UNIVERSITY
OF TURKU

FOOD HOARDING OF AN AVIAN PREDATOR UNDER FOOD LIMITATION AND CLIMATE CHANGE

Giulia Masoero

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
SARJA – SER. AII OSA – TOM. 373 | BIOLOGICA – GEOGRAPHICA – GEOLOGICA | TURKU 2020

UNIVERSITY
OF TURKU

FOOD HOARDING OF AN AVIAN PREDATOR UNDER FOOD LIMITATION AND CLIMATE CHANGE

Giulia Masoero

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
SARJA – SER. AII OSA – TOM. 373 | BIOLOGICA – GEOGRAPHICA – GEOLOGICA | TURKU 2020

University of Turku

Faculty of Science and Engineering
Department of Biology
Section of Ecology
Doctoral Programme in Biology, Geography and Geology (BGG)

Supervised by

Professor emeritus Erkki Korpimäki
University of Turku, Finland

Professor Toni Laaksonen
University of Turku, Finland

Dr Chiara Morosinotto
Novia University of Applied Sciences, Finland
University of Turku, Finland

Reviewed by

Professor Ryan Norris
University of Guelph, Canada

Docent Hannu Pietiäinen
University of Helsinki, Finland

Opponent

Professor Alexandre Roulin
University of Lausanne, Switzerland

The originality of this publication has been checked in accordance with the University of Turku quality assurance system using the Turnitin OriginalityCheck service.

Cover Image: Martina Cadin

ISBN 978-951-29-8185-4 (PRINT)
ISBN 978-951-29-8186-1 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)
Painosalama Oy, Turku, Finland 2020

To my grandma,
thank you for believing in me and
helping me get this far

UNIVERSITY OF TURKU
Faculty of Science and Engineering
Department of Biology
Section of Ecology
GIULIA MASOERO: Food hoarding of an avian predator under food limitation and climate change
Doctoral Dissertation, 171 pp.
Doctoral Programme in Biology, Geography and Geology (BGG)
October 2020

ABSTRACT

Hoarding behaviour (storing food for later use) has evolved to reduce the risk of starvation when resources are scarce. In this thesis, I studied the food-hoarding behaviour of Eurasian pygmy owls (*Glaucidium passerinum*) under spatio-temporally varying environmental conditions. I investigated differences between age and sex classes, the effect of intra-specific competition, predator responses to the abundance of the main prey, and the effect of climate on the behaviour. The data were collected starting in 2003 in western Finland, where the abundance of voles fluctuates in three-year population cycles. The number of stores per year and the biomass of prey items stored increased with vole abundance. Females and yearlings had larger and heavier stores than males and adults, respectively. At times of low vole abundance, adult owls stored more small birds and fewer small mammals than yearlings. Females stored more small mammals than males, and showed a tendency to store fewer birds. The numbers of yearlings of both sexes and adult females increased with increasing vole abundance. Owls were less likely than expected to have a neighbour of the same class (sex or age) when the main prey was abundant, suggesting high sex- or age-specific competition. Food stores, however, were mostly larger when the nearest neighbour was of the same sex. In years of low vole abundance, increasing conspecific density reduced the total prey number stored by an owl, suggesting a high cost of competition. The thesis also reveals a strong effect of autumn and winter climate on food-hoarding pygmy owls and on the quality of the stored food. Pygmy owls may be partly able to adapt to climate change by delaying the initiation of food-hoarding. Numerous weather variables nonetheless affect their hoarding behaviour and the perishability of the cached food. Rotten food may be of poor quality and may be connected to a lower recapture probability. In female owls, rotted food hoards, often consumed, are linked with a lower future recapture probability, presumably indicating that they either die or emigrate permanently from the area. Detailed knowledge of age- and sex-related differences in hoarding behaviour under fluctuating abundances of the main prey can thus provide a fundamental tool to better understand the dynamics of a predator population and its response to climate change.

TURUN YLIOPISTO
Luonnontieteiden ja tekniikan tiedekunta
Biologian laitos
Ekologia
GIULIA MASOERO: Food hoarding of an avian predator under food limitation and climate change
Väitöskirja, 171 s.
Biologian, maantieteen ja geologian tohtoriohjelma
Syyskuu 2020

TIIVISTELMÄ

Varastointikäyttäytyminen, eli ravinnon säilöminen myöhempää käyttöä varten, on kehittynyt vähentämään nälkiintymisen riskiä niukkojen ravintovarojen aikoina. Väitöskirjassani tutkin varpuspöllön (*Glaucidium passerinum*) varastointikäyttäytymistä ajallisesti ja paikallisesti vaihtelevissa ympäristöoloissa. Selvitin sukupuolten ja ikäluokkien välisiä eroja, lajinsisäisen kilpailun ja tärkeimpien saalisryhmien runsauden vaihtelun, sekä ilmaston vaikutuksia käyttäytymiseen. Tutkimusaineisto on kerätty vuodesta 2003 alkaen Kauhavan ympäristöstä läntisestä Suomesta, jossa myyrien populaatiotiheydet vaihtelevat kolmen vuoden sykleissä. Sekä varpuspöllöjen vuosittainen varastojen lukumäärä että varastoitujen saaliiden kokonaisbiomassa kasvoivat myyrätiheyden noustessa. Naaraiden varastot olivat kooltaan ja painoltaan suurempia kuin koiraiden varastot, samoin kuin nuorten pöllöjen varastot verrattuina aikuisten varastoihin. Myyrätiheyden ollessa alhainen aikuiset pöllöt varastoivat enemmän lintuja ja vähemmän pikkunisäkkäitä kuin nuoret. Naaraat taas varastoivat enemmän pikkunisäkkäitä kuin koiraat, ja olivat myös taipuvaisia varastoimaan vähemmän pikkulintuja. Nuorten naaraiden ja koiraiden, sekä aikuisten naaraiden lukumäärä kasvoi myyrätiheyden noustessa. Pöllöillä oli ravintotilanteesta riippumatta odotettua harvemmin samaa sukupuolta tai ikäluokkaa oleva naapuri talvella, mikä kielii kovasta sukupuolten ja ikäluokkien sisäisestä kilpailusta. Varastot olivat kuitenkin enimmäkseen suurempia niillä pöllöillä, joiden naapuri oli samaa sukupuolta. Huonoina myyrävuosina yksittäisen varpuspöllön varastoimien saaliiden lukumäärä laski lajikumppanien määrän kasvaessa, mikä viittaa lajinsisäisen kilpailun korkeisiin kustannuksiin. Väitöskirjani tuo myös ilmi, miten suuri vaikutus syystalven sääoloilla on varastoiviin varpuspöllöihin ja varastoidun ravinnon laatuun. Varpuspöllöt pystyvät osittain sopeutumaan ilmastonmuutokseen viivyttämällä varastoimisen aloitusta, mutta lukuisat säätekijät, erityisesti nollan molemmin puolin sahaavat lämpötilat vaikuttavat niiden varastointikäyttäytymiseen ja varastojen säilyvyyteen. Pilaantuneen varaston ravintoarvo on todennäköisesti huono, ja saattaa olla yhteydessä alentuneeseen todennäköisyyteen tavata sama yksilö uudestaan. Naaraspöllöjä, joilla oli pilaantuneita varastoja ja joita ne usein myös käyttivät, tavattiin harvemmin uudestaan, mikä kertoo niiden todennäköisesti joko menehtyneen tai lähteneen alueelta muualle. Täsmällinen tieto varastointikäyttäytymisen eroista sukupuolten ja ikäluokkinen välillä tärkeimpien saalislajien tiheyksien vaihdellessa voikin olla ratkaiseva avain petoeläinten populaatiodynamiikan ja ilmastonmuutosvasteen ymmärtämisessä.

Table of Contents

List of Original Publications

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

I **Masoero G.**, Morosinotto C., Laaksonen T., Korpimäki E. Food hoarding of an avian predator: sex- and age-related differences under fluctuating food conditions. Behavioral Ecology and Sociobiology, 2018, 72: 159.

II **Masoero G.**, Laaksonen T., Morosinotto C., Korpimäki E. Age and sex differences in numerical responses, dietary shifts, and total responses of a generalist predator to population dynamics of main prey. Oecologia, 2020, 192: 699–711.

III Koivisto E.*, **Masoero G.***, Morosinotto C., Le Tortorec E., Korpimäki E. Conspecific density drives sex-specific spatial wintertime distribution and hoarding behaviour of an avian predator. Submitted manuscript.

IV **Masoero G.**, Laaksonen T., Morosinotto C., Korpimäki E. Climate change and perishable food hoards of an avian predator: is the freezer still working? Global Change Biology. Early view.

*These authors contributed equally to this work.

The original publications have been reproduced with the permission of the copyright holders.

Author contributions to the original publications:

	I	**II**	**III**	**IV**
Original idea	GM, EK, CM, TL	EK, GM, TL, CM	Ekoi, CM, EK	EK, GM, TL
Data collection	EK, GM, CM	EK, GM, CM	EK, GM, CM	EK, GM, CM
Statistical analyses	GM	GM	GM, ELT	GM, TL
Writing the first draft	GM	GM	EKoi, GM	GM
Writing of the final draft	GM, EK, CM, TL	GM, EK, TL, CM	EKoi, GM, CM, EK	GM, EK, TL, CM

GM = Giulia Masoero, EK = Erkki Korpimäki, TL = Toni Laaksonen, CM = Chiara Morosinotto, EKoi = Elina Koivisto, ELT = Eric Le Tortorec

1 Introduction

1.1 Food as a limiting resource

Densities of animal populations are related to three main demographic components: births, deaths and movements (reviewed in Murray & Sandercock, 2020). The relationships among these components in turn are influenced by several factors, including weather, resource abundance (such as food or breeding-sites), and the presence of enemies (such as predators and competitors). These are therefore called ‘limiting factors’, and determine the abundance of a species in a specific area. Variation in food abundance and availability in particular, by affecting not only individual reproduction and survival (Lack, 1947; Martin, 1987; Reznick et al., 2000) but also emigration and immigration rates (Newton, 2006), can strongly limit animal populations and determine whether they will thrive, decline, or even become extinct (Stephens et al., 2007; Newton, 2013).

Food shortages may arise in situations or seasons in which there is an increase in demand, a decrease in food abundance or availability, or both (Roberts, 1979; Vander Wall et al., 2006; Stephens et al., 2007). An increase in demand is usually due to an increase in energy consumption, for example during reproduction. A decrease in food abundance or availability can arise due for example to cyclical fluctuations in resources or adverse weather conditions. Variations in food shortages may be occasional (due to specific weather conditions) or more regular, occurring in a specific season or every few years.

