

Conspecific density drives sex-specific spatial wintertime distribution and hoarding behaviour of an avian predator

Elina Koivisto*†, Giulia Masoero†, Chiara Morosinotto, Eric Le Tortorec & Erkki Korpimäki

E. Koivisto, G. Masoero, C. Morosinotto, E. Korpimäki, Section of Ecology, Department of Biology, FI-20014 University of Turku, Finland

G. Masoero, Department of Biology, University of Ottawa, 30 Marie Curie, Ottawa, Canada & Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland

C. Morosinotto, Department of Biology, University of Padova, Via U. Bassi 58/B, 35131 Padova, Italy & National Biodiversity Future Center (NBFC), Piazza Marina 61, 90133 Palermo, Italy

E. Le Tortorec, Department of Biological and Environmental Sciences, University of Jyväskylä, PO Box 35, FI-40014 University of Jyväskylä, Finland

** Corresponding author's e-mail: elanko@utu.fi*

† These authors contributed equally

Received 15 August 2023, accepted 19 January 2024

Most studies on intraspecific competition, *i.e.*, competition among individuals of the same species, have been conducted during the breeding season. Yet, at northern latitudes, intraspecific competition is expected to be particularly strong under the harsh weather conditions of the non-breeding season with limited number of resources available per individual. We studied the food-hoarding behaviour of wintering Eurasian Pygmy Owls (*Glaucidium passerinum*) along with sex- and age-specific spatial distribution in relation to fluctuating main prey abundance (voles) and conspecific density using a 15-year dataset. In low vole abundance years, increasing conspecific density reduced the total prey number stored by an owl, suggesting high costs of exploitative competition. The distance between the stores of nearest neighbours was greater when both were females, suggesting that the spatial avoidance is driven by sex-specific competition. However, food stores of females had a larger amount of prey items, especially when the nearest neighbour was of the same sex. The number of stores hoarded by an owl increased with increasing conspecific densities. Distributing the prey items to multiple store-sites instead of one (shifting from larder-hoarding towards scatter-hoarding) can help to reduce the overall loss to potential pilfering when conspecific density is high. These results combined suggest that high conspecific density inflames sex-specific interference competition, rather than solely exploitative competition, and in turn drives the observed sex-specific spatial distribution. Adopting a sex-specific spatial distribution according to hoarding and aggressive behaviour can be a way to reduce the severity of intraspecific competition locally and could have cascading effects on the prey community.



1. Introduction

Competition, together with food abundance and predation risk, is one of the central drivers of animal behaviour, spatial distribution, and population dynamics (Sih *et al.* 1985, Gurevitch *et al.* 2000). High densities of competitors may lead to demographic or individual density-dependent effects, *i.e.*, causing a decrease in fitness components such as survival (Armstrong *et al.* 2002) or fecundity (Korpimäki 1987, Ferrer & Donazar 1996, Both 1998). Competition occurs among individuals exploiting the same resources belonging either to the same or different species (intraspecific or interspecific competition, respectively). Individuals within a species usually occupy highly similar niches, and thus competition is expected to be intense (Schoener 1974). Intraspecific competition is consequently often found to have a higher impact on fitness than interspecific competition (Carrete *et al.* 2006, Svanbäck *et al.* 2008, Morosinotto *et al.* 2017a).

When resources become a limiting factor, either due to a decrease in their availability or to a higher number of competing individuals, intraspecific competition gets more intense and may affect reproductive success (Morosinotto *et al.* 2017a), food consumption and somatic growth rate (Amundsen *et al.* 2007). In general, 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*; Miller 1967, Charnov *et al.* 1976, Schoener 1983, review in Dhondt 2012). It may also involve direct interactions, such as fighting, theft or ritualised combat, where some individuals aggressively interfere with the use of resources by other competitors (*interference competition*; Miller 1967, Schoener 1983, review in 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.

As competition is costly (*e.g.*, Abramsky *et al.* 2001, review in Dhondt 2012), animals have evolved ways to reduce the costs of competition and to minimize the risk of aggressive interactions (*e.g.*, Valeix *et al.* 2007, review in Dhondt 2012).

