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**CAVITY-USE AND
SPATIAL ECOLOGY OF
THE EURASIAN PYGMY
OWL IN THE MANAGED
BOREAL FORESTS**

Daniele Baroni



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*To the pygmy owls,
with the hope that this contribution
will help so as his magic habitat
will not be destroyed anymore in the future*

UNIVERSITY OF TURKU

Faculty of Science

Department of Biology

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ABSTRACT

The loss and degradation of boreal old-growth forest is threatening biodiversity and a wide range of ecosystem services. Especially in Europe, the boreal forest has been subject to intensification of forestry practices, leading to habitat alteration and loss of nesting site for many taxa. This threat has strongly affected secondary cavity nesters, and many of them are declining among forest birds in Europe. I investigated cavity-use and spatial ecology of a forest-dwelling predator occurring at low densities across its distribution range, the Eurasian Pygmy Owl *Glaucidium passerinum*, which requires tree cavities for both nesting and food hoarding.

I first studied the abundance of suitable tree cavities at the landscape level, and examined the preferences of the owls for different cavity characteristics in two experiments and several years of nest-box monitoring data. I thereafter focused on how cavity distribution in space and time may limit their use during and outside of the breeding season. Using long-term data on the use of nest-boxes resembling tree cavities by individually marked pygmy owls, I compared the habitat and the distances among the nest-boxes used during two different seasons. Moreover, as most of the previous information are from nest-box occupancy, estimating the pygmy owl's true abundance remains a significant challenge. I therefore used passive acoustic monitoring with a large grid of detectors, and examined the habitat of pygmy owl calling sites and estimated their abundance. Finally, I used GPS-tracking as an essential conservation tool to fill the gaps of knowledge regarding their spatial ecology. For the first time, we used a small archival global positioning system (GPS) tag to identify and characterize breeding territories of the pygmy owl. We obtained 14 individual home ranges for males during the breeding period 2021 in two different study areas at the latitudinal extremes of the species distribution in Europe: 8 males in the boreal forest in Finland, where there is evidence that the species is declining, and 6 males in the Alps in Italy, where it is expanding its range.

My results show that natural cavities were scarce in the landscape (ca. 6.5/km²). However, natural cavity abundance per se does not seem to limit the breeding density of this predator, as suggested by a low occupancy rate in natural cavities and nest-boxes. Cavities whose characteristics prevent the nest from being reached by predators were clearly preferred, as the owls selected cavities with more than 5 cm width of the front wall and the nests had 15–30 cm of entrance-bottom distance within the cavity. While the number of cavities per se may not limit the nesting of the owls, they may be limited by suitable habitat with abundant food supply around

available cavities, or by lack of cavities in suitable habitats. Comparing the habitat and the distances among the nest-boxes used during two different seasons, I found that pygmy owls appear to be more demanding in their requirements for breeding than for food-hoarding habitat, because of the importance of spruce forests as a nesting habitat and nesting sites being farther from houses than food-hoarding sites. Also, I highlight the need of many different cavities within the home range of each individual, as individually marked pygmy owls mainly used different nest-boxes for nesting and food-hoarding, and they also used different nest-boxes in different years.

The results of the passive acoustic survey also demonstrated that the pygmy owl can be considered an old-growth forest specialist. Indeed, my results with habitat data at three spatial scales, and for both calling and nesting sites, show that increasing availability of old-growth forests was consistently the most important habitat variable increasing occupancy probability of the pygmy owls in a landscape dominated by managed forests. When I clustered the detections into territories, I estimated a density of pairs or territorial males that was altogether three times the number of pairs breeding in nest-boxes. Considering the number of natural cavities and nest-boxes, we however estimate that nest-boxes were preferred over natural cavities for breeding. From the GPS-tags study, I found that home ranges are bigger than previously estimated with telemetry data, and there is difference between the two study areas, with owls in the alpine forests having smaller home ranges (90% AKDE 1.47 ± 0.28 km²) than in the boreal forest (90% AKDE 3.08 ± 1.48 km²). I also show that pygmy owls are strictly diurnal, being active from sunrise to sunset in southern Europe, and at almost any time of the day in the North, because nights are not completely dark in the northern summer. Pygmy owls performed long hunting trips, travelled more than expected (4.66 ± 1.79 km per day in the boreal forest and 5.93 ± 1.98 in the alpine forests) and spent most of the time inside coniferous forest, strongly avoiding open habitats and forest edges.

All my findings are consistent with the hypothesis that pygmy owl can be considered an old-growth forest species, and I provide for the first time insights on habitat selection for the sites used for nesting and food hoarding sites, for advertising and for hunting. It is crucial information for conservation management strategies, as the pygmy owl's home ranges are large, diverse, and all its essential properties must be protected. Effective conservation strategies for this old-growth forest specialist should also include the maintenance of high-quality habitat that contains suitable cavities, supporting the need for protection of mature and old-growth forests as a whole, and not just of cavity bearing trees alone.

KEYWORDS: Boreal forest, Conservation, Forest management, Tree cavity occupancy, Population limitation, Secondary cavity nesting, Food depletion, Passive acoustic survey, GPS tracking

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TIIVISTELMÄ

Boreaalisen vanhan metsän häviäminen ja heikentyminen uhkaa biologista monimuotoisuutta ja laajaa ekosysteemien kirjoa. Erityisesti Euroopassa boreaalinen metsä on kärsinyt metsien voimakkaasta käytöstä, mikä on johtanut elinympäristöjen muuttumiseen ja monien lajien pesimispaikkojen häviämiseen. Tämä muutos on vaikuttanut toissijaisesti kolopesijöihin, ja monet niistä ovat vähenemässä Euroopan metsälintujen keskuudessa. Tutkin alhaisilla tiheyksillä esiintyvän metsässä elävän saalistajan, varpuspöllön (*Glaucidium passerinum*), pesäkolojen käyttöä ja alueellista ekologiaa. Laji käyttää koloja sekä pesimiseen että ravinnon varastointiin.

Tutkin ensin sopivien puunkolojen runsautta maisematasolla ja pöllöjen mieltymyksiä erilaisiin kolojen ominaisuuksiin kahdessa kokeessa ja useiden vuosien pesäpaikan seurantatiedoilla. Tämän jälkeen keskityin siihen, miten kolojen jakautuminen tilassa ja ajassa voi rajoittaa niiden käyttöä lisääntymiskauden aikana ja sen ulkopuolella. Yksilöllisesti merkittyjen varpuspöllöjen puunkoloja muistuttavien pesäpönttöjen käyttöä koskevan pitkän aikavälin tiedon avulla vertasin pönttöjen ympäristöä ja etäisyyksiä kahden eri vuodenajan aikana. Lisäksi, koska suurin osa aiemmista tiedoista on peräisin pönttöjen käytöstä, varpuspöllön todellisen runsaslukuisuuden arvioiminen on edelleen merkittävä haaste. Siksi käytin passiivista akustista seuranta suurella havaintopaikkamäärällä, ja tutkin varpuspöllöjen soidinlaulupaikkojen elinympäristöä ja arvioin niiden runsauden. Lopuksi käytin GPS-seuranta olennaisena suojelutyökaluna, jolla voitiin täyttää aukot, jotka liittyvät pöllöjen alueellista ekologiaa koskevaan tietoon. Ensimmäistä kertaa käytimme pientä GPS-paikanninta varpuspöllön elinpiirin tunnistamiseen ja karakterisointiin. Saimme 14 yksilöllistä koiraiden reviiriä lisääntymiskaudella 2021 kahdelle eri tutkimusalueelle lajien levinneisyyden ääripäässä Euroopassa: 8 koirasta Suomen boreaalisessa metsässä, jossa lajin vähenemisestä on näyttöä, ja 6 koirasta Alpeilla Italiassa, jossa se laajentaa levinneisyysaluettaan.