Some animals specialize in food supplies that fluctuate more than 100-fold from year to year (Newton, 2013; Newton, 2006). Populations of seed-eating boreal mammals and finches, for example, follow variations in the size of tree-seed crops (Morris et al., 1958; Enemar et al., 1984; Lindström et al., 2005). Trees of many species require more than one year to accumulate sufficient nutrients to produce a fruit crop, leading to considerable differences in crop size, with good crops usually followed by poor ones (Koenig & Knops, 1998; Koenig & Knops, 2000). Another example is provided by the regular fluctuations of three to five years in populations of microtine rodents (Elton, 1942; Krebs & Myers, 1978) that characterize boreal predator-prey interactions, influencing populations of avian and mammalian predators (Korpimäki & Norrdahl, 1991; Korpimäki & Hakkarainen, 1991;

Korpimäki, 1992; Newton, 2002; Lehikoinen, Ranta, et al., 2011). Fluctuations in food availability can nonetheless present spatial variability, and a year of good food availability in one region might be a poor year in another. The abundance of the main food can determine variation in the local population abundance, via changes both in movement and settlement patterns (simultaneous changes) and in survival and reproduction (delayed changes). Foraging decisions related to food resources are therefore a fundamental driving force of population dynamics (Holt & Kimbrell, 2007).

1.1.1 Food-hoarding behaviour

To cope with periods of food limitation, animals have evolved several diverse strategies, including hibernation, migration to areas with good food availability, and the ability to store energy (Brodin & Clark, 2007; Lack, 1968; Geiser, 2004; Smith & Reichman, 1984). One way to store energy is within the body as fat, carbohydrates or proteins; this strategy, however, significantly reduces mobility, and is therefore not favourable for species forced to remain active for purposes of foraging or to escape predation (Smith & Reichman, 1984). Analogous to storing resources inside the body, hoarding can provide a way to store food externally (Brodin & Clark, 2007; Vander Wall, 1990).

Food hoarding is usually defined as the handling of food to preserve it for later use (Vander Wall, 1990). In this thesis, the terms *caching* and *storing* are used as synonymous with hoarding. Food is usually hoarded when resources are abundant, and used later when resources are scarce or not easily available. Hoarding food thus increases the predictability of food resources and reduces the amount of energy spent searching for food during adverse environmental conditions. Food-hoarding behaviour is common among many different animals species; most commonly vertebrates such as mammals and birds, but also several species of arthropods. The type of food cached can be very diverse, including for example seeds, nuts, fruits, mushrooms, insects, small mammals, and birds. The duration for which food can be stored can range from a few hours or days to months or even years. Food-hoarding species can be defined as either *scatter-hoarding* (the food is stored in a number of dispersed caches) or *larder-hoarding* (all the food is stored in one or a few central stores; Morris, 1962; Vander Wall, 1990).

Factors promoting the evolution of food-hoarding behaviour can come from the external environment, from the species' own characteristics, or from the interaction of the two. Food hoarding is more common at higher latitudes than at lower ones, due to greater environmental variability (Smith & Reichman, 1984). At high latitudes wintering conditions may be harsh, and snow cover and cold climate may create a situation of food scarcity (e.g. snow cover hiding food; prey hibernating or migrating south), but may also favour the preservation of the food itself (Källander & Smith, 1990; Roberts, 1979; Smith & Reichman, 1984). Small-sized species need more food per gram of body weight than large-sized ones because of their higher metabolic rates (Brown et al., 2004; Peters, 1983). They cannot survive long periods of starvation, and are therefore more likely to have evolved strategies to cope with periods of food limitation (Geiser, 2004; Smith & Reichman, 1984; Lack, 1968).

1.1.2 Age and sex differences

Inter-individual differences in foraging behaviour are common among different animals species, and are connected to differences in individual personality (e.g. Start & Gilbert, 2017) or to differences related to age or sex class. Age and sex differences usually arise out of differences in experience, skills or morphology.

In general, juveniles appear to perform more poorly than adult ones, both as hunters and as breeders (Orians, 1969; Wunderle, 1991; Daunt et al., 1999; Laaksonen et al., 2002; Rutz et al., 2006; Marchetti & Price, 1989). In many species, young individuals forage differently from older ones, have different hunting skills (which generally improve with experience) and prey upon different species. To explain this age-effect, at least three hypotheses have been put forward (Forslund & Pärt, 1995; Martin, 1995):

- The *constraint hypothesis* (Curio, 1983): young individuals are constrained by their inferior foraging skills, they are still learning and practising;
- The restraint hypothesis (Curio, 1983): young individuals restrain their efforts, especially in breeding, in order not to jeopardise their survival and future breeding success;
- The differential mortality hypothesis (Curio, 1983; Forslund & Pärt, 1995): in cross-sectional data, older age groups may no longer include lower-quality individuals that are present in younger cohorts.

Differences in foraging behaviour and skills have also been reported in many species between sexes (e.g. Clarke et al., 1998; Ishikawa & Watanuki, 2002; Rose, 1994), especially in sexually size-dimorphic species (Earhart & Johnson, 1970; Korpimäki & Hakkarainen, 2012; Keynan & Yosef, 2010). Many species of owls and diurnal raptors are characterised by reverse size dimorphism (females are larger than males). Of the numerous hypothesis explaining this dimorphism, the following two have received the most support (Krüger, 2005; Massemin et al., 2000; Hakkarainen & Korpimäki, 1991):

- The *small male hypothesis*: smaller-sized males are more efficient hunters than larger-sized females because they have to provide food for the incubating female (Sergio et al., 2007; Hakkarainen & Korpimäki, 1991; Penteriani et al., 2013). Males are often better than females at catching prey that is skilled at manoeuvring (Mills et al., 2019). Furthermore, in females large size may be selected for to favour the production of large eggs and prolonged incubation (Reynolds, 1972; Snyder & Wiley, 1976; Lundberg, 1986; Mueller, 1986).
- The intersexual-competition hypothesis: differences in body size reduce competition between the sexes. Sex-specific foraging behaviours have also been observed in species in which the sexes do not differ in size (Gray & Hamer, 2001; Lewis et al., 2002), showing that the reduction of foraging competition between the sexes is beneficial regardless of size.

Individual differences in foraging behaviour related to age and sex class are thus likely to be reflected in differences in their food-hoarding behaviour; these variations, however, have not been thoroughly investigated.

1.1.3 Predator responses

Interactions between predators and their prey can determine fluctuations in the populations of all interacting species, thereby profoundly affecting the dynamics of the whole community (Vermeij, 1994; Abrams, 2000; Winnie & Creel, 2017). Predation can be density-dependent if the proportion of prey consumed increases with rising prey density, and predators can respond to changing prey density in two different ways (Newton, 2013; Solomon, 1949). With the *functional response*, the proportion of individuals of a certain prey species in the diet of a predator varies with the abundance of that species (e.g. Oaten & Murdoch, 1975). Predators may also switch to alternative prey species when the density of the main prey species declines (e.g. O'Donoghue et al., 1998; Korpimäki, 1987b; Korpimäki et al., 1989; Korpimäki & Norrdahl, 1991). With the *numerical response*, predator density increases with an rise in the density of the prey species (e.g. O'Donoghue et al., 1997; Salamolard et al., 2000; Korpimäki et al., 1989; Korpimäki & Norrdahl, 1991). Changes in predator numbers are usually induced by variations in the fitness of individuals (survival or reproduction), or in emigration and immigration rates.

Intraspecific age- and sex-related differences in behaviour can affect how individuals will respond to varying prey density. It has been shown that numerical responses can vary in relation to age or sex. In wintering birds of prey, the number of first-year individuals was lower and the sex ratio biased toward males when the main prey was less abundant (e.g. Village, 1985; Côté et al., 2007; Korpimäki &

Hakkarainen, 2012). The functional response can also vary with the predator's sex (Parajulee et al., 1994) or social status (Nilsen et al., 2009). The total response is the outcome of a combination of the age and sex structure of the predator population and their dietary shifts, which can thus affect the predator's impact on the prey community.

1.1.4 Intraspecific competition

Competition can strongly affect foraging behaviour and population dynamics. A high density of competitors may lead to a decrease in fitness (reduction in survival or reproduction rates), with consequences at both the individual and the population level (density-dependent effects; e.g. Matthysen, 2005; Fowler, 1981; Murdoch, 1994; Saether et al., 2002; Newton, 2013; Both, 1998). Individuals may compete for several kinds of resources (e.g. food, water, territory, light, mates, etc.) required for survival or reproduction. Generally, competition may involve indirect interactions through *resource depletion*, where some individuals are more effective at exploiting a certain resource, reducing the amount available to others (*exploitative competition*; Dhondt, 2012). Or it may involve direct interactions, such as fighting, theft or ritualised combat, where some individuals aggressively reduce others' access to and use of resources (*interference*; Dhondt, 2012). Negative effects of competition may further arise via *resource depression* (*sensu* Charnov et al., 1976), a process that does not require the actual capture of any prey by the predator. The presence of a predator may in fact bring about a decrease in the capture rate of the prey in its vicinity, due to the detrimental effects of its foraging activity on the behaviour and micro-distribution of prey.

Intraspecific competition takes place when the competing individuals belong to the same species (as opposed to *interspecific* competition, between individuals of different species). Intraspecific competition may intensify when resources become a limiting factor, due either to an increase in population density or to a decrease in resource availability. When resources are abundant and of good quality, animals may be able to compensate for the negative impact arising from a large number of competitors (Bårdsen & Tveraa, 2012).

Behaviours such as niche separation or spatial segregation can help in reducing the costs of competition and can arise from different competing abilities. Behavioural differences between age and sex classes can lead to differences in their competing abilities. thereby affecting their spatial distribution. Their ability to compete may also depend on current environmental conditions (e.g. Coulson et al., 2001).

1.1.5 Climate change and food hoarding

Recent global climatic changes have been affecting the population abundance, geographical range, phenology and behaviour of many species, and have even led to the decline or local extinction of some populations (Møller et al., 2010; Pearce-Higgins & Green, 2014; Dunn & Møller, 2019). Changes in temperature and precipitation have been occurring globally and at a rapid pace (IPCC, 2014). The earth's average temperature is rising, but increases have been greater at northern latitudes and during winter and spring (Houghton et al., 2001; IPCC, 2014). These temperature changes, and the consequently modified patterns of air circulation, are affecting global precipitation patterns: precipitation is increasing at high latitudes and during autumn and winter. The global climatic trends observed during the past decades are expected to accelerate during the coming years (IPCC, 2014), and are likely to affect many animal species.

Climatic conditions have always influenced animal populations, mainly through their survival, reproduction and geographical range, but also by way of the availability and quality of food and other resources (Dempster, 1975; Newton, 2013). Weather can therefore strongly affect foraging behaviour in general; in particular, it can have a profound effect on food-hoarding species, which usually rely on the preservation of food by cold or dry conditions that limit its degradation.

Predicting the susceptibility to climate change of food-hoarding species is a challenging task, thoroughly analysed by Sutton and colleagues (2016), and depends on certain fundamental factors (Fig. 1):

– Duration of food hoard. Food hoarders can store food to be consumed in the future, after a brief interval (from a few hours to a few days) or a long one (several weeks, months or even years). The longer the food is hoarded, the greater the susceptibility of the species to climate change.