Among these strategies, there is the selection of the habitat or territory where to live, trying to avoid areas with a high density of competitors (Avgar *et al.* 2020) or with scarce resources, and the niche separation between age classes or sexes (*e.g.*, Svanbäck & Bolnick 2007). The difference in competitive abilities among individuals can affect their spatial distribution (ideal despotic distribution; Fretwell 1972), where highly territorial dominant individuals will first occupy the best unoccupied sites (ideal pre-emptive distribution; Pulliam & Danielson 1991), while inferior competitors will have to settle for less favourable habitats (*e.g.*, Ziv *et al.* 1993, Calsbeek & Sinervo 2002). Niche separation can rise from difference between age and sex classes in their respective competitive ability, as they often exhibit differences in foraging due to experience, skills, or life history strategy (Marchetti & Price 1989, Smith & Metcalfe 1994, Coulson *et al.* 2001, Ishikawa & Watanuki 2002, Field *et al.* 2007, Faegre *et al.* 2020, Masoero *et al.* 2020). This marked difference in experience and size leads to separation in prey selection. For example, many birds of prey show pronounced reversed sex-specific size dimorphism (*i.e.*, females are the larger sex; Massemin *et al.* 2000, Krüger 2005, Korpimäki & Hakkarainen 2012). Larger females are capable of hunting for larger-sized prey, whereas smaller males can be more efficient hunters in catching agile prey, like birds (Mills *et al.* 2019), especially in structurally complex environments such as forests (Hakkarainen & Korpimäki 1991, Pérez-Camacho *et al.* 2015, 2018).

A vast majority of studies on intraspecific competition in birds have been conducted during the breeding season, as direct effects on reproductive success are often of primary interest (*e.g.*, Dann & Norman 2006, Denac 2006, Garabedian *et al.* 2022). Yet, at northern latitudes, intraspecific competition is expected to be particularly strong under the harsh climatic conditions of the non-breeding season, which can lead to food limitation, significant source of mortality during wintertime (Taylor 1994, Hakkarainen *et al.* 2002, Reigert & Fuchs 2011), and to skewing of the adult sex ratio

by sex-biased mortality (Chang & Wiebe 2016). Here, we investigate the wintertime sex- and age-specific spatial distribution of a small avian predator, the Eurasian Pygmy Owl (*Glaucidium passerinum*; hereafter “Pygmy Owl”), and its impact on the food hoarding of individuals (terms “storing” and “caching” are also used hereafter) using 15 years of data on food-store composition and captured individuals collected in Finland. The main prey of Pygmy Owls are voles of the genera *Myodes* and *Microtus* (Kellomäki 1977, Halonen et al. 2007, Masoero et al. 2020), which in North Europe exhibit three-year high-amplitude population cycles (Korpimäki et al. 2005), resulting in pronounced among-year fluctuations in the abundance of main food for Pygmy Owls.

During the breeding season, Pygmy Owls were found to avoid breeding close to conspecifics, but this avoidance decreased when voles were abundant (Morosinotto et al. 2017a). In autumn and early winter, Pygmy Owls store prey in natural cavities and nest boxes (Solheim 1984a, Terraube et al. 2017, Masoero et al. 2018, 2020). This behaviour has probably evolved to reduce starvation risk during winter, when resources are scarce (Vander Wall 1990). Like many species of birds of prey, also Pygmy Owls present reversed sexual size dimorphism, with females being larger than males, and show both age- and sex-specific differences in prey use (Masoero et al. 2018, 2020). When comparing the food-storing behaviour between the sexes and age classes, females and yearlings hoarded stores with a greater number of prey items than males and adults respectively (Masoero et al. 2018), stored more small mammals and tended to store fewer birds under low food availability (Masoero et al. 2020).

Based on the previous knowledge on the density-dependent effects during the breeding season as well as the age- and sex-specific differences in hoarding behaviour, we expected that: 1) spatial distribution of Pygmy Owls will depend on age- and sex-specific hoarding strategies, as avoiding neighbours with similar hunting strategies reduces exploitative intraspecific competition, 2) owls will have more stores when conspecific density is high to decentralize stored prey items to avoid potential pilfering and interference competition, and 3) overall, high conspecific density, as well as the age and sex

spatial distribution, will modify hoarding success (number of stored prey), especially when voles are scarce.

