of the boreal owl to use nest boxes shows an inconsistency over the Holarctic region (0–66%, Table 1). Some studies have found that boreal owls preferred to use nest boxes rather than natural cavities (e.g., Korpimäki 1984, 1985, Löfgren et al. 1986, Korpimäki and Hakkarainen 2012, Mezzavilla and Lombardo 2013, Ravussin et al. 2015). The authors explain that the preferences of boreal owls for nest boxes are due to higher reproductive success, better protection of nests against water collecting, and better protection of nests against predators such as pine martens (Korpimäki 1984, López et al. 2010, Ravussin et al. 2015, Hruška 2020). Other studies have documented that boreal owls did not use nest boxes or the nest-box occupancy rate was too low (less < 2%); such locations often occurred in Canada and Northern America (Hayward et al. 1993). The unwillingness of the boreal owl to use nest boxes was likely caused by sufficient availability of adequate natural cavities or imprinting for tree cavities (Hayward et al. 1993, Mossop 1997, Koopman et al. 2007, Meyer 2019, Domahidi et al. 2020). The nest-box occupancy rate is often connected with food availability, although such a relationship cannot work in temperate populations (Zárybnická et al. 2015e). *Study II* documented that the occupancy rate differed significantly between

the two study habitats, even though food abundancy and the boreal owl population sizes were comparable. Additionally, in neither study area there was evidence of increased competition for posted nest boxes with other animals significantly affecting the occupancy rate of these artificial nest sites. Therefore, the difference in the use of nest boxes between the two populations of boreal owl breeding in the Czech Republic was most likely can be explained by the different forest cover structures found in the two study areas (for details, see **Study II**).

Natural nest-site opportunities for boreal owls are represented almost solely by the cavities excavated by black woodpeckers (Korpimäki and Hakkarainen 2012). Their availability increases with increasing age of the forests, and simultaneously, it is higher in deciduous and pine forests than spruce forests, and finally, their abundance is higher in non-managed than in intensively managed forest stands (Kosiński and Kempa 2007, Miller 2010, Walankiewicz et al. 2014). In study areas of **Study II**, the species and the age of forest structure differed substantially. The forest structure associated with the abundance of black woodpecker populations and the availability of tree cavities excavated by this species being much higher in mature Scots pine-dominated forests of the Trebon Basin than in young restored forests of the Ore Mts. (major management interventions in the past due to atmospheric pollution; for detail, see Drdáková 2004, Kopáček and Veselý 2005). Simultaneously, pygmy owls — which almost solely use natural tree cavities for their breeding and avoid nest boxes in Central European conditions (Glutz von Blotzheim and Bauer 1980) — were substantially higher in their population size in the Trebon Basin than the Ore Mts. In **Study II**, it was suggested that the lack of natural tree cavities was the main reason for a substantially higher readiness of boreal owls to occupy nest boxes in the Ore Mts. Therefore, it is appropriate to install nest boxes in these young forests and forest stands at the end of intensive logging and clear-cutting to promote nesting opportunities for the breeding populations of the boreal owl in the Czech Republic.

4.3.1 Nest boxes as a good opportunity for the boreal owl

The use of nest boxes as conservation and monitoring tools in different types of habitats and environments and the biological consequences of this technique can, in some cases, bring positive as well as negative results (Mänd et al. 2005, Gottschalk et al. 2011). For example, nest boxes can increase intraspecific brood parasitism or