– Type of food hoarded. Susceptibility increases with increasing perishability of the food. Non-perishable foods include nuts and seeds, while fruits, mushrooms and meat are highly perishable.

– Location of the food hoard. Food can be stored in the ground or in trees; the more exposed the food store to environmental conditions, the more susceptible the species.

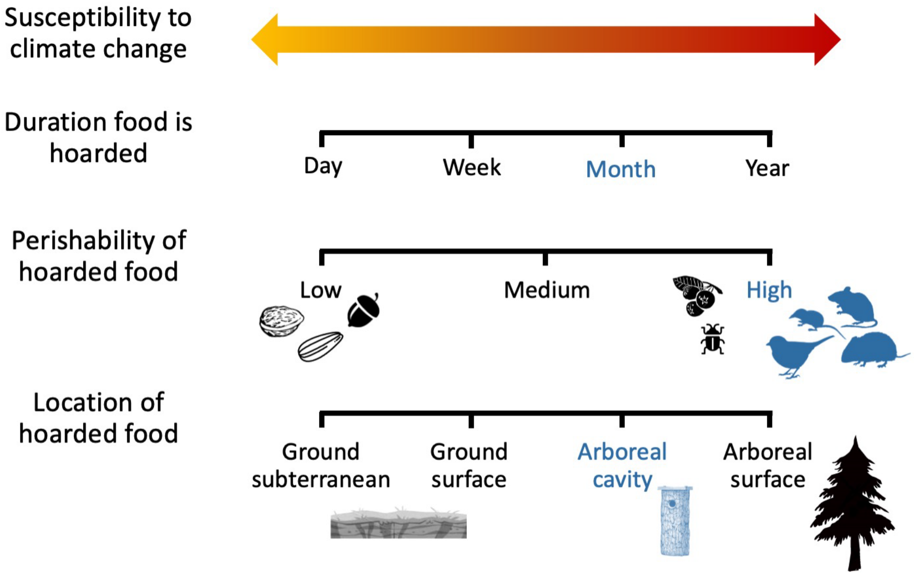

Figure 1. Three factors mainly affecting susceptibility of food-hoarding species to climate change. Values of each factor for pygmy owl are highlighted in blue. Figure reproduced and modified from Sutton et al. 2016. *Food storage in a changing world: implications of climate change for food-caching species*. Climate Change Responses 3:12.

1.2 Why investigate foraging in winter?

The vast majority of previous studies on intraspecific variation in foraging and its implication at the population level have been conducted during the breeding season, whereas the wintering season has generally been understudied. Numerical and functional responses of predators to food availability, as well as intraspecific competition, have been conducted during the reproductive season (but see e.g. Korpimäki et al., 1991; O'Donoghue et al., 1998; O'Donoghue et al., 1997). The effects of weather on foraging behaviour during breeding have received extensive attention (reviewed in Both, 2010), but with regard to the non-breeding season – with some exceptions (Sutton et al., 2019; Terraube et al., 2017; Halonen et al., 2007; Sechley et al., 2015) – they have been surprisingly understudied.

Seasonal variations in resource abundance, however, are particularly strong at high latitudes, and food availability for over-wintering predators can be particularly poor. In addition, climate change has been shown to be more intense at higher than at lower latitudes, and during autumn and winter. Investigating the effect of food limitation during winter on food-hoarding individuals and their behaviour could thus provide fundamental insight into the ecology of the species, and thus into predator-prey and community dynamics.

1.3 The study system

In the boreal environments of northern Europe, voles and lemmings show population cycles of three to five years that to a great extent govern the abundance and reproductive success of numerous species of mammalian and avian predators (Korpimäki, 1992; Korpimäki et al., 1989; Lehikoinen, Ranta, et al., 2011; Newton, 2002). Among avian predators, the Eurasian pygmy owl (*Glaucidium passerinum*; hereafter pygmy owl) is one of the smallest European species relying on voles as main prey (Schönn, 1980; Mikkola, 1983). Food availability has a profound impact on pygmy owl populations; in particular it has been shown that the breeding densities of pygmy owls can be higher, and their food stores more numerous, in years of vole abundance than in years of scarcity (Suhonen, 1993; Solheim, 1984b; Ekman, 1986; Solheim, 1984a), while times of food depletion may induce irruptive migrations in autumn (Lehikoinen, Hokkanen, et al., 2011).

Pygmy owls are generalist predators whose diet is related to prey availability, thus differing according to geographic area and season (Schönn, 1980; Mikkola, 1983; Ekman, 1986; Schulenburg & Wiesner, 1986). In northern Europe, their diet includes small mammals such as bank voles (*Myodes glareolus*), voles of the genus Microtus (the field vole *M. agrestis*; the sibling vole *M. rossiaemeridionalis*; hereafter 'Microtus voles'), shrews (the common shrew *Sorex araneus*; the pygmy shrew *S. minutus*), mice (the Eurasian harvest mouse *Micromys minutus*; the house mouse *Mus musculus*), and small passerine birds. During autumn and winter their avian prey species are usually resident forest passerines, such as tit species, small finches and goldcrests *Regulus regulus* (Halonen et al., 2007), but during the breeding season pygmy owls prey upon all migratory small birds breeding in the area (Kellomäki, 1977).

The pygmy owl inhabits old and mature coniferous forests in the boreo-alpine areas of Eurasia (Fig. 2), and nests in natural tree cavities, usually excavated by woodpeckers, or artificial nest-boxes (Strom et al., 2001; Halonen et al., 2007; Barbaro et al., 2016; Morosinotto et al., 2017). During late autumn and winter, cavities or boxes are also used to store large quantities of food (Fig. 3; Solheim, 1984b; Terraube et al., 2017).

Figure 2. Location of study area; geographical range of pygmy owl in Europe shown in orange. (Map modified from: BirdLife International and Handbook of the Birds of the World (2016) 2009. *Glaucidium passerinum*. IUCN Red List of Threatened Species. Version 2020-1).

Among avian predators (owls, diurnal raptors and shrikes), some form of food hoarding is fairly common during periods of food scarcity or during the breeding season (Källander & Smith, 1990; Korpimäki, 1987c; Yosef & Pinshow, 1989). The pygmy owl, however, is the only European species to store large quantities of prey items in cavities, establishing larders for the winter (Fig. 3; Mikkola, 1983; Solheim, 1984b; Schulenburg & Wiesner, 1986). Other owl species, as well as diurnal raptors and shrikes, hoard prey during the breeding season or are scatter-hoarders; the food is usually dispersed among a number of cavities or placed on tree branches or bushes (Vander Wall, 1990). The food hoarding behaviour of pygmy owls has previously been described in several studies in terms of store content, which varies with the availability of the main prey (i.e. the abundance of voles of the genera *Myodes* and *Microtus*; Mikkola, 1983; Solheim, 1984b; Halonen et al., 2007; Terraube et al., 2017). The beginning of the food-hoarding season seems to be related to a drop in daily temperatures below 0 °C in autumn (Solheim, 1984b; Schulenburg & Wiesner, 1986). During the food-hoarding season, increased precipitation is associated with a decline in prey biomass in food hoards and in the body condition of female pygmy owls (Terraube et al., 2017), and an increase in the snow-cover with a decline in the number of stored small mammals (Halonen et al., 2007).

Figure 3. Examples of food hoards of pygmy owls in nest-boxes. 3a shows a food hoard collected in a year of vole scarcity, composed mainly of birds. 3b shows a food store mainly composed of voles.

1.4 Aims of the thesis

In this thesis, I have studied winter foraging, its connection with predator population structure and dynamics, and the potential impact of climatic factors. I have therefore investigated the food-hoarding behaviour, a specific type of foraging behaviour, of a generalist avian predator, in a season of its life cycle which is as yet poorly known. The availability of a long-term dataset (starting in 2003) for capture-mark-recapture of pygmy owls and their food-hoard content therefore provides an ideal situation. The study species also hoards food of a highly perishable nature (small mammals and birds) in tree cavities for a prolonged period (usually several weeks or a few months), thus showing high susceptibility to climate change (Fig. 1). In the winter small mammalian prey are usually hidden by the snow, while most of the potential avian prey have migrated to the south. Stored food can thus be critical for wintering pygmy owls when fresh food is unavailable.

I started the work of the thesis by investigating the main characteristics of the food-hoarding behaviour of pygmy owls, and by describing differences among age and sex classes in autumn, when voles are abundant (**I**, **II**); while food-hoard content has been described in several previous studies, little is still known as to differences in food-hoarding behaviour according to individual age and sex. I then focused on the numerical and functional responses of pygmy owls of different age- and sex classes to a fluctuating abundance of their main prey, and how these are combined in the total predator response (**II**). Intraspecific competition is the main topic in **III**, where I looked at ways in which the spatial distribution of pygmy owls of different age- and sex classes may be affected by food abundance, and how the density of conspecifics may affect the number of stores and the amount of food stored. The subject of the last study (**IV**) was the impact of climate on the food-hoarding behaviour of pygmy owls, in particular on the initiation, accumulation, consumption and degradation of the hoarded food, and how these changes in food degradation may affect the subsequent recapture of hoarding individuals.

2 Materials and Methods

2.1 Study area

The research was carried out in Western Finland (63°N, 23°E), in the vicinity of the towns of Kauhava and Lapua (Fig. 2). The study area covers approximately 1000 km^2, consisting of commercially managed forest (some 70%, including saplings and clear-cut areas) agricultural lands (around 25%), and peatland bogs and settlement areas (Hakkarainen et al., 2003; Morosinotto et al., 2017). The tree composition of the forest area consists predominantly of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), with smaller proportions of deciduous trees, mostly birch-dominated. Due to the management of forested habitats the area mostly consists of young and medium-growth forest, as the proportion of old-growth areas is low. A total of 305 areas of forests (hereafter 'forest-sites') were provided with two nest-boxes for pygmy owls each, on average 80-100 m apart and usually on spruce trees at a height of approximately 1.5 m. The diameter of the boxes (45 mm) corresponds to the cavity of a three-toed woodpecker (*Picoides tridactylus*), and prevents other owl species from entering the boxes. Positioning two nest-boxes per forest-site allowed pygmy owls to have at least one box available, since Siberian squirrels (*Pteromys volans*) can occupy these boxes for roosting and reproducing all year round (Morosinotto et al., 2017).

2.2 Data collection

2.2.1 Food hoarding data

Detailed data on the food-hoarding behaviour of pygmy owls were collected from 2003 down to 2018. In the study area, two inspections of all the nest-boxes were usually carried out during each autumn: the first between the last week of October and the first week of November, the second between the last week of November and the first half of December (Fig. 4). During the autumn inspections, all prey items were identified, counted, weighed and marked (by toe-clipping in birds and tail-clipping in mammals), and the freshness of the food hoard was assessed, by visual inspection and smell, as either fresh or rotten (malodorous and degraded appearance). A third inspection was carried out in spring, between late March and early April, before the start of the nesting period. At this stage only prey species and number were collected, due to the highly degraded state of the food hoard.