Tulokseni osoittavat, että luonnonkolot olivat niukat ympäristössä (n. 6,5/km²). Luonnonkolojen runsaus sinänsä ei kuitenkaan näytä rajoittavan tämän petoeläimen pesimätiheyttä, kuten luonnonkolojen ja pönttöjen alhainen käyttöaste osoittaa. Kolot, joiden ominaisuudet estävät saalistajia pääsemästä pesään, olivat selvästi suosituimpia, koska pöllöt valitsivat kolot, joiden etuseinän leveys on yli 5 cm, ja pesien suuauko ja pohjan etäisyys oli 15–30 cm. Vaikka kolojen lukumäärä sinänsä ei välttämättä rajoita pöllöjen pesimistä, niitä saattaa rajoittaa sopiva elinympäristö, jolla on runsaasti ravintoa käytettävissä olevien kolojen ympärillä, tai kolojen puute

sopivissa elinympäristöissä. Verrattaessa kahden eri vuodenajan aikana käytettyjen pesäkolojen elinympäristöä ja etäisyyksiä havaitsin, että varpuspöllöt vaikuttavat vaativammilta lisääntymisvaatimuksiltaan kuin ruokavarastoinnin elinympäristövaatimuksiltaan. Kuusimetsät ovat tärkeämpiä pesimisympäristönä ja pesimispaikat kauempana taloista kuin ruokavarastointipaikat. Korostan myös monien erilaisten kolojen tarvetta jokaisen yksilön reviirillä, sillä yksilöllisesti merkityt varpuspöllöt käyttivät pääasiassa eri eri pönttöjä pesintään ja ruokavarastoina, ja eri vuosina myös eri pesäpaikkoja.

Passiivisen akustisen kartoituksen tulokset osoittivat myös, että varpuspöllöä voidaan pitää vanhaa metsää suosivana lajina. Tulokseni kolmesta alueellisesta mittakaavasta sekä kutsu- että pesimispaikoista osoittavat, että vanhojen metsien lisääntyvä saatavuus oli jatkuvasti tärkein luontotyyppimuuttuja, joka lisäsi varpuspöllöjen esiintyvyyttä talousmetsien hallitsemassa maisemassa. Kun ryhmittelin havainnot alueiksi, arvioin parien tai reviirillisten koiraiden tiheyden, joka oli yhteensä kolme kertaa pöntöissä lisääntyvien parien määrä. Kun otetaan huomioon luonnonkolojen ja pesäkolojen määrä, arvioimme kuitenkin, että pönttöjä pidettiin parempina lisääntymiseen kuin luonnonkoloja. GPS-tutkimuksen perusteella havaitsin, että reviirit ovat suurempia kuin telemetriatietojen perusteella aiemmin arvioitiin, ja näiden kahden tutkimusalueen välillä on ero: pöllöillä on alppimetsissä pienemmät reviirit (90 % AKDE $1,47 \pm 0,28 \text{ km}^2$) kuin boreaalisessa metsässä (90 % AKDE $3,08 \pm 1,48 \text{ km}^2$). Osoitan myös, että varpuspöllöt ovat tiukasti päiväaktiivisia, ne liikkuvat Etelä-Euroopassa auringonnoususta auringonlaskuun ja lähes mihin aikaan päivästä tahansa pohjoisessa, koska yöt eivät ole täysin pimeitä pohjoisen kesäaikaan. Varpuspöllöt tekivät pitkiä saalistusretkiä, liikkuivat odotettua enemmän ($4,66 \pm 1,79 \text{ km}$ päivässä boreaalisessa metsässä ja $5,93 \pm 1,98$ alppimetsässä).

Kaikki havaintoni ovat sopusoinnussa sen hypoteesin kanssa, että varpuspöllöä voidaan pitää vanha metsän lajina, ja esitän ensimmäistä kertaa tuloksia elinympäristöjen valinnasta pesimis- ja ruokavarastointipaikoille, soidinlauluun ja saalistamiseen. Tämä on olennaisen tärkeää luonnonsuojelustrategioiden kannalta, sillä varpuspöllön reviirit ovat laajat ja monipuoliset, ja kaikkia niiden olennaisia ominaisuuksia on suojeltava. Tämän vanhoja metsiä suosivan lajin tehokkaiseen suojelustrategioihin olisi kuuluttava myös laadukkaiden elinympäristöjen säilyttäminen, joissa on sopivia koloja, ja joilla tuetaan varttuneiden ja vanhojen metsien suojelua kokonaisuutena eikä pelkästään koloja sisältävien puiden suojelua.

Table of Contents

List of Original Publications	9
1 Introduction	10
1.1 Tree cavity nest-web and forest management	10
1.2 Aims of the Thesis	11
2 Materials and Methods	14
2.1 The study species	14
2.2 The study areas	15
2.3 Natural cavity survey	17
2.4 Use of nest-boxes for nesting and for food hoarding by individually marked pygmy owls	17
2.5 Passive acoustic survey	18
2.6 GPS tracking	18
2.7 GIS and habitat variables	20
2.8 Statistical methods	22
3 Results	23
4 Discussion	25
5 Conclusions	27
Acknowledgements	28
List of References	29
Original Publications	33

List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

- I **Baroni, D.**, Korpimäki, E., Selonen, V., Laaksonen, T., 2020. Tree cavity abundance and beyond: Nesting and food storing sites of the pygmy owl in managed boreal forests. *Forest Ecology and Management*, 460, 117818.
- II **Baroni, D.**, Masoero, G., Korpimäki, E., Morosinotto, C., Laaksonen, T., 2021. Habitat choice of a secondary cavity user indicates higher avoidance of disturbed habitat during breeding than during food-hoarding. *Forest Ecology and Management*, 483, 118925.
- III **Baroni, D.**, Hanzelka, J., Raimondi, T., Gamba, M., Brommer, J., Laaksonen, T. Passive acoustic monitoring reveals the importance of old-growth forests in a low-density predator of the managed boreal forest. *Manuscript*.
- IV **Baroni, D.**, Cecere, J.G., Bocca, M., Koliopoulos, S., Vertua, I., Piironen, A., Imperio, I., Laaksonen, T. Differences in space use of the forest-dwelling pygmy owl in boreal and alpine forests revealed by GPS tracking. *Manuscript*.

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1 Introduction

1.1 Tree cavity nest-web and forest management

In natural forests, the decay processes potentially lead to the formation of natural cavities in most of the trees worldwide. The diversity and abundance of this widespread resource allowed numerous groups of forest-dwelling organisms (e.g. fungi, arthropods, birds and mammals) to inhabit tree cavities (Gibbons and Lindenmayer, 2002; Hansell, 2002; Aitken and Martin, 2007; Goldingay, 2009; Cockle et al., 2010; Cockle et al., 2011a and 2011b; Bunnell, 2013; van der Hoek et al., 2017). Birds take part of the nest web communities and evolved cavity-nesting as a widespread behaviour in all the forests of the world. However, both the availability and the quality of natural cavities may limit the breeding densities of many bird species (Newton, 1994). Tree age is the main factor responsible for the decay processes, providing a softened wood easy to excavate by woodpeckers, facilitating the chemical digestion of wood by fungi and the invertebrate colonization of wood. Considering the formation processes, tree cavities are mainly divided in two categories: decay-formed cavities and excavator-formed cavities (i.e. excavated vs. non-excavated cavities). Excavated cavities may be built in younger trees, while non-excavated cavities often take many decades to develop. Moreover, the excavators provide, in few weeks, new useable nest cavities, while decay-formed cavities take more time before they are large enough to be used as a nest-site by birds. The difference between excavated and non-excavated tree cavities is crucial concerning forest management. Indeed, in managed forest without retention trees, almost only excavated cavities are found (Aitken et al., 2002; Martin et al., 2004; Aitken and Martin, 2007; Cockle et al., 2011; Andersson et al., 2018). Moreover, the proportion of non-excavated cavities increases with cavity density (Remm and Löhmus, 2011).

The formation rate of new cavities strictly depends on forest management. Clear-cutting is the main non-natural cause of loss of cavities in the boreal forest, because the development and the abundance of natural cavities can be suppressed by forestry. Cavity-bearing trees are removed during logging and the regeneration rates of tree cavities are slow (Edworthy and Martin, 2013). Also, natural cavities are more abundant in mature and old-growth forests, because a tree is more likely to support

a cavity with its increasing age, size and declining health (Wesołowski and Martin, 2018). Forestry limits non-excavated cavities because they need decades to century to form, and regular cutting activities usually stop this process well before. Density of excavated cavities is also higher in natural forests, because woodpeckers often reuse previous nest sites instead of excavating a new cavity annually in managed forest, as a response to the lack of large trees with softened workable wood (Holt, 1996; Aitken et al., 2002). Moreover, because non-excavated cavities persist longer (Wesołowski, 2012), the median life of natural cavities is shorter in managed forests. Thus, forest management results in a lower number of new cavities added annually and in shorter persistence times. Old, unmanaged forests host the highest densities of natural cavities worldwide (Remm and Löhmus, 2011).