breeding density, which leads to a decrease in reproductive success (for details, see Schlaepfer et al. 2002, Mänd et al. 2005). Additionally, the great crested flycatcher (*Myiarchus crinitus*) located in nest boxes, suffered from higher predation than nests situated in natural cavities (Miller 2002). The occupancy rate of nest boxes by boreal owls significantly decreases with their age due to increased risk of nest predation by martens or food depletion in the vicinity of old nest boxes (Sonerud 1985, 1989, Korpimäki 1993, Korpimäki and Hakkarainen 2012, Sonerud 2021), and the quality of nest boxes and the absence of maintenance can lead to an increase in the presence of nest parasites and affect nest box use by target species (Lambrechts et al. 2012, Zárybnická unpublished data). From the perspective of the boreal owl inhabiting the study areas, the above-mentioned suggestions were not confirmed. First, the boreal owl does not exhibit brood parasitism (Horníček et al. 2017). Second, in **Study II**, boreal owl did not use nest boxes if natural nest cavities were available. Third, only 8% of the nests were destroyed by pine martens in the Ore Mts. (n = 76), and one nest failed due to pine martens in the Trebon basin (n = 5). The information on nest predation from other areas varies. For example, in Germany, martens predated 59% of owl nests placed in boxes but only 24% in natural cavities (Meyer 2003). In the Spain Pyrenees, the trend was the opposite; martens destroyed 50% of nests in natural cavities, and only 15% were in boxes (López et al. 2010). During the long-term study in the Ore Mts., it was found that the predation rate of boreal owl nests by pine martens wildly varied among years, reaching from 0% to 50% (Drdáková 2003, Zárybnická unpublished data, Zárybnická et al. 2015e). Zárybnická et al. (2015c) found that the predation rate by pine martens is significantly related to the availability of *Apodemus* mice; however, most authors do not consider this factor when they evaluate nest predation. In **Study II**, it was not compared to nest predation in nest boxes and natural cavities. However, Hruška (2020) performed long-term research (2006–2020, 123 nests) on a boreal owl population nesting in natural cavities in a hilly area of Central Czechia (the Vysočina hills) and found that pine marten destroyed from 6% to 50% of all nests each year. The author also identified that up to 25% of all nests failed due to flooding in some years, and even nestlings from one nest drowned (see also, Llambías and Fernandez 2009). Such losses usually do not occur in nest boxes due to their regular maintenance and have never been identified as a reason for nest failure in the Ore Mts. (Zárybnická, unpublished data), suggesting that nest boxes can provide better conditions for boreal owl nesting than natural cavities. Fourth, a significantly higher

nest box occupancy was found in the Ore Mts. than in the Trebon Basin, even though the mean age of nest boxes was about 1.7 years older in the Ore Mts. than in the Trebon Basin, and the predation rate here reached only 8% compared to other studies (see above). And finally, the same quality, maintenance, and installation were used in the study areas of *Study II*. Specifically, nest boxes were installed high enough above the ground, regularly relocated and maintained, which kept nest boxes dry and clean, and also the surrounding of the nest box entrance was kept free of branches.

The high density of nest opportunities can cause other effects, such as changes in the social mating system (Johnson and Kermott 1991, Petit 1991). The boreal owl is primarily monogamous, but some 10–20% of males become polygynous and mate with two or three females simultaneously in food peak years (Carlsson 1991, Hakkarainen and Ekorpimäki 1998). Polygynous boreal owl males typically exhibit higher offspring productivity and lifetime reproductive success than monogamous males (Korpimäki 1992). However, the secondary females of polygynous males produce fewer offspring than primary females or monogamous females (Korpimäki 1991). As a result, increased nest opportunities, combined with adequate food conditions and the availability of females, can result in conflict over parental care (Korpimäki et al. 2011). However, in long-term research in the Ore Mts., only rare polygynous males have been identified, usually one male each year. Only once were four polygynous males identified (16% of checked males) in the *Apodemus* peak year, and the reproductive success of these nests (the number of fledglings in relation to hatchings) reached, on average, 95% (Zárybnická unpublished data). Thus, nest boxes do not seem to affect the parental social system of the boreal owl. Instead, food availability has been suggested to be a primary driver of the mating system and reproductive success of this owl (Korpimäki 1992, Zárybnická 2009b, Zárybnická et al. 2015e). I conclude that installing nest boxes in areas with sufficient amount of cavities did not have a negative effect (in a sense of ecological trap) on the populations of boreal owls monitored in *Study II*, as it prefers natural cavities in these locations.

4.3.2 Recommendations for nest box deployment

It has been documented that nest boxes can effectively support the boreal owl population and be a suitable tool for collecting biological information and material. At

the same time, nest boxes can lose their supporting function for the target species under specific environmental conditions. In addition, the results of the presented studies contribute to maximizing the use of nest boxes for the conservation of the cold-adapted boreal owl, which may be threatened in the future by climate change and increased anthropogenic activity in the Czech Republic. Based on *Study I*, *Study II*, and the literature review summarized the following recommendations to maximize the effectiveness of nest boxes for boreal owls in the Czech Republic and Central Europe, respectively. To efficiently support the boreal owl population, it should be follow these recommendations and their combinations:

1. To deploy nest boxes in the biotopes where natural cavities are lacking in short or long term. An example of such biotopes is a forest habitat that suffers from vegetation loss due to, for example, intensive management, atmospheric pollution, climatic (e.g., windthrow calamity, heavy snowfall), or biotic processes such as the outbreak of insects (e.g., European spruce bark beetle, *Ips typographus*) and fungi, especially at higher elevations and mountain areas.