For the first three articles forming part of this thesis (**I**, **II**, **III**), I used the data collected during the two inspections of the autumn food-hoarding season, pooled to obtain a total number of prey items per box. In **IV**, the data collected in the two autumn inspections were kept separate, and the data from the spring inspection were included in the analyses.

2.2.2 Pygmy owl data

Data on pygmy owl individuals were collected at the boxes in autumn when food stores were found (data for all four articles) or in spring during the breeding season (data used in **IV**; Fig. 4). In autumn, the individual owls collecting the food hoards were identified either via direct capture (nest-box trap, a replica of the box equipped with a swing door) or via indirect identification (RFID method; Gibbons & Andrews, 2004). Trapped individuals were provided with an aluminium ring and an RFID tag, a microchip with a unique identification code inserted subcutaneously in the upper back. In the spring, female pygmy owls were captured by hand in the nest-box while brooding the chicks. Males were usually attracted in the vicinity of the nest with a playback recorder and captured using a telescopic fishing pole with a loop on top. Both in spring and autumn, supplementary data from untrapped individuals were collected by setting up the RFID-reader antenna around the entrance of the box. Captured owls we also sexed and aged, their wing and tail length were measured, and they were weighed with a Pesola spring balance. Individuals were sexed using these measurements (pygmy owls are sexually size-dimorphic; Mikkola, 1983), and aged according to wing moult (Lagerström & Syrjänen, 1990). Individuals were then divided into ‘yearlings’ (in their hatching year) and ‘adults’ (older than one year).

2.2.3 Vole abundance data

In the study area, the main species consumed by pygmy owls are bank voles and species of the genus *Microtus*. The first species is more commonly found in forested areas, while the second group of species is present in more open areas (e.g. agricultural fields and clear-cut areas). In the area, the abundance of vole species fluctuates synchronously in three-year cycles, with an amplitude of 100- to 200-fold (Korpimäki et al., 2005).

The abundances of bank voles and *Microtus* voles have been estimated by snap trapping twice a year (early May and mid-September; Fig. 4) since 1973 at two locations, situated in the western and central part of the study area. The two sampling sites were 14 km apart; at each one, some 50-100 Finnish metal mouse snap traps were set at 10-m intervals to cover 0.5 to 1.0 ha. The traps were baited with multigrain bread, placed in vole runways, and checked daily for three consecutive days. The four main habitat types were sampled, i.e. spruce-dominated forest, pine-dominated forest, agricultural land currently under cultivation, and abandoned agricultural land. The results of the three-night trapping periods were then pooled and standardized as the number of animals caught per 100 trap-nights, creating one autumn abundance index for each group (see Korpimäki et al. 2005 for further details). The standardized abundances of bank voles and Microtus voles estimated from snap-trappings were then pooled in an overall 'vole index'.

From previous studies (Huitu et al., 2003; Korpimäki et al., 2005), it is known that densities of Microtus and bank voles fluctuate in synchrony in the study area, and that the regional synchrony of vole population cycles extends up to 80 km; thus the validity of the vole abundance index created can be extended to the whole study area.

2.2.4 Weather data

Climate data were obtained from the Finnish Meteorological Institute (FMI), recorded in the middle of the study area (Kauhava airport) since 1973. According to a recent review (Sutton et al., 2016), the most influential weather variables for the quality of hoarded food are temperature, freeze-thaw events, and precipitation. Snow cover may be important in determining the accumulation of new prey items and the consumption of hoarded ones (Halonen et al., 2007). We therefore considered the following nine variables, grouped into three main categories: 1) precipitation (number of days with total precipitation >0.1mm, cumulative precipitation), 2) snow cover (average snow cover depth, number of days with > 10 cm), and 3) temperature (average of mean, minimum and maximum daily temperatures, number of freezing days, number of freeze-thaw events). The number of freezing days was calculated as the number of days with a maximum daily temperature below the average initial freezing point of meat (-1.9 °C). Freeze-thaw events were defined as the number of days on which the minimum temperature was below the average initial freezing point of meat (-1.9 °C) and the maximum temperature was above it, following Sutton at al. (2019). Each variable was calculated over three different periods of the year (Fig. 4), except for only two snow-cover variables due to the lack of snow in October during 2003-2018). The periods were: immediately before and at the start of the autumn food-hoarding season (1 - 30 October), during the hoarding season, when food is most commonly hoarded (15 October - 15 December), and in wintertime, when hoarded food is usually consumed (15 December - 15 March).

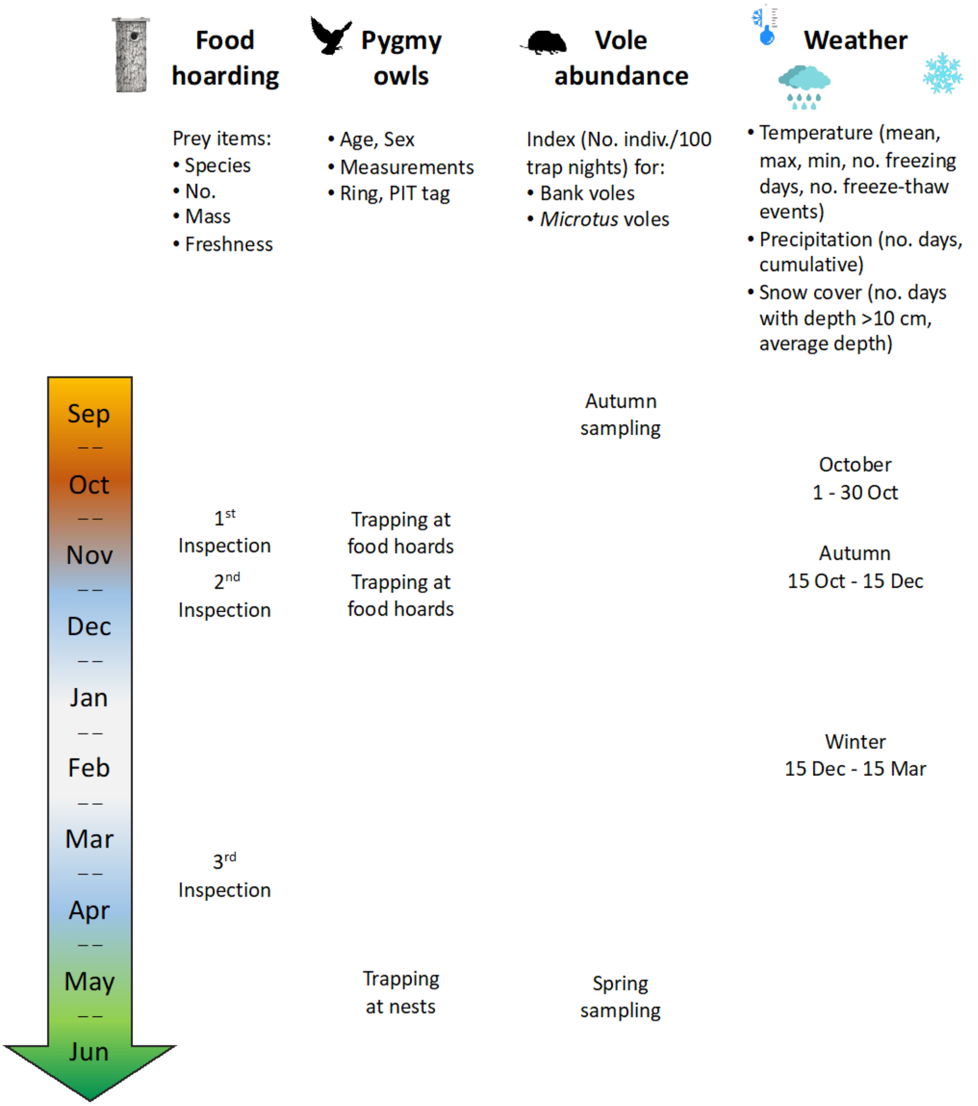

Figure 4. Reference figure for data used in the thesis and the temporal scale of their collection. Detailed data on food hoarding and captured pygmy owls were collected starting in 2003. Snow cover was not measured in October due to the lack of snow during the study years.

2.3 Statistical methods

In the thesis, I analysed the data collected using both generalised linear models (GLMs) and generalised linear mixed-effects models (GLMMs) fitted using maximum likelihood (Laplace approximation). The likelihood family was chosen according to the type of response variable modelled (Zuur et al., 2009). Count data were analysed with a Poisson likelihood family, corrected in case of overdispersion as quasi-poisson (e.g. GLMs in **II** for the age and sex population structure model) or negative binomial (e.g. GLMMs in **II** for food store composition models). Proportional data were analysed with a binomial family, corrected as quasi-binomial (e.g. GLMMs in **I** for the number of occupied sites).

The explanatory variables included the age and sex of the owl that had hoarded the store, and a measure of autumn vole abundance in the environment (usually referred to as 'vole index'; **I**, **II**, **IV**). For the purposes of study **III**, however, it was important to compare responses under similar vole abundance conditions on the density effects and spatial distribution of the owls. We therefore divided the continuous variable for vole abundance into three categories ('low', 'intermediate' and 'high'). In most of the GLMMs, the 'Individual identity' of the owl (the numeric code of the owl metal ring) and/or 'site' (the forest-site where each nest-box pair was located) were used as random effects. 'Individual identity' was used to control for possible repeated measures of the same individual, either in different boxes within the same year (e.g. if an individual had multiple stores) or between multiple years. 'Site' was included as a random effect to take into account spatial and temporal pseudo-replication, since most forest-sites had two nest-boxes available and were used multiple times during the study period. In **II**, I analysed the number of wintering individuals in relation to vole abundance of the current autumn. In this model, I took into account the non-independence of errors due to temporal autocorrelation by adding an autoregressive term of order 1 (corAR1).

In **I** and **II**, interactions were included in some of the models. I started with a full model, and using backward stepwise selection achieved a model with only significant interactions (significance evaluated with the function 'Anova' in the R package *car* v. 2.1-6). In **III** and **IV**, the goal was to identify the model that best described the various response variables, so I used AICc (Akaike Information Criterion corrected for small sample size) model selection. The models were ranked in order of AICc, and the best-ranking model was retained. If the difference between models in terms of AICc (ΔAICc) was <2 and of similar weight, I retained the simpler model, with a lower number of interactions

In **I** and **III**, I used R-GIS spatial methods to calculate distances between boxes or stores and density of individuals. Distances between every store of each individual (with at least two stores), and between an individual and its nearest neighbour, during a particular year were calculated from the coordinates of the boxes, using the function 'gDistance' in the package GIStools (R package v. 0.7-4; Brunsdon & Chen, 2014). Density values were calculated using the function 'density' in the package spatstat (R package v. 1.59-0; Baddeley et al., 2015), which calculates a kernel smoothed intensity function from a pattern of points.