The Palearctic region's forests hold the lowest densities of cavities in the world, due to the colder and drier climate, and to the heavier forest management (Remm and Löhmus, 2011). Moreover, both tree species richness and the number of bird species breeding in tree cavities are higher in North America's boreal forest than in Europe (Latham and Ricklefs, 1993; van der Hoek et al., 2017). In boreal Europe, the two main tree species are Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, but both have a low probability of bearing natural cavities (Andersson et al., 2018). Deciduous trees nearly always constitute a small minority in these forests, but the proportion of trees containing natural cavities is higher for these species: birches *Betula* sp., European aspen *Populus tremula*, rowan *Sorbus aucuparia*, grey alder *Alnus incana* and willows *Salix* spp (Remm and Löhmus 2011; Bunnell 2013; Andersson et al., 2018).

The loss and degradation of boreal old-growth forest is threatening biodiversity and a wide range of ecosystem services. Especially in Europe, the boreal forest has been subject to intensification of forestry practices (Kouki et al., 2019), leading to habitat alteration and loss of nesting site for many taxa (Björklund et al., 2015; Fraixedas et al., 2015; Virkkala, 2016). This threat has strongly affected secondary cavity nesters and old-growth forest specialists (Virkkala, 2004), and many of them are declining among forest birds in Finland (Korpimäki et al., 2021). However, the lack of basic knowledge regarding their spatial ecology calls for studies aiming to find out the habitat requirements of the species. Indeed, understanding the species-specific details of resource selection provides insight into how quality and alteration of habitats influence their spatial occurrence and behaviour.

1.2 Aims of the Thesis

I investigated cavity-use and spatial ecology of a forest-dwelling predator occurring at low densities across its distribution range, the Eurasian Pygmy Owl *Glaucidium passerinum*, which requires tree cavities for both nesting and food hoarding.

In chapter I, I studied the abundance of suitable tree cavities at the landscape level, and examined the preferences of the owls for different cavity characteristics in two experiments and several years of nest-box monitoring data. I specifically aimed to quantify the abundance of natural cavities and to measure the occupancy of both nest-boxes and tree cavities, as a large availability of potential cavities is likely to be associated with a low site occupancy by the owl, and vice versa. However, since not all the cavities may be suitable as a nest or a food-hoarding site, I examined the preferences of pygmy owls for cavity characteristics. To this end, I examined four characteristics of the cavities that could affect their occupancy: I examined the pattern of occupancy with respect to the length of the entrance corridor, the distance between the entrance hole and the bottom of the cavity, the height of the cavity above the ground, and the entrance hole orientation. To my knowledge, this is the first attempt to examine the preferences of a secondary cavity nester for both nest and food hoarding sites. The results of this study also help in assessing whether or not artificial nest-boxes mimic the natural conditions, e.g. when they are placed relatively low above the ground. This is important information for evaluating the generality and applicability of the use of artificial nest-boxes in the understanding of functional and evolutionary ecology of owl populations.

In chapter II, I focused on how cavity distribution in space and time may limit their use during and outside of the breeding season. Using long-term data on the use of nest-boxes resembling tree cavities by individually marked pygmy owls, I compared the habitat and the distances among the nest-boxes used during two different seasons (food hoarding and nesting), and in the context of environmental change due to forest management. Specifically, using individually marked pygmy owls, I investigated whether differences exist between the habitat surrounding the food-hoarding sites in the autumn and the nesting site in the following spring. I tested whether the distance between food-hoarding sites and subsequent nest is affected by main food availability, and I assessed whether any sex or age differences exist in either the habitat or the distance between cavities used by an individual.

In chapter III, I used passive acoustic monitoring with a large grid of detectors, to study habitat selection of pygmy owl calling sites, and to estimate their abundance and the proportion of pairs nesting in natural cavities or in nest-boxes. I specifically distinguish habitat preferences based on calls and based on nest sites, to describe home range scale habitat selection of pygmy owls. To include in the analyses the information of actual size of home ranges, I also used, for the first time, miniaturized GPS-tags on pygmy owl males. Moreover, as one of the main aims of the study is to explore the effects of forest management, I specifically produced forestry data GIS layers to test whether the area of old-growth forests may alter the species occupancy patterns, both for calling and for nesting sites.

Finally, the chapter IV is based on the use of GPS-tracking as an essential conservation tool, to fill the gaps of knowledge regarding the pygmy owl spatial ecology. For the first time, I used a small archival global positioning system (GPS) tag to identify and characterize breeding territories of the pygmy owl. I estimated the home-range size and habitat composition, the home-range scale habitat selection for hunting activity, and the differences in home range size and activity rhythms between two study areas in the boreal forest and in the alpine forests. I was specifically interested in what kind of forests the pygmy owl maybe preferring (main tree species, forest age), as this is relevant for guidance of forestry practice.

2 Materials and Methods

2.1 The study species

The Eurasian pygmy owl (hereafter “pygmy owl”) is an elusive forest specialist and an obligate secondary cavity nester, which prefers coniferous-dominated forests. This predator is occurring at low densities across its distribution range. It is known to be declining in the boreal forest (Meller et al., 2019; Korpimäki et al. 2020; Honkala et al., 2021) and expanding its range in central and southern Europe (Maffei *et al.*, 2018; Scherzinger and Mebs, 2020; Lehikoinen, 2021).

The approximate measures of known nest sites of pygmy owls have a 4–5 cm diameter of the cavity entrance of, a 5.5 cm entrance corridor length, an inner chamber diameter of 14 cm and average depth of 21 cm (Schönn, 1978; Wiesner, 2001). Most of the woodpecker cavities used for breeding by pygmy owls have been found at 1–8 m above the ground (average 3 m; min. 0.6 to max. 18.7 m) (Scherzinger, 1969; Schönn, 1978; Wiesner, 2001). Nest-showing is performed by males, beginning 2 months before egg laying, and the females select the nest site. Once the cavity has been chosen, no apparent nest material is added (except prey remains such as fur and feathers), but the female may do some cleaning (Cramp, 1985). Differently from other European cavity-nesting owl species, the pygmy owls do not use cavities for roosting. However, the cavities are crucial for food hoarding, which the pygmy owls do in the late autumn for the winter when they are no longer able to hunt main foods (voles) protected by snow layer (Solheim, 1984; Schulenburg and Wiesner, 1986; Terraube et al., 2017; Masoero et al. 2018; Halonen et al., 2007; Suhonen et al., 2007).

The pygmy owls readily accept woodpecker-type nest-boxes, both for reproduction and food hoarding, because they mimic the natural preferred sites (Sonerud et al., 1972; Syrjänen et al. 2006; Morosinotto et al. 2017; Masoero et al. 2018). In Finland, most pygmy owl nests in natural cavities are in cavities excavated by great-spotted or three-toed woodpeckers *Picoides trydactylus* (Pakkala et al., 2018).

The population dynamics of pygmy owls strongly depend on the population fluctuations of voles of the genera *Microtus* and *Myodes*, which are their main prey species (Kellomäki, 1977, Lehikoinen et al., 2011a,b, Morosinotto et al. 2017, Korpimäki et al., 2020). In southern Finland, populations of these voles follow 3-

year population cycles, fluctuating in a succession of low, increase and decrease years (Korpimäki et al., 2005).

The pygmy owl is a possible indicator of valuable old-growth forests or bird species richness. Pygmy owl was regarded as among the most important indicator species of species richness of bird fauna in the study of Pakkala et al. (2014) and several other bird species have been shown to be indicators of other species groups of mature or old-growth forests as well, such as, e.g. the white-backed woodpecker *Dendrocopos leucotos* (Martikainen et al., 1998), the three-toed woodpecker *Picoides trydactylus* (Roberge et al., 2008), the northern goshawk *Accipiter gentilis* (Burgas et al., 2014), or the Western capercaillie *Tetrao urogallus* (Pakkala et al., 2003; Mikoláš et al., 2015). Based on the information of indicator species, Virkkala et al. (2022) recently predicted suitable nesting habitats of six indicator hawk and woodpecker species from valuable forests modelling.

2.2 The study areas

All the work presented in chapters I-III was conducted in two study areas located in south-western and central-western Finland, whereas in chapter IV, in addition to Finland, a study area in Italy was also included.

The main study area, i.e. the one included in all the chapters of the Thesis, lies in the vicinity of Turku (municipalities of Rusko, Masku, Mynämäki and Nousiainen, 60°N, 22°E) and covers approx. 500 km². The second area, included in chapters I and II, is located approx. 300 km north of the first one in the Kauhava, Lapua and Lappajärvi municipalities, South Ostrobothnia, covering approx. 1000 km² (63°N, 23°E). Both study areas mainly consist of managed Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* forests, with small numbers of deciduous trees such as birch (*Betula pendula* and *B. pubescens*) and European aspen *Populus tremula*. Norway spruce-dominated forests are found on wet and moist soils, and Scots pine-dominated forests on drier and rocky soils. Forests in these areas are interspersed with a quite high proportion of agricultural land and a few peatland bogs. The study area in the vicinity of Turku lies between the hemi-boreal and the southern boreal vegetation zone, while the Kauhava study area is located on the border between the south- and mid- boreal vegetation zones (Ahti et al., 1968).