2. To deploy nest boxes in the biotopes where forest management plans intensive logging and clear-cutting.

3. To deploy nest boxes in forest habitats where the black woodpecker population is limited or occurs in lower densities.

4. To deploy nest boxes preferably in coniferous forest habitats, especially at middle and high elevations (above 600 m a. s. l.), providing optimal climate conditions for the boreal owl.

5. To deploy nest boxes in forest habitats where the abundance of the tawny owl is low to eliminate the interspecific competition.

6. Erected nest boxes require regular maintenance and service at least once per year. Mainly, they require (a) repairing to avoid water leaking inside the box or wind blowing throughout the box, (b) remaining branches from the surrounding of the nest-box entrance, (c) relocating nest boxes if nest predation is recorded, and (d) removing old content of nest boxes, mainly food and nest remains, to eliminate the presence of parasites.

4.4 Vocalization of the boreal owl

Study III, using passive acoustic monitoring, confirmed the influence of environmental factors on spontaneous owl-calling behavior. Boreal owl vocalizations varied significantly between years, within the breeding season (depending on food abundance), and over the course of the night. More specifically, the frequency of sampling points in which boreal owls were recorded was higher in the year of increased prey abundance and at the beginning of the breeding season. The duration (the number of minutes per hour) of territorial vocalization of boreal owls increased in the year with a higher food supply, later in the breeding season, and showed two peaks during the night. However, weather conditions, other breeding pairs of boreal owls, and the vocalization of other species did not affect the vocalization of the boreal owl.

The reproductive behavior of the boreal owl varies significantly depending on the changing availability of its main prey. For example, the size of the clutch, the number of fledglings, and the date of nesting change depending on food availability. In *Study III*, a relationship between food supply and the number of hooting males was additionally demonstrated. In years with low food supply, the duration of territorial hooting and the frequency of sites at which boreal owl vocalizations were recorded decreased. Also, Kloubec and Pačenovský (1996) documented a positive relationship between the territorial calling of boreal owls and the number of prey items in food material collected from owl nests. Ratajc et al. (2022) explained the reduction in the number of male territorial hooting to their absence, such as in years with low prey abundance, males likely leave their territories to find a suitable prey-rich area (primarily mixed forests of lower elevations), or do not nest (Korpimäki and Hakkarainen 2012). Additionally, with changing food availability during and between breeding seasons, interspecific predation pressure may also change and thus influence the abundance of hooting individuals. Although the effect of interspecific interaction on the vocal activity of the boreal owl was not found in *Study III*, Pepłowska-Marczak (2019) reported that the boreal owl reduces its vocal activity in the presence of its competitor, the tawny owl, and limits it to short territorial and contact vocalizations. Also, Ratajc et al. (2022) did not record any vocal activity of the boreal owl using vocal provocation in an area with higher tawny owl densities. However, they did record a few hooting individuals after additional surveys. Therefore, to most accurately

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determine population abundance in the study area, it is necessary to monitor vocally active individuals over longer time horizons.