Models were usually constructed through the ‘lmer’ and the ‘glmer’ functions in the package *lme4* (R package v. 1.1-13; Bates et al., 2015), in conjunction with package *lmerTest* (R package v. 2.0-33; Kuznetsova et al., 2016). The package glmmADMB (R package v. 0.8.3.3) was used in the case of negative binomial models (Bolker et al., 2012). Least square means (i.e. marginal means) were obtained through the package *lsmeans* (R package v. 2.27-2; Lenth, 2016). All statistical tests and calculations were performed using the latest version of R available at the time (R Core Team, 2019).

3 Results and Discussion

3.1 Voles as a limiting resource

Throughout the thesis, a recurring theme is the impact of vole abundance on the population of over-wintering pygmy owls and their food-hoarding behaviour. Fluctuations in vole abundance were the main driver of variation in many of the characteristics of food-hoarding behaviour. I first showed that vole abundance in autumn positively affected the number of individuals hoarding food in winter, the number of food stores, and the size of food stores (**I**). Second, I described in detail the numeric responses and dietary shifts of this small avian predator in relation to the autumn abundance of voles (**II**). High vole abundance correlated with the presence of a larger number of individuals, especially yearlings and females. All age and sex classes showed dietary shifts towards different alternative prey items (other small mammals, such as shrews or mice, or small birds). Overall, the numeric response and the dietary shifts were combined in the total response of pygmy owls. I was also able to show that the number of birds (the most important alternative prey) consumed, in particular tits, increased with low vole abundance. In **III**, I investigated how vole abundance influences the effect of conspecific density on food-hoarding behaviour. In years of vole scarcity, when food resources are limited, there seemed to be higher exploitative competition (low number of prey stored), while in years of vole abundance conspecific density probably played a lesser role. In **IV**, I examined the impact of climate on specific aspects of food-hoarding behaviour, taking autumn vole abundance into account. With regard to vole abundance, the results (Fig. 3 in **IV**) showed how the initiation of food-hoarding was delayed and more prey items were accumulated in autumns of high food abundance in the environment. Furthermore, even if a larger number of prey items was consumed during the winter in years of vole abundance than of scarcity, the probability of using the food hoard and the proportion of prey items were lower. Having more fresh prey available in the environment was probably connected to lesser use of old prey items cached, inducing a delay in the initiation of hoarding and a reduced use of hoards.

Previous studies have shown that good vole abundance is linked with high breeding densities of pygmy owls and high numbers of food stores, as well as a high number of prey items stored (Solheim, 1984b; Solheim, 1984a; Ekman, 1986;

Suhonen et al., 2007; Terraube et al., 2017; Lehikoinen, Ranta, et al., 2011), and that food scarcity may induce irruptive migrations in the autumn (Lehikoinen, Hokkanen, et al., 2011). My results confirm this previous knowledge, but also deepen our understanding of the mechanisms whereby food limitation acts on a food-hoarding predator.

3.2 Age and sex differences in food-hoarding behaviour

In **I**, I mainly analysed the age and sex differences in the food-hoarding behaviour of pygmy owls, and found that yearling owls and females have overall larger and heavier food-stores than adult owls and males, respectively. In **II**, I investigated the age and sex differences in the content of food hoards. Yearling owls mainly hoard small mammals, whereas the food store composition of adult owls varies more according to vole abundance, with more hoarded birds in years of low vole abundance. Females also appear to hoard more voles than males, which in turn hoarded more birds in years of low vole abundance.

These results seem to support the idea that yearlings and females may need to invest more in autumn hoarding than adults and males, because they may not be able to rely on daily hunting success in winter. With regard to age differences, I did not find any support for the *constraint* hypothesis; it appears that food hoarding is not limited by hunting experience or skills, although yearlings nonetheless have lower foraging plasticity than adults. In years of vole scarcity, the best option for inexperienced owls may be to hoard small mammals, which are easier to capture than birds (Temeles, 1985) even if less frequently encountered in low years, while adults, being more experienced, would be better at hunting birds (Sasvári et al., 2000; Rutz et al., 2006). Females may have to invest more energy in collecting a larger food hoard, due both to their larger size and to the need to maintain good body condition for the breeding season (Hirons, 1985; Korpimäki, 1987a). This finding is consistent with the *small male* hypothesis, put forward to explain sexual size dimorphism in birds of prey (Korpimäki & Hakkarainen, 1991; Lee & Severinghaus, 2004). Overall, differences between the age and sex classes were greater when voles were scarce, indicating that yearlings and females may be less able to cope with food scarcity.

3.3 Numerical responses and dietary shifts with fluctuating densities of the main prey

My purpose in **II** was to investigate the numerical responses and dietary shifts of wintering pygmy owls in relation to the abundance of their main prey, and their age-and sex-related differences. To study predator responses, I used the data on food-hoarding individuals and the content of their food hoards (as a proxy for diet) collected during the autumn.

The number of food-hoarding adult males wintering in the area remained relatively stable between years, while yearlings of both sexes and females showed pronounced numerical responses to fluctuations in vole abundance. Adults presented wider dietary shifts according to vole abundance, hoarding more birds in years of vole scarcity, whereas yearling owls had a less diverse diet and mainly captured small mammals. Female pygmy owls generally cached more voles than males, and shifted to other small mammals in years of vole scarcity. Males showed a tendency to shift to birds when vole abundance was low.

More experienced adult males are likely to have greater plasticity in their foraging behaviour than young ones or females, and are better able to adjust their foraging effort to varying environmental conditions. Similar age differences have previously also been found in other species (Daunt et al., 2007; Sasvári et al., 2000). Adult males may have better bird-hunting skills than yearlings or females, and may therefore be better at relying on the every-day hunting of avian prey (available throughout the winter). This higher competitiveness would also allow them to persist in the study area and show no numerical response to variations in the main prey.

Taken together, these age- and sex-specific differences in the numerical response and dietary shifts generate differences in the total response of the predator. The different age and sex classes of a single predator species seem to act functionally as different predator types (‘trophic species’, *sensu* Sih et al., 1998). Since it has previously been shown that differences in foraging between predators with different personalities can be an important determinant of prey abundance, community composition and trophic cascades (Start & Gilbert, 2017), my results suggest that differences between age and sex classes can also impact the prey community. Foraging segregation between individuals of different age and/or sex may mean an lesser impact on the population of a single prey species, especially in a context of fluctuating densities of the main prey. When the main prey is abundant, the density of the predator increases and most alternative prey species are released from predation. On the other hand, when the main prey is scarce, species-specific consumption is be higher, but the prey community as a whole will benefit by an overall decline in predation pressure, due both to the lower number of wintering individuals and to the predation pressure being shared among a larger number of prey species.

3.4 Intraspecific competition and food hoarding

In **III**, I presented findings with regard to the effect of fluctuating main prey abundance and conspecific density on spatial distribution and food-hoarding behaviour. Food-hoarding pygmy owls were less likely to have a nearest neighbour of the same sex when the main prey was abundant, suggesting high intrasexual competition. However, food stores were unexpectedly larger when the nearest neighbour was of the same sex. Choosing a different-sex neighbour might thus be a way to promote mating opportunities in the following breeding season, although I found no evidence of that.

When voles are scarce in the environment, a high conspecific density reduces the total amount of prey stored; no such effect was found in years of vole abundance. When resources are scarce, high conspecific densities may lead to reduced storing success in food-hoarding predators, which in turn may imperil their over-winter survival. Dietary differences between sexes (Chapter **II**; Mills et al., 2019), and the consequent sex-specific spatial segregation (**III**), may in any case be beneficial in reducing the costs of competition. When conspecific density was high, the owls also allocated their prey items to multiple food stores rather than just one, showing a shift from a larder-hoarding strategy towards a slightly more scatter-hoarding one. Overall, allocating the prey to several food stores reduces the transportation distance and thus the energetic costs for food-hoarding owls. Allocating prey items to multiple stores may also be a way to decentralize stored prey items so as to avoid potential pilfering, or to reduce the overall costs of losing one store when the density of conspecifics is high (Vander Wall and Jenkins 2003). It is known that pygmy owls may visit other individuals' food stores (Masoero et al. 2018); multiple food stores are thus likely to reduce pilfering from conspecifics or other small predators, such as weasels and stoats, whose densities would also increase in years of good vole abundance.

The competitive abilities of individuals are probably connected to their response to fluctuating densities of the main prey (chapter **II**). When food is abundant, the variance in competitive abilities within the population may be high, since inexperienced or lower-quality competitors may be able to overwinter in the area. On the other hand, when the abundance of the main prey is a limiting factor, it is likely that only better competing individuals will manage to persist and survive in the area, while others may have to disperse and/or perish, due to the higher risk of starvation. As shown in **II**, the individuals usually present in constant numbers are adult males, which also show a higher plasticity in dietary shifts with vole abundance.

Prey populations are also probably affected by interactions between predators, and modify their spatial distribution accordingly (Byholm et al., 2012; Morosinotto et al., 2010; Ritchie & Johnson, 2009). The sex-specific diet and spatial settlement of wintering pygmy owls can therefore further affect the habitat selection of their main and alternative prey (voles and small passerine birds, respectively), presumably influencing their survival under the harsh winter conditions of boreal forests.

3.5 Effect of weather on food-hoarding behaviour and the consequences

In **IV**, I offered a comprehensive view of the effects of winter weather on food-hoarding behaviour and its consequences for the local survival of individuals. I did so by analysing how weather factors can determine the initiation of hoarding and the accumulation, consumption and rotting of the hoards, taking into account the abundance of the main prey and the age and sex of the hoarder, so as to gain a better understanding of the weather responses. I then investigated the use of rotten food and the future recapture probability of individuals with a rotten food hoard.

I found that pygmy owls initiate food hoarding early in the autumn, when there is a high number of freeze-thaw events before the food-hoarding season; they have also tended to start later in recent years. Pygmy owls used their hoards more with more frequent freeze-thaw events and a deeper snow cover in autumn and winter, and lower precipitation in winter. More food hoards were found rotten with more frequent precipitation days during the autumn food-hoarding season. Food hoards were found decayed more often at the time of the second autumn inspection (late November - early December), if they were already present at the first inspection, one month earlier. I also found that rotten food hoards were used more in years of vole scarcity. In female owls, having rotten food hoards was linked with a lower future recapture probability, presumably indicating that they had either died or permanently emigrated from the area.