In the study area north of Turku, 121–234 (mean = 198) nest-boxes were maintained each year during 2014–2021. Only one nest-box was provided in each location and the sites were typically one km or more apart from each other. In Kauhava, two nest-boxes (80–100 m apart) were set up during 2003–2019 in 126–261 different forest sites (mean = 223 sites per year). All the nest-boxes were already installed in the beginning of the study period (the first years), and they have been thereafter moved only when their forest patch disappeared due to clear-cutting of the forest. Nest-boxes

were relatively homogeneously distributed across the forests of the whole study area. The entrance hole diameter was 45 mm, with a length of the entrance corridor of 5–8 cm. The cavity was ~ 30 cm deep, with a layer of sawdust provided on the bottom. The boxes were set-up at 1.5 m height from the ground (to entrance-hole) in order to facilitate their check. All boxes were checked twice in the spring (April to May) for the presence of the nests and (once Turku area) or twice (Kauhava) in the autumn (late October to early December) for the presence of food-hoards.

The study area in Italy, included in chapter IV, is covering approx. 600 km² in the Western Italian Alps (Aosta Valley, 45°N, 7°E). The pygmy owl occurs between 900 and 2300 m a.s.l. in subalpine forests, composed of a mixture of larch (*Larix decidua*), Norway spruce, Scots pine and mountain pine (*Pinus mugo uncinata*) trees (Maffei et al., 2018). Here, 272 great spotted woodpecker excavated cavities were found and checked during 2019-2021, from a min. of 82 to a max. of 272 cavities every year.

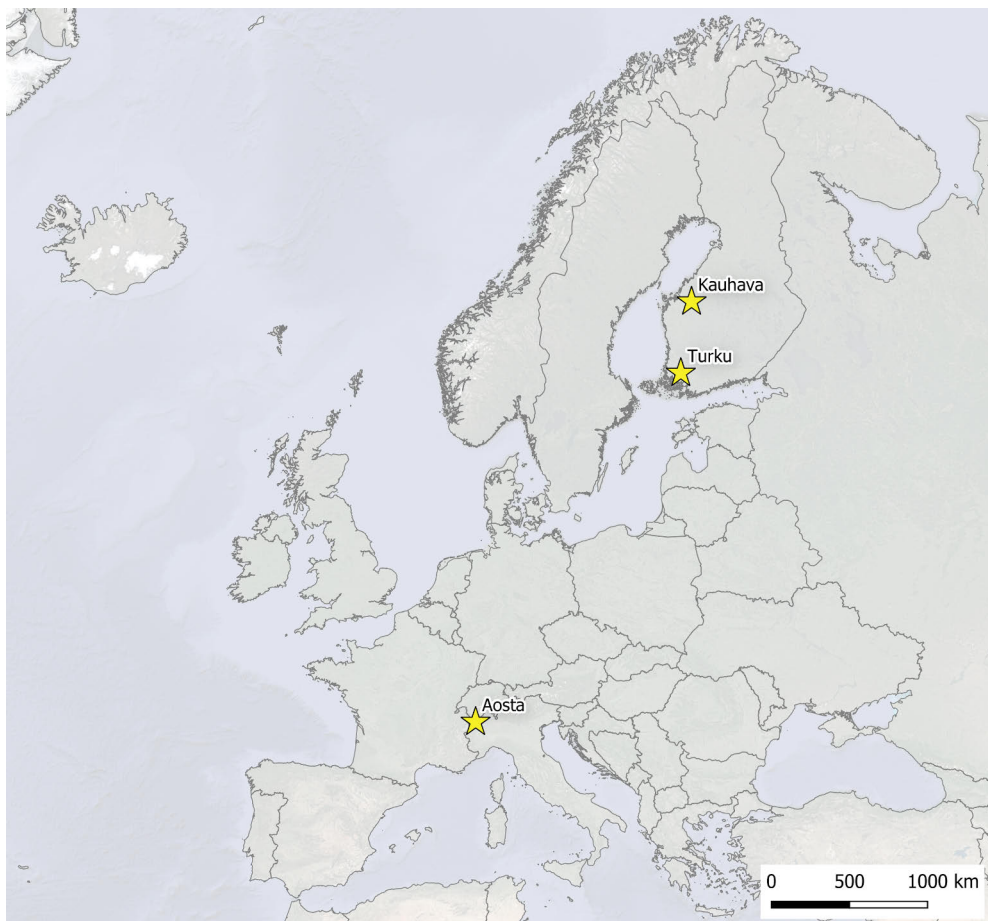


Figure 1. The three study areas included in the Thesis: Kauhava (chapters I and II) and Turku (chapters I, II, III and IV) in Finland, and the Aosta Valley (chapter IV) in Italy.

2.3 Natural cavity survey

We surveyed 50 grids that were 4 ha in size (Fig. 1), in the ~500 km² area north of Turku, and 60 grids in the ~ 1000 km² area in Kauhava. The grids were always in the SW corner of a 1 km² cell, randomly selected from the Finland Uniform Coordinate System (YKJ). All potential trees were examined for cavities within every grid cell. Many tree holes are not real cavities, but just small platforms not deep enough to be considered a potential nest site, and from the ground it is impossible to evaluate the quality of most of the cavities (Hoyt, 1957; McClelland, 1979; Bull and Meslow, 1988; Hooper et al., 1991; Ojeda et al., 2007; Cockle et al., 2010; Ouellet-Lapointe et al., 2012). Therefore, the cavities found during systematic searches by ground surveys were examined in a separate visit, in 2016–17 by climbing and in 2018–19 with a camera mounted on telescopic poles (Wildlife Windows Ltd). In addition to the cavities found in the grid surveys, cavity trees found opportunistically during other fieldwork in the area were marked and later examined for occupancy in the same way as the ones in the grids.

Moreover, to analyse nest site preferences in relation to cavity characteristics, we measured from the boxes both the length of the entrance corridor and the hole orientation in degrees. We also carried out two experiments providing cavities that were either cleaned or not cleaned from old nest material to find out whether the accumulation of nest material prevents breeding of the pygmy owls and to test whether pygmy owls show any preference for the height of the cavities above the ground.

2.4 Use of nest-boxes for nesting and for food hoarding by individually marked pygmy owls

Pygmy owls were captured using nest-box traps during the hoarding season (a replica of the box equipped with swing door) (Terraube et al., 2017; Masoero et al., 2018). During the nesting period, males were captured broadcasting an “advertising call” close to the nest in combination with a wooden copy of a small owl, so that the male approaches it and can be caught using a neck-loop (Korpimäki et al., 2020). Females were captured directly by hand inside the nest-box while they were brooding chicks. Moreover, nestlings were ringed every year before fledging. Trapped owls were individually marked with an aluminum leg ring, their wing and tail lengths were measured, and they were weighted, sexed, and aged. From 2011, the owls were also individually marked using PIT tags (Passive Integrated Transponder tags), small electromagnetic microchips implanted subcutaneously (Masoero et al., 2018). Data on encounters of individual owls were collected by placing the antenna of the reader around the entrance hole of the nest-boxes used as a food- hoarding or nesting site for one to two weeks.

2.5 Passive acoustic survey

In chapter III, I deployed a wide-scale autonomous recording units (ARUs) survey, involving 292 sites in a single season (year 2021). I used AudioMoths version 1.1 (Hill et al., 2018), in 292 sites on a regular grid with spacing of 1 km. I selected every 1-km grid cell from the Finland Uniform Coordinate System (YKJ), and put the recorder within the 100 m radius buffer around the centroid of the grid cell. If there was no forest within the buffer, we skipped that grid cell. We conducted the passive acoustic survey between 16th of March and 25th of April 2020. This period is the month preceding the egg-laying phase (Korpimäki et al., 2020), when singing activity peaks and the breeding territories are established (Schönn, 1978). We set the sample rate to 48 kHz, gain at the level between “medium” and “high”, sleep duration at 0 seconds, and recording duration at 3600 seconds (1 hour). Since continuous 24-h monitoring quickly decreases their autonomy, ARUs were programmed to record between 00:00 and 7:00 and between 16:00 and 20:00 UTC hours every day. Recording was limited to these times to include the pygmy owl daily activity peaks, around sunrise and sunset (Schönn, 1978). The ARUs produced approx. 70 hours of recordings from every site. They were attached to tree trunks at approximately 1.5 – 2 m above ground. To protect the devices from rain and moisture, we sealed them inside a plastic bag, together with a silica gel pack (Suppl. Mat.). We used 90 ARU devices (Audiomoth), progressively set up in 3 consecutive phases in the field, to cover the whole sample of survey sites. The ARUs were progressively moved, changing the batteries and downloading the data between following deployments, using a spatial moving window, so that preceding and succeeding adjacent devices were at least partly overlapping their recording schedule.