In the Czech Republic, boreal owl vocalizations occurred at more sampling points in late March/early April compared to late April/early May (*Study III*). Also, in Northern and Central Europe, the peak of vocal activity has usually been recorded during February/March and March/April, when most individuals vocalize (Mikkola 1983, Kloubec 2007, Korpimäki and Hakkarainen 2012). The decrease of vocalization at the end of the season may be mainly related to nesting, since after egg-laying, the nesting pair typically uses only contact voices for communication (Korpimäki 1981, Vacík 1991). However, egg laying dates may vary over the years depending on snow cover height, which affects food availability at the beginning of the breeding season (Korpimäki and Hakkarainen 2012, Šindelář et al. 2015, Kouba et al. 2020). As a result, for an effective estimation of boreal owl population abundance, it is advisable to monitor vocally active individuals early and later in the breeding season, mainly during the peak vocalization phase, which usually starts between early March and late April (Korpimäki and Hakkarainen 1991, Zárybnická et al. 2015c). The length of the hoot lengthened as the breeding season progresses, predominantly in years with a higher food supply (*Study III*). For example, Korpimäki and Hakkarainen (2012) point to the lengthening of the vocal activity of the boreal owl as the season progresses, predominantly in unpaired individuals. Therefore, during the second acoustic monitoring later in the breeding season, unpaired vocalizing male boreal owls could be frequently detected. Finally, boreal owls showed two peaks of vocal activity during the night, between 23:00–24:00 and 03:00–04:00, while they reduced their vocal activity between 24:00–03:00 (*Study III*). Similarly, the vocalization of boreal owls dropped around midnight and was associated with systematically changing sunset and sunrise during the breeding season in studies conducted based on human-acoustic monitoring (e.g., Kloubec and Pačenovský 1996). The biphasic circadian rhythm was also observed in males based on prey deliveries to their nests that peaked after sunset and before sunrise and shifted during the breeding season (Klaus et al. 1975, Zárybnická 2009a, Zárybnická et al. 2012). The circadian activity with peaks between 22:00–23:00 and 03:00–05:00 was also found in females based on their nest activities (measured as the frequency of departures and arrivals from and to their nests; Drdáková 2008).

In *Study III*, no effect of weather conditions on the vocal activity of the boreal owl was found, though some studies have noted a reduction in vocal activity of the boreal owl in response to worsening weather conditions, which may lead to an underestimation of the abundance of the monitored population (e.g., wind and rain; Kloubec and Pačenovský 1996, Lengagne and Slater 2002, Kloubec 2007, Zuberogoitia et al. 2018). However, during the study, bioacoustic monitoring was conducted primarily during suitable weather conditions. This is likely why no relationship was found between the vocalizations of the boreal owl and the presence of rain or wind. Moreover, high ambient noise increases the difficulty of detecting vocalizing owls and can cause a high number of false positives or increase the rate of false negative detections in automatic species recognition (Buxton and Jones 2012, Rognan et al. 2012, Zuberogoitia et al. 2018). As a result, most authors avoided acoustic monitoring during unsuitable weather conditions, whereas recording several nights in a row will increase the likelihood of detection and acquisition of a quality recording, especially in environments where weather conditions can change rapidly (Tripp and Otter 2006, Frommolt 2017, Abrahams 2019).

4.4.1 Recommendations for bioacoustic monitoring of spontaneous vocal activity

Based on the above-mentioned environmental factors influencing the spontaneous vocal activity of the boreal owl in the Czech Republic, *Study III*, and previous studies, it should be kept the following recommendations in order to maximize the effectiveness of acoustic monitoring of boreal owl's populations and get a reliable estimate of the population abundance:

1. To estimate the abundance of the boreal owl using autonomous recording units, it is necessary to monitor this owl population for at least two years.
2. To deploy autonomous recording units at the peak of the vocal activity of the boreal owl; in order to that, acoustic units should be applied no less than twice per season and always for at least two nights.
3. In the conditions of the Czech Republic, monitor vocal activity from sunset to sunrise, or at least between 22:00–24:00 and 03:00–5:00 (two peaks of vocal activity).
4. To deploy autonomous recording units during suitable weather conditions, i.e., mainly under eliminated rain and wind.

5. To deploy autonomous recording units at a distance of about 1 km, but no less than 0.5 km, but no more than 3.0 km from each other.

5. Conclusion

This dissertation summarizes the results of three studies on the influence of selected environmental factors on the distribution, use of nest boxes, and spontaneous vocal activity of breeding populations of the boreal owl in the Czech Republic found through different types of monitoring.