This study revealed a strong effect of winter climate on food-hoarding pygmy owls and the quality of their stored food. In high latitude ecosystems, including this study area, the autumns have already become warmer and winters milder and with increasing precipitation, and future changes are predicted to continue along this path (Collins et al., 2013; Ruosteenoja et al., 2011). Unexpectedly, I found that pygmy owls may be partly able to adapt to climate change by delaying the initiation of food-hoarding. Nonetheless, numerous weather variables are affecting their hoarding behaviour and the perishability of cached food. Rotten food, often consumed, may be of poor quality and may be connected to a lower recapture probability of female owls. This is further supported by the finding that rainy days during the food-hoarding season induced a lower biomass of prey items in food stores, in turn reducing the body condition of female pygmy owls. Global warming, and climate change in general, can thus impair the over-winter survival of pygmy owls by acting on the frequency of freeze-thaw events on precipitation patterns, and on the structure of the snow cover.

4 Conclusions

In this thesis, I investigated the food-hoarding of pygmy owls, a highly specific kind of foraging behaviour. The long-term dataset collected during the food-hoarding season can nonetheless provide useful insights into many aspects of the ecology of a species. Indeed, the data analysed shed light on important issues, such as age- and sex-related differences in foraging, intraspecific competition, predator responses and even climate change.

The results highlighted strong differences in food-hoarding behaviour between age classes and sexes (**I, II**) reflecting individual competing abilities (**III**) and their functional and numerical responses to fluctuating abundance of the main prey (**II**). Adult males showed a greater dietary plasticity than other age and sex classes, probably connected to their higher competitiveness and appearing in their lack of a numerical response to the main prey abundance. Yearling individuals and females are presumably lower-quality competitors, relying more on the abundance of the main prey; they therefore show high numerical responses (**II**), and are prone to irruptive migration in years of vole scarcity (Lehikoinen, Hokkanen, et al., 2011). Moreover, yearling individuals with adult neighbours likely incurred a high cost for competition, and thus showed lower food-hoarding success (**III**). Dietary differences between the sex classes would therefore influence the spatial distribution of pygmy owls at the landscape level (**III**). Individuals of the same sex avoided each other, suggesting high sex-specific competition.

Taken together, the results also suggest that predator responses to climate change may not be homogenous between sexes or age classes (**IV**). Due to their lower foraging plasticity (**II**), yearlings and females may be less able than adult males to adapt to global warming and increased precipitation, if this entails a change in main prey availability. Furthermore, with the arrival of autumn, female owls that bred in the area may face a difficult choice. They either have to abandon the study area (**II**; Lehikoinen, Hokkanen, et al., 2011) and risk not finding a wintering place with available food resources, or stay and risk paying the cost of having a rotted food store (**IV**).

Behaviour is a fundamental component of the individual response to environmental variation, and investigating age- and sex-related differences is therefore crucial for understanding how populations are influenced by environmental variations. In coping with environmental change, different behavioural personality types may be beneficial to the persistence and stability of a population. Differences among individuals ensure that at least some of them may be able to cope with the change (*insurance effect*; Wolf & Weissing, 2012). In contrast, age- and sex-specific behavioural differences mean that a whole age or sex category will be affected, with negative consequences for the whole population.

Predator-prey interactions rely on a delicate balance between prey and predator populations, and are affected by climate parameters (Bretagnolle & Terraube, 2019). The mismatches, regime changes and trophic cascades induced by global change can therefore have a negative impact at the level of individuals, populations (predator or prey abundances) and communities (e.g. Post et al., 1999; Mills et al., 2013). My findings, together with global predictions (Collins et al., 2013; Ruosteenoja et al., 2020), thus suggest that climate change has the potential to strongly impair the foraging behaviour and food intake of wintering predators, potentially impacting the entire boreal food web.

Acknowledgemets

Time flies and I can’t believe I managed to do everything. During the past four years my life changed entirely, I had to face many personal and work-related challenges, but it was also an amazing adventure and I loved every minute of it! So first of all I want to thank all the people that one way or another helped me achieve this wonderful goal: Grazie! Thanks! Kiitos! Merci! Gracias! Obrigada!

I’d like to thank my amazing team of supervisors (Erkki Korpimäki, Toni Laaksonen and Chiara Morosinotto) that managed to be there for me, but also to leave me the space to investigate and discover! Thank you Erkki for forging me as a scientist and researcher, since that first e-mail exchange when I was still looking for a PhD, to now. Thanks for making me discover Kauhava and its fascinating owls, for your enthusiasm and passion. Thank you Toni for listening to me, for all the statistical chats and advice you gave me, and for our chats when I needed to talk about “my future”. Thanks for always finding the time, even when you had a crazy schedule! Finally, thank you Chiara for your incredible presence and just for “being there” when I needed you, from discussing complicated science and statistical analysis during full-on migraine attack or simply chatting about other important things in life, such as the recipe of “glossy peppers”. And just to remind you, I’m still waiting for mail delivery of the lasagne with the little worms that say “ciao”! Thanks also for the great times during conferences!

I’m extremely grateful to my opponent Professor Alexandre Roulin for agreeing to act as my opponent during the public defence, I’m sure it will be an interesting discussion! My gratitude also goes to Professor Ryan Norris and Docent Hannu Pietiäinen for their work to pre-examine this thesis, I very much appreciated your comments.

Thanks to all the thesis co-authors that are not my supervisors: Elina Koivisto and Eric Le Tortorec. It was great to share science with you and thanks for teaching me a lot. Elina, thank you also for all the great tea breaks and lunches.

Thank you Martina Cadin, I appreciated very much your dedication to the project and your interested questions that lead to the wonderful cover of this thesis you made for me.

Thanks for the people that helped me in the field counting voles or enjoying the amazing nature that Kauhava can hide. Hope I can share some trips in the field with you again. A particular thanks to Jorma, for all the chats about birds and for helping me with the bird ringing and all the paperwork in Finnish!

In these past few years I also had a lot of fun outside of work! Thanks to all the incredible friends that I met during this journey, thanks for the Friday (plus Wednesday) Beers and the 21th Century Peggy group: Aino, Ana, Antoine, Barbara, Carly, Chiara, Christie, Daniele, Elie, Giovanna, Glenda, Ian, Jasper, Jennie, Julien, Katrine, Kinga, Luca, Luca, Maria, Mario, Martin, Michael, Nina, Océane, Pablo, Pere, Robin, Sandra, Simon, Sophie, Tiia, Tom, Vérane. Thanks for all the nice moments, the trips, the adventures, the saunas, the distractions, the chats and the parties. I learned so much from you all, and I had quite some fun hanging out with you guys, I'm happy to have friends all over the world thanks to you! Thank you to the Biology people and to the second floor in particular! Arriving early and exchanging a "good morning" and some chats with Tapio and Timo was a nice way to start the day. Thanks to Hanna for introducing me to climbing, it took away a good part of the stress related to the thesis, and to you and Kalle for the mushrooms and apple parties. Thank you so much Aino for being a great climbing partner and office-mate, and an even greater friend!

And now to the friends in Italy… Thank you Annesa for being the best friend one could ever hope to have and being always there for me despite the distance. Thank you Ilenia for your amazing friendship and for sharing the love for nature, since the first thesis together! Thank you Alberto for your friendships, our talks every time I come back and for the sand martins. Andrea, I want to thank you for always pushing me in believing in myself and not give into the impostor syndrome too much, your friendship has been a constant source of strength. Thank you also to the whole Gioie&Disagi group (Andrea, Enrico, Gaia, Giacomo, Giovanni, Irene, Mara, Marco, Stefano e Clara). Thank you Enrico and Dan for being the best bachelor and master supervisors one could hope for and helping me get here.

And last but not least, a huge thank you to my family for always supporting me in this crazy choice to study birds. First of all, a gigantic hearth-felt thank you to my grandma, who passed away a couple of months before my defence and to whom this thesis is dedicated. I remember that I had just started my master and I wanted to go to a conference, you were interested, asked me many questions and then provided me with my very first "travel grant". I have many other amazing memories to thank you for. Grazie di aver sempre creduto in me. A huge thank you to mamma and papà for everything you gave me and your support, and to my brother Pietro. Thanks also to Dora for being the best little sister a big sister can hope for. Danke Alexandra for the great chats about the academic world and for being such a good friend. Obrigada Limao. An enormous Grazie to all my family!

Finally, a gigantic thank you to all the pygmy owls for being such a great study species! I hope I can study you again in the future!

Turku, October 2020
Giulia Masoero

List of References

Abrams, P.A. (2000). The evolution of predator-prey interactions: Theory and evidence. *Annual Review of Ecology and Systematics*, **31**: 1, 79–105.

Baddeley, A., Rubak, E. & Turner, R. (2015). *Spatial Point Patterns: Methodology and Applications with R*. London, UK: Chapman and Hall/CRC Press.

Barbaro, L., Blache, S., Trochard, G., Arlaud, C., de Lacoste, N. & Kayser, Y. (2016). Hierarchical habitat selection by Eurasian pygmy owls *Glaucidium passerinum* in old-growth forests of the southern French Prealps. *Journal of Ornithology*, **157**: 1, 333–342.

Bårdsen, B.-J.J. & Tveraa, T. (2012). Density-dependence vs. density-independence - linking reproductive allocation to population abundance and vegetation greenness. *Journal of Animal Ecology*, **81**: 2, 364–376.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. R package v. 1.1-15. *Journal of Statistical Software*, **67**: 1, 1–48.

Bolker, B., Skaug, H., Magnusson, A. & Nielsen, A. (2012). Getting started with the glmmADMB package. *R package ver. 2.0–8*, 12.

Both, C. (1998). Experimental evidence for density dependence of reproduction in great tits. *Journal of Animal Ecology*, **67**: 4, 667–674.

Both, C. (2010). Food availability, mistiming, and climatic change. In A. P. Møller, W. Fiedler, & P. Berthold, eds. *Effects of Climate Change on Birds*. Oxford, UK, UK: Oxford University Press.

Bretagnolle, V. & Terraube, J. (2019). Predator-prey interactions and climate change. In P. O. Dunn & A. P. Møller, eds. *Effects of Climate Change on Birds*. Oxford, UK: Oxford University Press: 199–220.

Brodin, A. & Clark, C.W. (2007). Energy storage and expenditure. In D. W. Stephens, J. S. Brown, & R. C. Ydenberg, eds. *Foraging. Behavior and Ecology*. The University of Chicago Press: 221–269.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, **85**: 7, 1771–1789.

Brunsdon, C. & Chen, H. (2014). GISTools: Some further GIS capabilities for R.

Byholm, P., Burgas, D., Virtanen, T. & Valkama, J. (2012). Competitive exclusion within the predator community influences the distribution of a threatened prey species. *Ecology*, **93**: 8, 1802–1808.

Charnov, E.L., Orians, G.H. & Hyatt, K. (1976). Ecological Implications of Resource Depression. *The American Naturalist*, **110**: 972, 247–259.

Clarke, J., Manly, B., Kerry, K., Gardner, H., Franchi, E., Corsolini, S. & Focardi, S. (1998). Sex differences in Adélie penguin foraging strategies. *Polar Biology*, **20**: 4, 248–258.

Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W.J., Johns, T., Krinner, G., Shongwe, M., Tebaldi, C., Weaver, A.J. & Wehner, M. (2013). Long-term Climate Change: Projections, Commitments and Irreversibility. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley, eds. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

Côté, M., Ibarzabal, J., St-Laurent, M.-H., Ferron, J. & Gagnon, R. (2007). Age-dependent response of migrant and resident *Aegolius* owl species to small rodent population fluctuations in the Eastern Canadian boreal forest. *Journal of Raptor Research*, **41**: 1, 16–25.

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. (2001). Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, **292**: 5521, 1528–1531.

Curio, E. (1983). Why de young birds reproduce less well? *Ibis*, **125**: 3, 400–404.

Daunt, F., Wanless, S., Harris, M.P. & Monaghan, P. (1999). Experimental evidence that age-specific reproductive success is independent of environmental effects. *Proceedings of the Royal Society B: Biological Sciences*, **266**: 1427, 1489–1493.

Daunt, F., Wanless, S., Harris, M.P., Money, L. & Monaghan, P. (2007). Older and wiser: Improvements in breeding success are linked to better foraging performance in European shags. *Functional Ecology*, **21**: 3, 561–567.

Dempster, J.P. (1975). *Animal population ecology*. Academic Press.

Dhondt, A.A. (2012). *Interspecific Competition in Birds*. 1st ed. Oxford University Press.

Dunn, P.O. & Møller, A.P. eds. (2019). *Effects of climate change on birds*. Second. Oxford University Press.

Earhart, C.M. & Johnson, N.K. (1970). Size dimorphism and food habits of North American owls. *The Condor*, **72**, 251–264.

Ekman, J. (1986). Tree use and predator vulnerability of wintering passerines. *Ornis Scandinavica*, **17**: 3, 261–267.

Elton, C. (1942). *Voles, mice and lemmings. Problems in population dynamics*. Oxford: Oxford University Press.

Enemar, A., Nilsson, L. & Sjostrand, B. (1984). The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland. A 20-year study. *Annales Zoologici Fennici*, **21**: 3, 321–338.

Forslund, P. & Pärt, T. (1995). Age and reproduction in birds - hypotheses and tests. *Trends in Ecology & Evolution*, **10**: 9, 374–378.

Fowler, C.W. (1981). Density Dependence as Related to Life History Strategy. *Ecology*, **62**: 3, 602–610.

Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu. Rev. Physiol*, **66**, 239–74.

Gibbons, J.W. & Andrews, K.M. (2004). PIT Tagging: Simple Technology at Its Best. *BioScience*, **54**: 5, 447.

Gray, C.M. & Hamer, K.C. (2001). Food-provisioning behaviour of male and female Manx shearwaters, Puffinus puffinus. *Animal Behaviour*, **62**: 1, 117–121.

Hakkarainen, H. & Korpimäki, E. (1991). Reversed sexual size dimorphism in Tengmalm's owl: is small male size adaptive? *Oikos*, **61**, 337–346.

Hakkarainen, H., Mykrä, S., Kurki, S., Korpimäki, E., Nikula, A. & Koivunen, V. (2003). Habitat composition as a determinant of reproductive success of Tengmalm's owls under fluctuating food conditions. *Oikos*, **100**: 1, 162–171.

Halonen, M., Mappes, T., Meri, T. & Suhonen, J. (2007). Influence of snow cover on food hoarding in pygmy owls *Glaucidium passerinum*. *Ornis Fennica*, **84**: 3, 105–111.

Hirons, G.J.M. (1985). The importance of body reserves for successful reproduction in the Tawny owl (*Strix aluco*). *Journal of Zoology*, **1**: 1, 1–20.

Holt, R.D. & Kimbrell, T. (2007). Foraging and Population Dynamics. In D. W. Stephens, J. S. Brown, & R. C. Ydenberg, eds. *Foraging. Behavior and Ecology*. Chicago: The University of Chicago Press.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., Van Der Linden, P.J., Dai, X., Maskell, K. & Johnson, C.A. (2001). *Climate Change 2001: The Scientific Basis*. Cambridge, UK, UK: Cambridge University Press.

Huitu, O., Norrdahl, K. & Korpimäki, E. (2003). Landscape effects on temporal and spatial properties of vole population fluctuations. *Oecologia*, **135**: 2, 209–220.

IPCC. (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC. Core Writing Team, R. K. Pachauri, & L. A. Meyer, eds. Geneva, Switzerland, Switzerland.

Ishikawa, K. & Watanuki, Y. (2002). Sex and individual differences in foraging behavior of Japanese cormorants in years of different prey availability. *Journal of Ethology*, **20**: 1, 49–54.

Källander, H. & Smith, H.G. (1990). Food storing in birds: an evolutionary perspective. In D. M. Power, ed. *Current Ornithology*. New York: Plenum Press: 147–207.

Kellomäki, E. (1977). Food of the pygmy owl *Glaucidium passerinum* in the breeding season. *Ornis Fennica*, **54**, 1–29.

Keynan, O. & Yosef, R. (2010). Temporal changes and sexual differences of impaling behavior in Southern grey shrike (*Lanius meridionalis*). *Behavioural Processes*, **85**: 1, 47–51.

Koenig, W.D. & Knops, J.M.H. (2000). Patterns of annual seed production by Northern Hemisphere trees: A global perspective. *American Naturalist*, **155**: 1, 59–69.

Koenig, W.D. & Knops, J.M.H. (1998). Scale of mast-seeding and tree-ring growth [5]. *Nature*, **396**: 6708, 225–226.

Korpimäki, E. (1987a). Breeding performance of Tengmalm's owl Aegolius funereus: effects of supplementary feeding in a peak vole year. *Ibis*, **131**: 1, 51–56.

Korpimäki, E. (1987b). Dietary shifts, niche relationships and reproductive output of coexisting kestrels and long-eared owls. *Oecologia*, **74**: 2, 277–285.

Korpimäki, E. (1992). Fluctuating food abundance cetermines the lifetime reproductive success of male Tengmalm's owls. *Journal of Animal Ecology*, **61**: 1, 103–111.

Korpimäki, E. (1987c). Prey caching of breeding Tengmalm's owls *Aegolius funereus* as a buffer against temporary food shortage. *Ibis*, **129**: April, 499–510.

Korpimäki, E. & Hakkarainen, H. (1991). Fluctuating food supply affects the clutch size of Tengmalm's owl independent of laying date. *Oecologia*, **85**: 4, 543–552.

Korpimäki, E. & Hakkarainen, H. (2012). *The boreal owl: ecology, behaviour, and conservation of a forest-dwelling predator*. Cambridge: Cambridge University Press.

Korpimäki, E. & Norrdahl, K. (1991). Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. *Ecology*, **72**: 3, 814–826.

Korpimäki, E., Norrdahl, K., Huitu, O. & Klemola, T. (2005). Predator-induced synchrony in population oscillations of coexisting small mammal species. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 193–202.

Korpimäki, E., Norrdahl, K. & Korpimaki, E. (1989). Predation of Tengmalm's Owls: Numerical Responses, Functional Responses and Dampening Impact on Population Fluctuations of Microtines. *Oikos*, **54**: 2, 154.

Korpimäki, E., Norrdahl, K. & Rinta-Jaskari, T. (1991). Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? *Oecologia*, **88**: 4, 552–561.

Krebs, C.J. & Myers, J.H. (1978). Population cycles in small mammals. *Advances in Ecological Research*, **8**, 267–399.

Krüger, O. (2005). The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. *Evolutionary Ecology*, **19**: 5, 467–486.

Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2016). lmerTest: Tests in linear mixed rffects models.

Laaksonen, T., Korpimäki, E. & Hakkarainen, H. (2002). Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's owls. *Journal of Animal Ecology*, **71**: 71, 23–31.

Lack, D. (1968). Bird migration and natural selection. *Oikos*, **19**: 1, 1–9.

Lack, D. (1947). The significance of clutch-size. *Ibis*, **89**: 2, 302–352.

Lagerström, M. & Syrjänen, J. (1990). Varpuspöllön iän määrittäminen (Summary: Ageing pygmy owls). *Lintumies*, **25**, 291–194.

Lee, Y.-F. & Severinghaus, L.L. (2004). Sexual and seasonal differences in the diet on Lanyu scops owls based on fecal analysis. *Journal of Wildlife Management*, **68**: 2, 299–306.

Lehikoinen, A., Hokkanen, T. & Lokki, H. (2011). Young and female-biased irruptions in pygmy owls *Glaucidium passerinum* in southern Finland. *Journal of Avian Biology*, **42**: 6, 564–569.

Lehikoinen, A., Ranta, E., Pietiäinen, H., Byholm, P., Saurola, P., Valkama, J., Huitu, O., Henttonen, H. & Korpimäki, E. (2011). The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. *Oecologia*, **165**: 2, 349–355.

Lenth, R. V. (2016). Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software*, **69**: 1, 1–33.

Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S., Hamer, K.C., Dall–Antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S. & Hamer, K.C. (2002). Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society B: Biological Sciences*, **269**: 1501, 1687–1693.

Lindström, Å., Enemar, A., Andersson, G., Proschwitz, T. von, Nyholm, N.E.I., Von Proschwitz, T. & Nyholm, N.E.I. (2005). Density-dependent reproductive output in relation to a drastically varying food supply: Getting the density measure right. *Oikos*, **110**: 1, 155–163.

Lundberg, A. (1986). Adaptive advantages of reversed sexual size dimorphism in European owls. *Ornis Scandinavica*, **17**: 2, 133–140.

Marchetti, K. & Price, T. (1989). Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biological Reviews*, **64**: 1, 51–70.

Martin, T.E. (1995). Avian Life-History Evolution in Relation to Nest Sites, Nest Predation, and Food.

Martin, T.E. (1987). Food as a Limit on Breeding Birds: A Life-History Perspective. *Annual Review of Ecology and Systematics*, **18**: 1987, 453–487.

Massemin, S., Korpimäki, E. & Wiehn, J. (2000). Reversed sexual size dimorphism in raptors: evaluation of the hypothesis in kestrels breeding in a temporally changing environment. *Oecologia*, **124**, 26–32.

Matthysen, E. (2005). Density-dependent dispersal in birds and mammals. *Ecography*, **28**: 3, 403–416.

Mikkola, H. (1983). *Owls of Europe*. T. and A. D. Poyser.

Mills, L.S., Zimova, M., Oyler, J., Running, S., Abatzoglou, J.T. & Lukacs, P.M. (2013). Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proceedings of the National Academy of Sciences of the United States of America*, **110**: 18, 7360–7365.

Mills, R., Taylor, G.K. & Hemelrijk, C.K. (2019). Sexual size dimorphism, prey morphology and catch success in relation to flight mechanics in the peregrine falcon: a simulation study. *Journal of Avian Biology*, **50**: 3, 1–14.