2.6 GPS tracking

I equipped 14 male pygmy owls with PinPoint 10 or 50 (Lotek), using a backpack Teflon harness. Devices (including the harness) weighed between 2.30 and 3.54 g, on average accounting for 4.67% (± 0.87) of the body mass (range 3.59 - 6.15%). I collected movement data during the chick-rearing phase of the breeding season 2021, except for two males in the Alps, which were tagged at an earlier stage (one during the incubation and the other 20 days before the egg-laying). Breeding males were caught by mist netting with a playback lure in the vicinity of the nest. After ringing and tagging the birds, we programmed the GPS tags to collect 1-2 hourly GPS locations per day, and released them at the site where they were captured. After 8-51 days (mean $18 \pm$ s.d. 12 days), we recaptured the owls and removed the devices. When recaptured, birds were also measured and aged according to Lagerström and Syrjänen (1990). To evaluate possible impacts of tags on bird health condition, we analysed changes in bird body mass by comparing their weights at the capture and recapture.



Figure 2. Male pygmy owl equipped with PinPoint 10, using a backpack Teflon harness (Nousiainen, June 2021; picture by S. Koliopoulos).

2.7 GIS and habitat variables

I included habitat analyses in chapters II, III and IV of the Thesis. I used pre-existing data, in some cases manually revised, and also newly built habitat variables, depending on the different purposes.

In chapter II, I compared habitat composition around the nest-boxes between boxes used either as a food-hoarding or as a nesting site by the same pygmy owl individual, considering a 500 m radius buffer. I calculated the proportion of agricultural areas, spruce- or pine-dominated forests, and clear-cuts and young stands. I also considered the biomass of the foliage (10 kg/ha) of spruce trees, broad-leaved trees and pine trees, and the canopy cover. In addition, I calculated for every nest-box, the distance in meters from the nearest main road, the nearest inhabited house, the nearest forest margin and the nearest agriculture field. The habitat types were identified using landscape maps based on SLICE dataset (Mikkola et al., 1999; Morosinotto et al., 2017). A forest classification was available for 2009 (METLA 2009). I manually measured the proportion of every habitat overlapping the Landsat Images (landsat.usgs.gov/) of the corresponding year to the landscape maps, in order to take into account yearly changes in forest cover (e.g. new clear-cuts), and to obtain more accurate measurements at the local scale. I calculated the tree biomass and canopy cover from 2013 Multi-source National Forest Inventory provided by the National Resources Inst. Finland (Mäkisara et al., 2016). Finally, the distances from the nest-boxes to the nearest habitat features (variables 9–12) were measured using QGIS tools (QGIS Development Team, 2020).

For chapter III and IV, I calculated the biomass of the foliage (10 kg/ha) of spruce and pine trees, i.e. the two dominant tree species in the study area. The two variables were calculated from 2013 Multi-source National Forest Inventory provided by the National Resources Inst. Finland (Mäkisara et al., 2016). Ages of the forests were calculated manually, drawing the polygons of clear-cutted forests in the last 80 years. For this purpose, we compared historical aerial photographs or satellite images available from 1949, 1959, 1995, 1998, 2006, 2010, 2013, 2015, 2017 and 2020 (available on <http://kartta.paikkatietoikkuna.fi/>) and from 1985 (Google satellite images). For chapter III, I was able to classify all the forest area, i.e. the area covered by the “canopy cover” layer from the National Forest Inventory, into the following three variables: clear-cuts and young stands (forest age < 15 years), forest areas (forest age > 15 years), and old forest (forest age > 80 years old). For chapter IV, I calculated the exact age of every forest patch. In addition, I included peatland areas from National Resources Institute Finland open source data and agricultural areas from CORINE land cover. Finally, I calculated for every site, the distance in meters from the nearest main road, and the nearest inhabited house. The distances from the ARU to the nearest habitat features were measured using QGIS tools (QGIS Development Team, 2020).

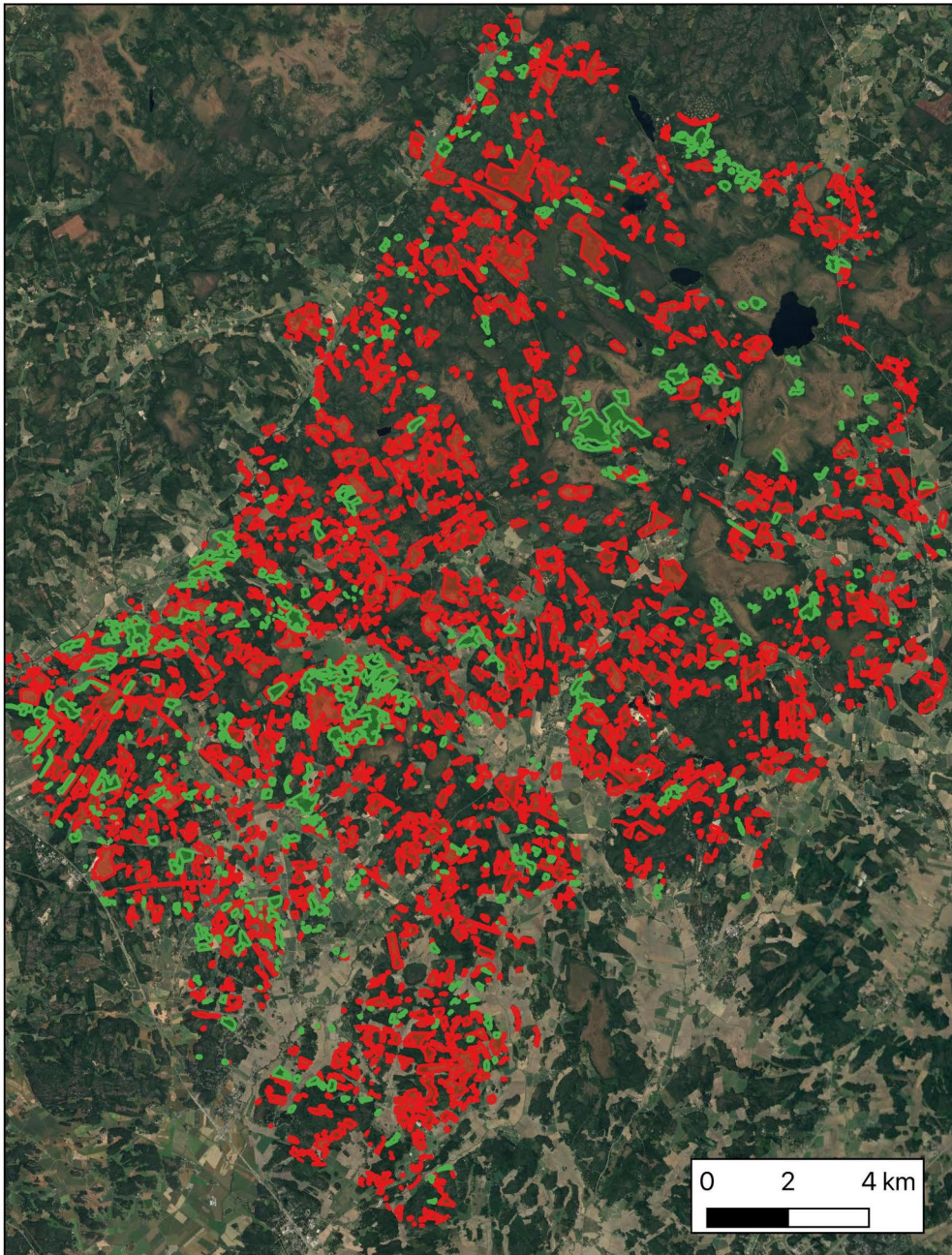


Figure 3. Manually drawn polygons of young forests, i.e. where forests have been clear-cut less than 15 years ago (red polygons) and of old forests, i.e. where forests have not been cut for at least 80 years (green polygons) in the study area north of Turku.