First, the effect of elevation and temperature on the distribution of the boreal owl was demonstrated using atlas data. The Czech boreal owl populations, compared to other owl species, prefers to inhabit the highest elevations and the coldest localities. Even though the boreal owl has been recorded in forest stand locations of lower elevations in the Czech Republic, the distribution of this species is still limited by elevation gradient and temperature. In Southern and Northern Europe, changes in the distribution and abundance of this species have already been detected ostensibly as a result of direct and indirect effects of global warming, forest habitat degradation, and changes in interspecific interaction. Although the boreal owl has been widely detectable in the last decades in the Czech Republic, there is a real risk that its abundance may begin to fluctuate or even decline due to consequences of intensive forest management, bark beetle calamities, and climate change. Therefore, there is a need for continual monitoring of trends in the distribution and abundance of the species and understanding methods to support local population effectively.

Second, the effect of forest structure on the nest box use by the boreal owl in two habitat-different forest stands of higher and lower elevations was determined using vocal activity and monitoring of nest-box populations. Only nest boxes erected in young restored forests in the historically air-polluted Ore Mts. were an effective tool to support populations of boreal owl. Simultaneously, it was discovered that boreal owls adjusted nest-box utilization according to habitat types, and the availability of natural tree cavities probably reduced their willingness to occupy nest boxes. These findings document that the effectiveness of nest boxes to supporting target species varies significantly between habitats. Therefore, deploying nest boxes should be considered carefully under local environmental conditions. Using the results obtained and previous studies, a list of recommendations for deploying nest boxes in the Czech Republic was compiled.

Finally, bioacoustic monitoring is an effective tool for assessing the distribution and abundance of local populations of nocturnal species. However, the effects of varying environmental conditions have to be considered, and mainly the variation among years associated with food abundance, within seasons associated with timing of breeding, and in the course of the night associated with circadian activity have to be well considered. Using the results obtained and previous studies, a list of recommendations for effective monitoring of boreal owl populations was compiled.

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7. Curriculum vitae & list of publication

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Education

1. Extension course	2020–present, Czech University of Life Sciences Prague, Institute of Education and Communication, V Lázních 3, 159 00 Praha 5, Malá Chuchle, Study for Teaching Vocational Subjects
2. Doctoral study	2017–present, Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Kamýcká 129, 165 00 Praha, Suchdol, Ecology
3. Master's degree	2015–2017, Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Kamýcká 129, 165 00 Praha, Suchdol, Nature Conservation, diploma thesis: The occurrence of Tengmalm's owl (*Aegolius funereus*) in relation to environmental factors and interspecific competition.
4. Bachelor's degree	2012–2015, Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Kamýcká 129, 165 00 Praha, Suchdol, Applied Ecology, Bachelor's thesis: The effect of ambient temperature on the temperature of the Tengmalm's owl (*Aegolius funereus*) clutches during incubation period.
5. High school	2008–2012, Gymnasium and Secondary Vocational School of Economics, Nádražní 90, 264 01 Sedlčany.

Scientific activity

Publications	1. **Ševčík, R.**, J. Riegert, J. Šindelář, and M. Zárybnická. 2019. Vocal activity of the Central European Boreal Owl population in relation to varying environmental conditions. Ornis Fennica **96**:1-12. 2. **Ševčík, R.**, J. Riegert, K. Šťastný, J. Zárybnický, and M. Zárybnická. 2021. The effect of environmental variables on owl distribution in Central Europe: A case study from the Czech Republic. Ecological Informatics. **64**:101375. https://doi.org/10.1016/j.ecoinf.2021.101375 3. **Ševčík, R.**, B. Kloubec, J. Riegert, J. Šindelář, M. Kouba, and M. Zárybnická. 2022. Forest structure determines nest box use by Central European boreal owls. Scientific Reports **12**:4735. https://doi.org/10.1038/s41598-022-08792-y
Conferences	1. Kostelecké inspirování 2017: Vocal activity of boreal owl in Central Europe: effect of food supply and environmental factors, 2. KAGÚP Chloumek 2018: Bioacoustic monitoring of boreal owl in the Ore Mountains: the effect of environmental conditions and interspecific competition 3. Zoologické dny 2020: The effect of elevation on the distribution of owls in the Czech Republic.
Work and research experience (cooperation)	1. 2022–present, Forestry and Game Management Research Institute (Supporting residual populations of the European hare (*Lepus europaeus*) in different types of agricultural landscapes: from research to applied conservation) – field and research worker. 2. 2021–2022, Institute of Vertebrate Biology CAS (Determining the food supply in little owl's territories using captures of small mammals and beetles from the family ground beetles (Carabidae)) – field work, data processing. 3. 2021, Czech Society for Ornithology (Bird monitoring in Special Protection Area Eastern Ore Mountains) – field work, data processing. 4. 2018–2020, Czech University of Life Sciences Prague, Faculty of Environmental Sciences, conference Kostelecké inspirování – organizer. 5. 2017, Program Work and Travel (CCUSA) in Yellowstone National Park – USA.