Møller, A.P., Fielder, W. & Berthold, P. eds. (2010). *Effects of Climate Change on Birds*. Second. Oxford, UK, UK: Oxford University Press.

Morosinotto, C., Thomson, R.L. & Korpimäki, E. (2010). Habitat selection as an antipredator behaviour in a multi-predator landscape: All enemies are not equal. *Journal of Animal Ecology*, **79**: 2, 327–333.

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. *Ecologyical Monographs*, **87**: 1, 4–20.

Morris, D. (1962). The behaviour of the green acouchi (Myoproctapratti) with special reference to scatter hoarding. *Journal of Zoology*, **139**: 4, 701–732.

Morris, R.F., Cheshire, W.F., Miller, C.A. & Mott, D.G. (1958). The Numerical Response of Avian and Mammalian Predators during a Gradation of the Spruce Budworm. *Ecology*, **39**: 3, 487–494.

Mueller, H.C. (1986). The Evolution of Reversed Sexual Dimorphism in Owls: An Empirical Analysis of Possible Selective Factors. *The Wilson Bulletin*, **98**: 3, 387–406.

Murdoch, W.W. (1994). Population Regulation in Theory and Practice. *Ecology*, **75**: 2, 271–287.

Murray, D.L. & Sandercock, B.K. eds. (2020). *Population ecology in practice*. 1st ed. Wiley-Blackwell.

Newton, I. (2006). Advances in the study of irruptive migration. *Ardea*, **94**: 3, 433–460.

Newton, I. (2013). *Bird populations*. London: William Collins.

Newton, I. (2002). Population ecology in Holarctic owls. In I. Newton, R. Kavanagh, J. Olsen, & I. Taylor, eds. *Ecology and conservation of owls*. Collingwood, VIC: CSIRO publishing: 3–29.

Nilsen, E.B., Linnell, J.D.C., Odden, J. & Andersen, R. (2009). Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. *Journal of Animal Ecology*, **78**: 4, 741–751.

O'Donoghue, M., Boutin, S., Krebs, C.J. & Hofer, E.J. (1997). Numerical responses of coyotes and lynx to the snowshoe hare cycle. *Oikos*, **82**: 1, 169–183.

O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L. & Hofer, E.J. (1998). Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology*, **79**: 4, 1193–1208.

Oaten, A. & Murdoch, W.W. (1975). Functional response and stability in predator-prey systems. *The American Naturalist*, **109**, 289–298.

Orians, G.H. (1969). Age and hunting success in the brown pelican (*Pelecanus occidentalis*). *Animal Behavior*, **17**: 1, 6–319.

Parajulee, M.N., Phillips, T.W. & Hogg, D.B. (1994). Functional response of Lyctocoris campestris (F.) adults: Effects of predator sex, prey species, and experimental habitat. *Biological Control*, **4**: 1, 80–87.

Pearce-Higgins, J.W. & Green, R.E. (2014). *Birds and climate change: Impacts and conservation responses*. Cambridge, UK: Cambridge University Press.

Penteriani, V., Rutz, C. & Kenward, R. (2013). Hunting behaviour and breeding performance of northern goshawks *Accipiter gentilis*, in relation to resource availability, sex, age and morphology. *Naturwissenschaften*, **100**: 10, 935–942.

Peters, R.H. (1983). *The ecological implications of body size*. Cambridge University Press.

Post, E., Peterson, R.O., Stenseth, N.C. & McLaren, B.E. (1999). Ecosystem consequences of wolf behavioral response to climate. *Nature*, **401**: 6756, 905–907.

R Core Team. (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Reynolds, R.T. (1972). Sexual Dimorphism in Accipiter Hawks: A New Hypothesis. *The Condor*, **74**: 2, 191–197.

Reznick, D., Nunney, L. & Tessier, A. (2000). Big houses, big cars, superfleas and the costs of reproduction. *Trends in Ecology and Evolution*, **15**: 10, 421–425.

Ritchie, E.G. & Johnson, C.N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**: 9, 982–998.

Roberts, R.C. (1979). The Evolution of Avian Food-Storing Behavior. *The American Naturalist*, **114**: 3, 418–438.

Rose, L.M. (1994). Sex differences in diet and foraging behavior in white-faced capuchins (Cebus capucinus). *International Journal of Primatology*, **15**: 1, 95–114.

Ruosteenoja, K., Markkanen, T. & Räisänen, J. (2020). Thermal seasons in northern Europe in projected future climate. *International Journal of Climatology*, joc.6466.

Ruosteenoja, K., Räisänen, J. & Pirinen, P. (2011). Projected changes in thermal seasons and the growing season in Finland. *International Journal of Climatology*, **31**: 10, 1473–1487.

Rutz, C., Whittingham, M.J. & Newton, I. (2006). Age-dependent diet choice in an avian top predator. *Proceedings of the Royal Society B: Biological Sciences*, **273**: 1586, 579–586.

Saether, B.-E., Engen, Steinar, Matthysen, E., May, R.M., Pianka, E.R., Promislow, D.E.L., Harvey, P.H., Sæther, B.-E., Bakke, Ø., Southwood, T.R.E., Fowler, C.W., ___., Gilpin, M.E., Ayala, F.J., Sæther, B.-E., Diserud, O., Engen, S., Fowler, C.W., Engen, S., Bakke, Ø., Islam, A., Aanes, S., Engen, S., Sæther, B.-E., Willebrand, T., Marcström, V., Ariño, A., Pimm, S.L., Coulson, T., Bjørnstad, O.N. & Grenfell, B.T. (2002). Demographic characteristics and population dynamical patterns of solitary birds. *Science (New York, N.Y.)*, **295**: 5562, 2070–3.

Salamolard, M., Butet, A., Leroux, A. & Bretagnolle, V. (2000). Reponse of an avian predator to variation in prey density at a temperate latitude. *Ecology*, **81**: 9, 2428–2441.

Sasvári, L., Hegyi, Z., Csörgõ, T. & Hahn, I. (2000). Age-dependent diet change, parental care and reproductive cost in tawny owls *Strix aluco*. *Acta Oecologica*, **21**: 4–5, 267–275.

Schönn, S. (1980). *Der Sperlingskauz*. Die Neue Brehm-Bücherei.

Schulenburg, J. & Wiesner, J. (1986). Zur Winternahrung des Sperlinkgskauzes (*Glaucidium passerinum*) in zwei unterschiedlichen Gebieten der DDR. *Acta ornithoecologica*, **1**: 2, 167–183.

Sechley, T.H., Strickland, D. & Norris, D.R. (2015). Linking the availability of cached food to climate change: an experimental test of the hoard-rot hypothesis. *Canadian Journal of Zoology*, **93**: 6, 411–419.

Sergio, F., Blas, J., Forero, M.G., Donázar, J.A. & Hiraldo, F. (2007). Size-Related Advantages for Reproduction in a Slightly Dimorphic Raptor: Opposite Trends between the Sexes. *Ethology*, **113**: 12, 1141–1150.

Sih, A., Englund, G. & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution*, **13**: 9, 350–355.

Smith, C.C. & Reichman, O.J. (1984). The Evolution of Food Caching by Birds and Mammals. *Annual Review of Ecology and Systematics*, **15**: 1984, 329–351.

Snyder, N.F.R. & Wiley, J.W. (1976). Sexual Size Dimorphism in Hawks and Owls of North America. *Ornithological Monographs*, : 20, i–96.

Solheim, R. (1984a). Breeding biology of the pygmy owl Glaucidium passerinum in two biogeographical zones in southeastern Norway. *Ann. Zool. Fennici*, **21**, 295–300.

Solheim, R. (1984b). Caching behaviour, prey choice and surplus killing by pygmy owls *Glaucidium passerinum* during winter, a functional response of a generalist predator. *Annales Zoologici Fennici*, **21**, 301–308.

Solomon, M.E. (1949). The natural control of animal populations. *The Journal of Animal Ecology*, **18**: 1, 1–35.

Start, D. & Gilbert, B. (2017). Predator personality structures prey communities and trophic cascades. *Ecology Letters*, **20**: 3, 366–374.

Stephens, D.W., Brown, J.S. & Ydenberg, R.C. eds. (2007). *Foraging. Behaviour and ecology.* The University of Chicago Press.

Strom, H., Sonerud, G.A., Strøm, H. & Sonerud, G.A. (2001). Home range and habitat selection in the Pygmy Owl Glaucidium passerinum. *Ornis Fennica*, **78**: 4, 145–158.

Suhonen, J. (1993). Predation risk influences the use of foraging sites by tits. *Ecology*, **74**: 4, 1197–1203.

Suhonen, J., Halonen, M., Mappes, T. & Korpimäki, E. (2007). Interspecific competition limits larders of pygmy owls *Glaucidium passerinum*. *Journal of Avian Biology*, **38**: 5, 630–634.

Sutton, A.O., Strickland, D., Freeman, N.E., Newman, A.E.M.M., Norris, D.R. & Sutton, A.O. (2019). Autumn freeze-thaw events carry over to depress late-winter reproductive performance in Canada jays. *Royal Society Open Science*, **6**: 4.

Temeles, E.J. (1985). Sexual size dimorphism of bird-eating hawks: The effect of prey vulnerability. *The American Naturalist*, **125**: 4, 485–499.

Terraube, J., Villers, A., Poudré, L., Varjonen, R. & Korpimäki, E. (2017). Increased autumn rainfall disrupts predator-prey interactions in fragmented boreal forests. *Global Change Biology*, **23**: 4, 1361–1373.

Vermeij, G.J. (1994). The evolutionary interaction among species: Selection, escalation, and coevolution. *Annual Review of Ecology and Systematics*, **25**: 1, 219–236.

Village, A. (1985). Turnover, age and sex-ratios of kestrels (Falco tinnunculus) in South Scotland. *Journal of Zoology*, **206**, 175–189.

Vander Wall, S.B. (1990). Food Hoarding in Animals. *Chicago: University of Chicago Press.*, **250**: xii, 1602–1603.

Vander Wall, S.B., Briggs, J.S., Jenkins, S.H., Kuhn, K.M., Thayer, T.C. & Beck, M.J. (2006). Do food-hoarding animals have a cache recovery advantage? Determining recovery of stored food. *Animal Behaviour*, **72**: 1, 189–197.

Winnie, J. & Creel, S. (2017). The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. *Food Webs*, **12**, 88–94.

Wolf, M. & Weissing, F.J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology and Evolution*, **27**: 8, 452–461.

Wunderle, J.M. (1991). Age-specific foraging proficiency in birds D. M. Power, ed. *Current Ornithology*, **8**, 273–324.

Yosef, R. & Pinshow, B. (1989). Cache size in shrikes influences female mate choice and reproductive success. *The Auk*, **106**: 3, 418–421.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer

UNIVERSITY
OF TURKU

Painosalama Oy, Turku, Finland 2020

ISBN 978-951-29-8185-4 (PRINT)
ISBN 978-951-29-8186-1 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)