2.8 Statistical methods

I analyzed the data collected using generalised linear models or generalised mixed-effects models, choosing the likelihood family according to the type of response variable in the model.

In the first chapter, I used mixed effects logistic regression model with occupancy of nest-boxes as a binomial response variable and their characteristics as predictors. Year and nest-box identity were included as random effects. Moreover, circular statistics (Rayleigh-test) were performed to assess whether the orientation of nest-boxes had an effect on the nest-box occupancy.

In chapter II, generalised linear mixed-effect models were used to analyse the relationship between the habitat variables and the cavity use, i.e. for food-hoarding or for nesting. Different models were built for every habitat variable, which was included as a response variable, while the explanatory variable was the type of cavity use (nesting or hoarding). Individual identity of the owl and year were included as random effects. In the models including sex and age, models were constructed with the habitat variable as a response, and age, sex and vole abundance included as explanatory variables. In the analyses on the distance between food-hoarding and nesting sites, I constructed generalised linear mixed-effect models with the log10-transformed variables using as random effects year and individual identity of the owl. I included vole abundance during the food-hoarding season, age and sex of the hoarding individual, and the habitat variables that had a significant effect in the habitat GLMMs as explanatory variables.

In chapter III, I used binomial generalised linear models to analyse the relationship between the habitat variables and the site occupancy by pygmy owls. Occupancy of each site of the passive acoustic monitoring where we placed an ARU was the response variable (0 = pygmy owl not detected, 1 = pygmy owl detected), and the habitat proportions surrounding the sites of the passive acoustic monitoring at three different scales (100, 400 and 1000 m) were the predictors.

In chapter IV, I used binomial generalised linear mixed-effect models to explore the relationship between the habitat variables and the probability of use by the GPS-tagged pygmy owls. The response variable had the following values: 1 = GPS fixes (habitat use) and 0 = random locations (habitat availability). We included as explanatory variables in the model all the habitat variables which characterize the habitat surrounding the surveyed sites and overall the whole study area, therefore potentially affecting the habitat selection by pygmy owls.

3 Results

The results of chapter I show that natural cavities were scarce in the landscape (ca. 6.5/km²). However, natural cavity abundance per se does not seem to limit the breeding density of this predator, as suggested by a low occupancy rate in natural cavities and nest-boxes (Turku: mean = 3%; Kauhava: mean = 4%). Cavities whose characteristics prevent the nest from being reached by predators were clearly preferred, as the owls selected cavities with more than 5 cm width of the front wall and cleaned the content to get 15–30 cm of entrance-bottom distance within the cavity. While the number of cavities per se may not limit the nesting of the owls, they may be limited by suitable habitat with abundant food supply around available cavities, or by lack of cavities in suitable habitats. Comparing the habitat and the distances among the nest-boxes used during two different seasons (II), I found that pygmy owls are more demanding in their requirements for breeding than for food-hoarding habitat, because of the importance of spruce forests as a nesting habitat and nesting sites being farther from houses than food-hoarding sites. Also, I highlight the need of many different cavities within the home range of each individual, as individually marked pygmy owls mainly used different nest-boxes for nesting and food-hoarding, and they also used different nest-boxes in different years.

The results of the passive acoustic survey (III) also demonstrated that the pygmy owl can be considered an old-growth forest specialist (Fig. 4). Indeed, my results with habitat data at three spatial scales, and for both calling and nesting sites, show that increasing availability of old-growth forests was consistently the most important habitat variable increasing occupancy probability of the pygmy owls in a landscape dominated by managed forests. When we clustered the detections into territories, we estimated a density of pairs or territorial males that was altogether three times the number of pairs breeding in nest-boxes. Considering the number of natural cavities and nest-boxes, we however estimate that nest-boxes were preferred over natural cavities for breeding. From the GPS-tracking study, we found that home ranges are bigger than previously estimated with radiotelemetry data, and there is difference between the two study areas, with owls in the alpine forests having smaller home ranges than in the boreal forest (alpine forests: 90% AKDE 0.95 ± 0.49 km²; boreal forest: 90% AKDE 3.08 ± 1.48 km²). I also show that pygmy owls are strictly diurnal,

being active from sunrise to sunset in South Europe, and at any time of the day in North Europe. Owls performed long hunting trips, travelled more than expected (4.66 ± 1.79 km per day in the boreal forest and 5.93 ± 1.98 in the alpine forests) and spent most of the time inside coniferous forest.

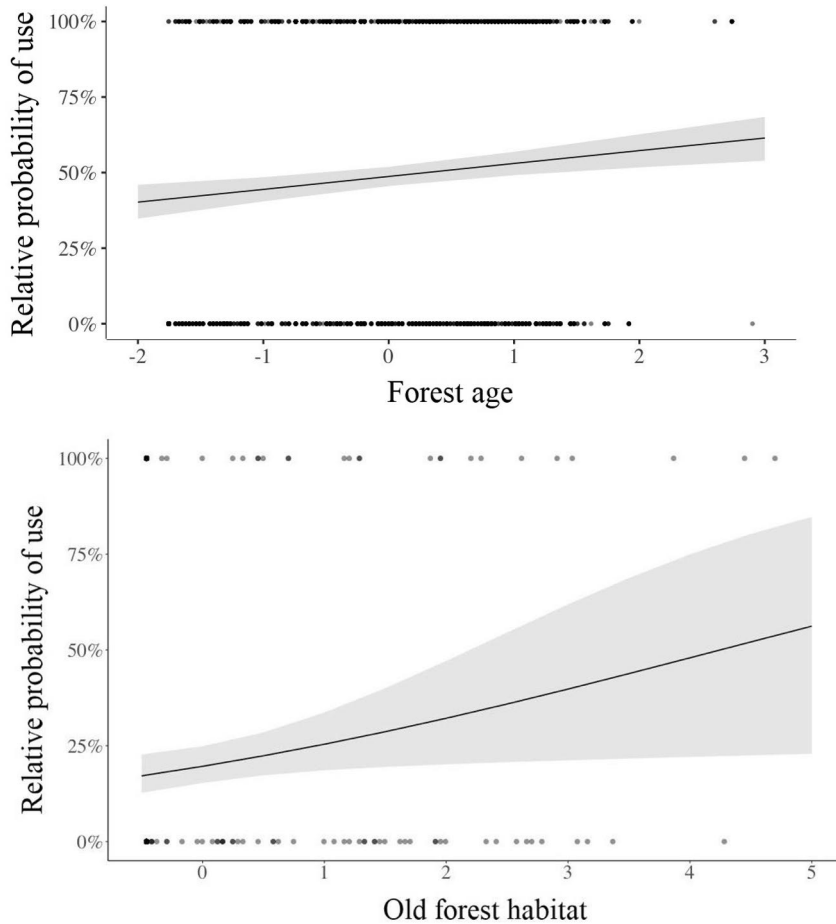


Figure 4. Two different results on the importance of old forests for the pygmy owls: prediction of the relative mean probability of use ($\pm 95\%$ C.I.) by the GPS-tagged pygmy owls in relation to the age of the forest (upper) and prediction of the relative mean probability of occurrence ($\pm 95\%$ C.I.) of pygmy owls in relation to the availability of old forest (at 100 m radii buffers) in the surroundings of the sites of the passive acoustic monitoring (lower) in the boreal forest. On the X-scales, the forest age (upper) refers to the mean age of the forest patch where the GPS tag fix or the random sites were found, and the old forest habitat (lower) refers to the proportion of older forests as percentage of surface area within the buffers. Both variables are scaled to zero mean and unit variance.

4 Discussion

The main results of the Thesis are focused first on tree cavity abundance and suitability for the pygmy owl. The results of the first two chapters indicate a clear selection for safe cavities, whose characteristics prevent the access of predators and their needs for several cavities in different seasons. Thereafter, in chapter III, I provided the first estimate of pygmy owls' real density at the landscape level, finding that the pairs nesting in nest-boxes were one-third of the overall populations also including the pairs nesting in woodpecker-excavated cavities and potential non-breeding individuals of both sexes. In chapters II, III and IV, I focused on habitat selection analyses, providing insights on some topics that have been less (or not at all) explored in previous studies on pygmy owl ecology and, more in general, on the boreal forest bird species: the preference for spruce forests as nesting habitat and not for food hoarding (results of chapter II), the importance of old-growth forests both for calling and for nesting sites (results of chapter III), and on older spruce (and larch) forests as preferred hunting habitat during the breeding period (results of chapter IV). Comparing the results of the different chapters, the importance of spruce forests was found both for nesting and for calling sites, and the importance of the age of the forest, i.e. a preference for older forests, was found both for calling sites and for hunting habitats. Therefore, I highlight how coherent the results of the different chapters are, e.g. in showing the importance of the conservation of old spruce forests for the pygmy owl in the boreal forest, where this species can be considered an old-growth forest specialist.