Grants

Principal investigator	IGA 2018 (20184222), 2018–2020, Habitat use by boreal owl with respect to spatiotemporal changes and intra/interspecific competition.
Co-investigator	CIGA 2017 (20174203), 2017, The effect of climatic factors on diet structure of Tengmalm's owl (*Aegolius funereus*). IGA 2016 (20164215), 2016–2018, The effect of food supply, habitat and intraspecific competition on utilization of nest boxes by boreal owl (*Aegolius funereus*). CIGA 2016 (20164202), 2016–2017, Monitoring of bird nesting using an "Intelligent Bird Box."

Languages and other knowledge and skills

Native language	Czech
Foreign language	English (B2)
Software skills	RStudio, Statistic, Avisoft SASLab Pro, AMSrv, ArcGIS, Microsoft Office, QGIS, Photoshop
Certificates	Certificate of professional competence for designing experiments and experimental projects under Section 15d (3) of Act No 246/1992 Coll., on the Protection of Animals against Cruelty, as amended (valid until 4. 6. 2028).
Driving license	Class B

8. Supplementary Information

Forest structure determines nest box use by Central European boreal owls

Richard Ševčík, Bohuslav Kloubec, Jan Riegert, Jiří Šindelář, Marek Kouba & Markéta Zárybnická

Table S1. The abundance of small mammals in snap traps in the Ore Mountains and the Trebon Basin in 2015–2017. The number of individuals, trapping index (i.e., the number of individuals per 100 trap-nights, mean ± SD), and the total proportion of particular species are shown.

Study area	Species	2015 No. of inds.	Trapping index	2016 No. of inds.	Trapping index	2017 No. of inds.	Trapping index	Total number	%
Ore Mts.	*Apodemus* mice	11	1.53 ± 1.11	0	0.00	30	4.17 ± 4.01	41	54.0
	Microtus voles	1	0.14 ± 0.34	0	0.00	1	0.14 ± 0.34	2	2.6
	Myodes voles	4	0.56 ± 0.68	1	0.14 ± 0.34	26	3.61 ± 6.53	31	40.8
	Sorex shrews	2	0.28 ± 0.68	0	0.00	0	0.00	2	2.6
	Total	18	2.50 ± 1.18	1	0.14 ± 0.34	57	7.92 ± 9.45	76	100.0
Trebon Basin	*Apodemus* mice	10	1.39 ± 1.88	2	0.28 ± 0.43	2	0.28 ± 0.43	14	53.9
	Microtus voles	1	0.14 ± 0.34	0	0.00	0	0.00	1	3.8
	Myodes voles	2	0.28 ± 0.68	4	0.56 ± 1.01	4	0.56 ± 0.86	10	38.5
	Sorex shrews	1	0.14 ± 0.34	0	0.00	0	0.00	1	3.8
	Total	14	1.94 ± 1.64	6	0.83 ± 1.39	6	0.83 ± 1.05	26	100.0

Table S2. The results of GLMM analysis (*lmer* function). The effect of the study area, year, and their interaction on the abundance of small mammals.

Model	AIC	df	Chi	% of explained variability	P
Apodemus mice					
null model	165.78	35			
null model + area	164.83	34	2.95	1.85	0.086
null model + year	163.58	33	3.25	3.71	0.071
null model + year*area	156.13	32	13.45	12.30	0.004
Myodes voles					
null model	181.94	35			
null model + area	182.83	34	1.11	0.63	0.292
null model + year	182.82	33	2.01	1.77	0.156
null model + year*area	184.53	32	4.29	4.21	0.232
Microtus voles					
null model	2.16	35			
null model + area	3.79	34	0.37	8.57	0.546
null model + year	3.91	33	1.89	36.95	0.170
null model + year*area	8.73	32	1.18	47.18	0.758
Sorex shrews					
null model	22.18	35			
null model + area	23.97	34	0.21	1.32	0.644
null model + year	22.19	33	3.78	24.70	0.052
null model + year*area	27.46	32	0.72	29.16	0.868

Table S3. Partial relationships of *Apodemus* mouse abundance between the study areas (Ore Mts., Trebon Basin) and years (2015–2017) using a post-hoc test (function *lsmeans* in lsmeans package).