The results in chapter I proved the importance of some cavity characteristics because the kind of cavities that are safe from predation were preferred by pygmy owls. The cavity abundance estimates are indicating that such suitable cavities are more abundant than the owls even in the heavily managed boreal forest. However, they may be limited by or by lack of cavities in suitable habitats. I explored this issue to some extent in chapter II and I found that while the number of cavities per se may not limit the nesting of the owls, they may be limited by suitable habitat with abundant food supply around available cavities. They also need more cavities in the winter than in the summer, as each individual needs one to six cavities for hoarding food, to survive over winter. The subsequent logical step was to estimate the real

density of breeding pygmy owls at the landscape level, and to compare this information with the previously known availability of suitable cavities. In chapter III, I found a density of pairs or territorial males that was altogether three times the number of pairs breeding in nest-boxes. Considering the number of natural cavities and nest-boxes, I however estimated that nest-boxes were largely preferred over natural cavities for breeding. Finally, it was crucial to get knowledge on the home range size, for which I analysed this trait in two different study areas. I found that in the boreal forest, the males explored larger areas, moved longer distances and spent less time at night roost sites than in the alpine forests. Indeed, I showed that pygmy owls are active only from sunrise to sunset in southern Europe, and at any time of the day in the North where the nights are light during chick-rearing in the early summer. These differences in home range size and activity rhythms show that the species also exhibits a certain degree of plasticity to adapt under these different environments.

5 Conclusions

A vast majority of my findings are consistent with the hypothesis that the pygmy owl can be considered an old-growth forest species. I also provide for the first time insights on habitat selection for the sites used for nesting and food hoarding sites, for advertising and for hunting. It is crucial information for conservation management strategies, as the pygmy owl's home ranges are large and diverse, and all its essential properties must be protected. Effective conservation strategies for this old-growth forest specialist should also include the maintenance of high-quality habitat that contains suitable natural cavities, supporting the need for protection of mature and old-growth forests as a whole, and not just of cavity bearing trees alone.

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Turku, April 2022
Daniele Baroni

List of References

- Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in north-western Europe. *Ann. Bot. Fenn.*, 5 (3), 169–211.
- Aitken, K.E.H., Martin, K., 2007. The importance of excavators in hole-nesting communities: availability and use of natural tree holes in old mixed forests of western Canada. *J. Ornithol.*, 148 (Suppl.), S425–S434.
- Aitken, K.E.H., Wiebe, K.L., Martin, K., 2002. Nest-site reuse patterns for a cavity nesting community in interior British Columbia. *Auk*, 119, 391–402.
- Andersson, J., Gómez, E.D., Michon, S., Roberge, J.-M., 2018. Tree cavity densities and characteristics in managed and unmanaged Swedish boreal forest. *Scand. J. Forest Res.*, 33 (3), 233–244.
- Björklund H., Valkama J., Tomppo E., Laaksonen T., 2015. Habitat effects on the breeding performance of three forest-dwelling hawks. *PLoS one*, 10(9), e0137877.
- Bull, E.L., Meslow, E.C., 1988. Breeding biology of the pileated woodpecker: Management implications. USDA Forest Service Gen. Tech. Rep. PSW-GTR-181, Pacific Northwest Research Station, Portland, Oregon.
- Bunnell, F. L., 2013. Sustaining cavity-using species: patterns of cavity use and implications to forest management. *Int. Sch. Res. Notices*, 2013.
- Burgas, D., P. Byholm, and T. Parkkima., 2014. Raptors as surrogates of biodiversity along a landscape gradient. *Journal of Applied Ecology*, 51:786-794.
- Cockle, K.L., Martin, K., Drever, M.C., 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic Forest. *Biol. Cons.*, 143 (11), 2851–2857.
- Cockle, K.L., Martin, K., Wesolowski, T., 2011a. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. *Front. Ecol. Environ.* 9 (7), 377–382.
- Cockle, K.L., Martin, K., Wiebe, K., 2011b. Selection of nest trees by cavity-nesting birds in the neotropical Atlantic forest. *Biotropica*, 43 (2), 228–236.
- Cramp, S., 1985. The birds of the western Palearctic. Volume IV. Terns to woodpeckers. Oxford University Press, Oxford.
- Edworthy, A.B., Martin, K., 2013. Persistence of tree cavities used by cavity-nesting vertebrates declines in harvested forests. *J. Wildl. Manag.*, 77 (4), 770–776.
- Fraixedas, S., Lindén, A., & Lehikoinen, A., 2015. Population trends of common breeding forest birds in southern Finland are consistent with trends in forest management and climate change. *Ornis Fennica*, 92(4), 187-203.
- Gibbons, P., Lindenmayer, D., 2002. *Tree Hollows and Wildlife Conservation in Australia*. CSIRO Publishing, Collingwood.
- Goldingay, R.L., 2009. Characteristics of tree holes used by Australian birds and bats. *Wildl. Res.*, 36 (5), 394–409.
- Halonen, M., Mappes, T., Meri, T., Suhonen, J., 2007. Influence of snow cover on food hoarding in Pygmy Owls *Glaucidium passerinum*. *Orn. Fenn.*, 84 (3), 105–111.
- Hansell, M., 2002. *Animal Architecture*. Oxford University Press, Oxford.

- Hill, A.P., Prince, P., Piña Covarrubias, E., Doncaster, C. P., Snaddon, J.L., Rogers, A., 2018. AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods Ecol. Evol.*, 9(5), 1199–1211.
- Holt, R.F., 1996. Habitat selection, demography and conservation implications for a cavity nesting community in a managed landscape. Ph.D. dissertation, University of Toronto, Toronto, Ontario.
- Honkala, J., Piha, M., Saurola, P. & Valkama, J., 2021. Breeding and population trends of common raptors and owls in Finland in 2020. – *Linnut-vuosikirja 2020*, 70–85 [in Finnish with English summary].
- Hooper, R.G., Krusac, D.L., Carlson, D.L., 1991. An increase in a population of red-cockaded woodpecker. *Wildl. Soc. Bull.*, 19, 277–286.
- Hoyt, J. S., 1957. The ecology of the pileated woodpecker. *Ecology*, 38, 246–256.
- Kellomäki, E., 1977. Food of the Pygmy Owl *Glaucidium passerinum* in the breeding season. *Ornis Fenn.*, 54 (1), 1–29.
- Korpimäki, E., 2021. Habitat loss and climate change as drivers of long-term declines of two forest-dwelling owl populations in boreal forest. - *Proceedings of the 5th World Owl Conference*. Airo, 29, 278-290.
- Korpimäki, E., Norrdahl, K., Huitu, O., Klemola, T., 2005. Predator-induced synchrony in population oscillations of coexisting small mammal species. *Proc. R. Soc. B.*, 272 (1559), 193–202.
- Korpimäki, E., Hongisto, K., Masoero, G., Laaksonen, T., 2020. The difference between generalist and specialist: the effects of wide fluctuations in main food abundance on numbers and reproduction of two co-existing predators. *J. Av. Biol.*, 51(8), 1–13. <https://doi.org/10.1111/jav.02508>.
- Kouki, J., Junninen, K., Mäkelä, K., Hokkanen, M., Aakala, T., Hallikainen, V., Korhonen, K.T., Kuuluvainen, T., Loiskekoski, M., Mattila, O., Matveinen, K., Punttila, P., Ruokanen, I., Valkonen, S., Virkkala, R., 2019. Forests. In: Kontula, T., Raunio, A. (Eds.), *Threatened habitat types in Finland 2018. Red List of habitats. Part I: Results and basis for assessment*. Finnish Environment Institute and Ministry of Environment, Helsinki. *The Finnish Environment 2/2019*, 113-124. <http://urn.fi/URN:ISBN:978-952-11-5110-1>
- Lagerström M., Syrjänen J., 1990. Varpuspöllön iän määrittäminen. *Lintumies*, 25, 291–294.
- Latham, R. E., Ricklefs, R. E., 1993. Patterns of tree species richness in moist forests: Energy-diversity theory does not account for variation in species richness. *Oikos*, 67(2), 325–333.
- Lehikoinen, A., 2021. Eurasian Pygmy Owl *Glaucidium passerinum*. In: Keller, V., Herrando, S., Vorisek, P., Franch, M., Kipson, M., Milanese, P., Martí, D., Anton, M., Klvanová, A., Kalyakin, M.V., Bauer, H.-G., Foppen, R.P.B. *European breeding bird atlas 2: Distribution, abundance and change*. European Bird Census Council & Lynx Edicions, Barcelona.
- Lehikoinen, A., Hokkanen, T., Lokki, H., 2011a. Young and female-biased irruptions in pygmy owls *Glaucidium passerinum* in southern Finland. *J. Avian Biol.*, 42 (6), 564–569.
- Lehikoinen, A., Ranta, E., Pietiäinen, H., Byholm, P., Saurola, P., Valkama, J., Huitu, O., Henttonen, H., Korpimäki, E., 2011b. The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. *Oecol.*, 165 (2), 349–355.
- Maffei, G., Baroni, D., Bocca, M., 2018. Uccelli nidificanti in Valle d'Aosta: distribuzione, ecologia, fenologia e conservazione. Testolin editore, Aosta.
- Mäkisara, K., Katila, M., Peräsaari, J., Tomppo, E., 2016. *The Multi-Source National Forest Inventory of Finland - methods and results 2013*.
- Martikainen, P., Kaila, L., Haila, Y., 1998. Threatened beetles in White-backed Woodpecker habitats. *Biol. Conserv.*, 12:293-301.
- Martin, K., Aitken, K.E., Wiebe, K.L., 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *The condor*, 106(1), 5-19.
- Masoero, G., Morosinotto, C., Laaksonen, T., Korpimäki, E., 2018. Food hoarding of an avian predator: sex and age-related differences under fluctuating food conditions. *Behav. Ecol. Sociobiol.*, 72 (10), 159.

- McClelland, B.R., 1979. The pileated woodpecker in forests of the northern Rocky Mountains. In: Dickson, J.G., Conner, R.N., Fleet, R.R., Kroll, J.C., Jackson, J.A. (eds). *The Role of Insectivorous Birds in Forest Ecosystems*. Academic Press, New York, New York. pp. 283–299.
- METLA, (Metsähallitus), 2009. “Kansallispuistojen ja retkeilyalueiden kävijöiden rahankäytön paikallistaloudelliset vaikutukset (in Finnish only).” 3017/52/200. Metsähallitus, Luontopalvelut yhteistyössä Metsäntutkimuslaitoksen kanssa.
- Meller, K., Björklund, H., Saurola, P. & Valkama, J., 2019. Breeding and population trends of common raptors and owls in Finland in 2018. *Linnut-vuosikirja 2018*, 80–95 [in Finnish with English summary].
- Mikkola, A., Jaakkola, O., Sucksdorff, Y., 1999. The Slices- project: national classification of land use, land cover and soil, and the production of databases. *Finnish Environment*, 342, 1–86.
- Mikoláš, M., Svitok, M., Tejkal, M., Leitão, P. J., Morrissey, R. C., Svoboda, M., Fontaine, J. B., 2015. Evaluating forest management intensity on an umbrella species: Capercaillie persistence in central Europe. *For. Ecol. Manag.*, 354, 26–34.
- Morosinotto, C., Villers, A., Thomson, R.L., Varjonen, R., Korpimäki, E., 2017. Competitors and predators alter settlement patterns and reproductive success of an intraguild prey. *Ecol. Monographs*, 87 (1), 4–20. <https://doi.org/10.1002/ecm.1238>.
- Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biol. Cons.*, 70 (3), 265–276.
- Ojeda, V.S., Laura-Suarez, M., Kitzberger, T., 2007. Crown dieback events as key processes creating cavity habitat for Magellanic woodpeckers. *Austral Ecol.*, 32, 436–445.
- Ouellet-Lapointe, U., Drapeau, P., Cadieux, P., & Imbeau, L., 2012. Woodpecker excavations suitability for and occupancy by cavity users in the boreal mixedwood forest of eastern Canada. *Ecoscience*, 19(4), 391–397.
- Pakkala, T., Pellikka, J., Lindén, H., 2003. Capercaillie *Tetrao urogallus* - a good candidate for an umbrella species in taiga forests. *Wildl. Biol.*, 9(4), 309–316.
- Pakkala, T., Lindén, A., Tiainen, J., Tomppo, E., Kouki, J., 2014. Indicators of forest biodiversity: which bird species predict high breeding bird assemblage diversity in boreal forests at multiple spatial scales? *Ann. Zool. Fenn.*, 51, 457–476.
- Pakkala, T., Tiainen, J., Piha, M., Kouki, J., 2018. How important are nest cavities made by the Three-toed Woodpecker *Picoides tridactylus* for cavity-nesting forest bird species? *Acta Ornithol.*, 53(1), 69–79.
- QGIS Development Team, 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available online: <http://qgis.osgeo.org>.
- Remm, J., Löhmus, A., 2011. Tree cavities in forests – The broad distribution pattern of a keystone structure for biodiversity. *Forest Ecol. Manag.*, 262 (4), 579–585.
- Roberge, J.-M., P. Angelstam, Villard, M.-A., 2008. Specialised woodpeckers and naturalness in hemiboreal forests - Deriving quantitative targets for conservation planning. *Biol. Conserv.*, 141, 997–1012.
- Scherzinger, W., 1969. Ein Schelm aus unseren Wäldern – der Sperlingskauz. *Vogelkosmos*, 6, 421–423.
- Scherzinger, W., Mebs, T., 2020. *Die Eulen Europas. Biologie, Kenzeichen, Bestände*. Kosmos, Stuttgart.
- Schönn, S., 1978. *Der Sperlingskauz*. Die Neue Brehm-Bücherei 513, Lutherstadt Wittenberg.
- Schulenburg, J., Wiesner, J., 1986. Zur Winternahrung des Sperlingskauzes (*Glaucidium passerinum*) in zwei unterschiedlichen Gebieten der DDR. *Acta Ornithoecol.*, 1, 167–183.
- Solheim, R., 1984. Caching behaviour, prey choice and surplus killing by Pygmy Owls *Glaucidium passerinum* during winter, a functional response of a generalist predator. *Ann. Zool. Fennici*, 21 (3), 301–308.
- Sonerud, G.A., Mjelde, A., Prestrud, K., 1972. Spurveuglehekking i fugleholk. *Sterna*, 11, 1–12.

- Suhonen, J., Halonen, M., Mappes, T., Korpimäki, E., 2007. Interspecific competition limits larders of pygmy owls *Glaucidium passerinum*. *J. Avian Biol.*, 38 (5), 630–634.
- Syrjänen, J., Lagerström, M., Rintamäki, P., 2006. Pirkanmaan varpuspöllötutkimuksen kaksi vuosikymmentä. *Lintuviesti*, 31, 8–21.
- Terraube, J., Villers, A., Poudré, L., Varjonen, R., Korpimäki, E., 2017. Increased autumn rainfall disrupts predator–prey interactions in fragmented boreal forests. *Glob. Change Biol.*, 23 (4), 1361–1373.
- Van der Hoek, Y., Gaona, G.V., Martin, K., 2017. The diversity, distribution and conservation status of the tree-cavity nesting birds of the world. *Divers. Distrib.*, 23 (10), 1120–1131.
- Virkkala, R., 2004. Bird species dynamics in a managed southern boreal forest in Finland. *For. Ecol. Manag.*, 195, 151–163.
- Virkkala, R., 2016. Long-term decline of southern boreal forest birds: consequence of habitat alteration or climate change?. *Biodivers. Conserv.*, 25(1), 151–167.
- Virkkala, R., Leikola, N., Kujala, H., Kivinen, S., Hurskainen, P., Kuusela, S., Valkama, J. Heikkinen, R.K., 2022. Developing fine-grained nationwide predictions of valuable forests using biodiversity indicator bird species. *Ecol. Appl.*, 32, e2505.
- Wesołowski, T., 2012. “Lifespan” of non-excavated holes in a primeval temperate forest: a 30 year study. *Biol. Conserv.*, 153, 118–126.
- Wesołowski, T., Martin, K., 2018. Tree holes and hole-nesting birds in European and North American forests. In: Mikusiński, G., Roberge, J.-M., Fuller, R.J. (Eds.). *Ecology and conservation of forest birds*. Cambridge University Press, New York, NY, pp. 79–134.
- Wiesner, J., 2001. Die Nachnutzung von Buntspechthöhlen unter besonderer Berücksichtigung des Sperlingskauzes in Thüringen. *Abh. Ber. Mus. Heineanum*, 5, 79–94.



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