Area	Year	Contrast	Estimate	df	t-ratio	P
Ore Mts.		2015 – 2016	1.53	20.0	1.54	1.000
Ore Mts.		2015 – 2017	-2.64	20.0	-2.66	0.134
Ore Mts.		2016 – 2017	-4.17	20.0	-4.21	0.004
Trebon Basin		2015 – 2016	1.11	20.0	1.12	1.000
Trebon Basin		2015 – 2017	1.11	20.0	1.12	1.000
Trebon Basin		2016 – 2017	0.00	20.0	0.00	1.000
	2015	Ore Mts. – Trebon Basin	0.14	28.4	0.13	1.000
	2016	Ore Mts. – Trebon Basin	-0.28	28.4	-0.26	1.000
	2017	Ore Mts. – Trebon Basin	3.89	28.4	3.58	0.011

Table S4. The number of sampling points, the number of sampling points with owl vocalization, the vocal occupancy rate (i.e., the number of vocalizing individuals per the number of sampling points), and the density of vocalizing individuals related to the study area (Ore Mts., Trebon Basin), year (2015–2017), and period (April, May).

Year	Species	Month	Ore Mts. No. of sampling points	No. of sampling points with vocalization	Vocal occupancy rate	Density per 10 km^2	Trebon Basin No. of sampling points	No. of sampling points with vocalization	Vocal occupancy rate	Density per 10 km^2
2015	Boreal owl	April	34	20	0.59	1.87	31	16	0.52	1.64
		May	26	13	0.50	1.59	31	18	0.58	1.85
	Tawny owl	April	34	14	0.41	1.31	31	15	0.48	1.54
		May	26	10	0.38	1.22	31	15	0.48	1.54
	Eagle owl	April	34	0	0.00	0.00	31	2	0.06	0.21
		May	26	0	0.00	0.00	31	1	0.03	0.10
	Pygmy owl	April	34	3	0.09	0.28	31	6	0.19	0.62
		May	26	2	0.08	0.24	31	11	0.35	1.13
	Long-eared owl	April	34	3	0.09	0.28	31	1	0.03	0.10
		May	26	3	0.12	0.37	31	0	0.00	0.00
	Mean ± SD		30.0 ± 4.2	6.8 ± 6.9	0.23 ± 0.22	0.72 ± 0.70	31.0 ± 0.0	8.5 ± 7.2	0.27 ± 0.23	0.87 ± 0.74
2016	Boreal owl	April	36	17	0.47	1.50	31	7	0.23	0.72
		May	35	6	0.17	0.55	21	4	0.19	0.61
	Tawny owl	April	36	17	0.47	1.50	31	15	0.48	1.54
		May	35	14	0.40	1.27	21	8	0.38	1.21
	Eagle owl	April	36	1	0.03	0.09	31	0	0.00	0.00

Year	Species	Month								
		May	35	0	0.00	0.00	21	0	0.00	0.00
	Pygmy owl	April	36	2	0.06	0.18	31	9	0.29	0.92
		May	35	2	0.06	0.18	21	1	0.05	0.15
	Long-eared owl	April	36	3	0.08	0.27	31	2	0.06	0.21
		May	35	3	0.09	0.27	21	0	0.00	0.00
	Mean ± SD		35.5 ± 0.5	6.5 ± 6.8	0.18 ± 0.19	0.58 ± 0.60	26.0 ± 5.3	4.6 ± 5.0	0.17 ± 0.17	0.54 ± 0.55
2017	Boreal owl	April	36	18	0.50	1.59	32	11	0.34	1.09
		May	36	14	0.39	1.24	32	11	0.34	1.09
	Tawny owl	April	36	11	0.31	0.97	32	18	0.56	1.79
		May	36	9	0.25	0.80	32	14	0.44	1.39
	Eagle owl	April	36	0	0.00	0.00	32	1	0.03	0.10
		May	36	0	0.00	0.00	32	1	0.03	0.10
	Pygmy owl	April	36	1	0.03	0.09	32	9	0.28	0.90
		May	36	2	0.06	0.18	32	5	0.16	0.50
	Long-eared owl	April	36	5	0.14	0.44	32	3	0.09	0.30
		May	36	3	0.08	0.27	32	2	0.06	0.20
	Mean ± SD		36.0 ± 0.0	6.3 ± 6.4	0.18 ± 0.18	0.56 ± 0.56	32.0 ± 0.0	7.5 ± 6.0	0.23 ± 0.19	0.75 ± 0.59

Table S5. The number of boxes, the number of boxes occupied by animal taxa (boreal owls, common goldeneyes, pine martens, passerine birds, bats, and insects), and the nest box occupancy rate (the number of occupied nest boxes per available nest boxes) related to the study area (Ore Mts., Trebon Basin), year (2015–2017), and period (spring: April-May, autumn: September-October).

Year	Species	Period	Ore Mts.			Trebon Basin		
			Number of boxes	Number of occupied boxes	Nest box occupancy rate	Number of boxes	Number of occupied boxes	Nest box occupancy rate
2015	Boreal owl	Spring	230	23	0.10	245	3	0.01
	Passeriformes	Spring	230	11	0.05	245	20	0.08
	Insect	Spring	230	0	0.00	245	0	0.00
	Pine marten	Spring	230	3	0.01	245	0	0.00
	Goldeneye	Spring	230	0	0.00	245	0	0.00
	Bats	Spring	230	0	0.00	245	0	0.00
		Mean ± SD	230.0 ± 0.0	6.2 ± 9.3	0.03 ± 0.04	245.0 ± 0.0	3.8 ± 8.0	0.02 ± 0.03
2016	Boreal owl	Spring	246	23	0.09	242	2	< 0.01
	Passeriformes	Spring	246	74	0.30	242	17	0.07
	Insect	Spring	246	0	0.00	242	2	< 0.01
	Pine marten	Spring	246	2	< 0.01	242	1	< 0.01
	Goldeneye	Spring	246	0	0.00	242	0	0.00
	Bats	Spring	246	0	0.00	242	0	0.00
		Mean ± SD	246.0 ± 0.0	16.5 ± 29.6	0.07 ± 0.12	242.0 ± 0.0	3.7 ± 6.6	0.02 ± 0.03
	Boreal owl	Autumn	246	0	0.00	56	0	0.00
	Passeriformes	Autumn	246	19	0.08	56	0	0.00
	Insect	Autumn	246	1	< 0.01	56	29	0.52

	Species	Season						
	Pine marten	Autumn	246	0	0.00	56	0	0.00
	Goldeneye	Autumn	246	0	0.00	56	0	0.00
	Bats	Autumn	246	0	0.00	56	0	0.00
	Mean ± SD		246.0 ± 0.0	3.3 ± 7.7	0.01 ± 0.03	56.0 ± 0.0	4.8 ± 11.8	0.09 ± 0.21
2017	Boreal owl	Spring	246	18	0.07	237	0	0.00
	Passeriformes	Spring	246	49	0.20	237	19	0.08
	Insect	Spring	246	0	0.00	237	26	0.11
	Pine marten	Spring	246	0	0.00	237	0	0.00
	Goldeneye	Spring	246	0	0.00	237	1	< 0.01
	Bats	Spring	246	0	0.00	237	0	0.00
	Mean ± SD		246.0 ± 0.0	11.2 ± 19.9	0.05 ± 0.08	237.0 ± 0.0	7.7 ± 11.7	0.03 ± 0.05
	Boreal owl	Autumn	246	1	< 0.01	200	0	0.00
	Passeriformes	Autumn	246	15	0.06	200	38	0.19
	Insect	Autumn	246	0	0.00	200	87	0.44
	Pine marten	Autumn	246	0	0.00	200	0	0.00
	Goldeneye	Autumn	246	0	0.00	200	0	0.00
	Bats	Autumn	246	0	0.00	200	3	0.02
	Mean ± SD		246.0 ± 0.0	2.7 ± 6.1	0.01 ± 0.02	200.0 ± 0.0	21.3 ± 35.5	0.11 ± 0.18