2. Material and methods

2.1. The study system

The study area consists of ca. 1,000 km² of forests and agricultural lands in the Kauhava region, western Finland (63°N, 23°E), where ca. 300 sites with two nest boxes per forest site were provided for Pygmy Owls (a landscape map of the study area with nest-box sites in Fig. S1 of Morosinotto et al. 2017a). The proportion of coniferous forests is 66% and that of agricultural land 25% of the study area. The management of the forest lands has created a mosaic of clear-cut and sapling areas as well as different-aged forests where the main tree species are scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and in smaller proportions some deciduous trees (Hakkarainen et al. 2003, Morosinotto et al. 2017a, Korpimäki et al. 2020). For more details on the habitat structure and vegetation age classes please see Morosinotto et al. (2017a) and Baroni et al. (2021). The data for this study were collected from 2003 to 2017.

Pygmy Owls inhabit mature and old coniferous forests of Europe and Asia (Schönn 1980, Strøm & Sonerud 2001, Barbaro et al. 2016, Morosinotto et al. 2017a). Natural tree cavities or artificial nest boxes are used in spring for breeding and late autumn and winter for storing food (Solheim 1984a, 1984b, Morosinotto et al. 2017a, Terraube et al. 2017). In autumn, all the box-sites were inspected twice (once in late October to early November and once in late November to early December) to collect data on the food stores and on the Pygmy Owl individuals storing the food items (for further details on the study system, see Terraube et al. 2017, Masoero et al. 2018). The total number of fresh prey items in the two autumn visits was calculated and, to avoid double-counting, prey items in food stores were marked with tail-clipping (mammals) or toe-clipping (birds).

From 2003 to 2017, we collected data for a total of 1018 food stores, of which 643 had an identified food hoarder. On average, the annual

percentage (mean \pm SD) of food stores with an identified hoarder was $63.2 \pm 12.7\%$. Most owls (82%) at food stores were captured with nest-box traps (a replica of the box equipped with swing door) or with a telescopic fishing pole with a noose at the top, a capture commonly used with larger owl species (e.g., Forsman 1983, Bull 1990) and therefore safe for Pygmy Owls. Captured owls were ringed with an aluminium leg ring for individual identification, weighed, sexed, and aged, and wing and tail lengths were measured. The rest of the identities of hoarders (18%) were obtained using Passive Integrated Transponder (PIT) tags, a small electromagnetic microchip implanted subcutaneously when capturing the owls (Masoero *et al.* 2018). Data on encounters of individual owls were collected by placing the antenna of the reader around the entrance hole of the food-store box. The antenna and reader were set up when the food store was found but capturing the owl with the nest box trap failed. The antenna was then kept in place at least for two weeks or until the reader recorded the identity. As females are larger than males, sex was determined based on wing length, tail length, and body mass (as in Masoero *et al.* 2018). The age was estimated according to wing moult (Lagerström & Syrjänen 1990), and individuals were divided into two classes: individuals at their hatching year (1y = yearlings) and older individuals (Ad = adults).

The abundance of the main prey (bank voles *Myodes glareolus* and *Microtus* voles, the fieldvole *M. agrestis* and the sibling vole *M. rossiaemeridionalis*; Kellomäki 1977, Halonen *et al.* 2007, Masoero *et al.* 2020) was estimated by snap trapping twice a year (early May and mid-September). In two locations 14 km apart within the study area, 50–60 metal mouse snap-traps were set up to cover 0.5 to 0.6 ha and the four main habitat types; agricultural and abandoned fields, and forests dominated by spruce or pine (Korpimäki *et al.* 2005). Live trapping was not feasible due to methodological constraints (see also Ethical approval section). The traps (baited with mixed-grain bread) were placed in vole runways and checked daily for three days. The regional synchrony of vole population cycles and thus indices of small mammals extend up to 80 km (Huitu *et al.* 2003, Korpimäki *et al.* 2005),

therefore the validity of this index could be extended to the whole study area. The abundance of vole species in the study area fluctuates in three-year cycles with a 100–200-fold amplitude (see Korpimäki *et al.* 2005 for more details). To obtain an autumn vole abundance index for the analyses, the results from the three-night trapping sessions done in September for both the bank voles and *Microtus* voles (voles only) were pooled and standardised as the number of animals captured per 100 trap nights. For the analysis the continuous vole abundance data was changed into a categorical variable. To consider the actual abundance of main food resources in the current autumn, the variable was divided into three levels: “low” (0.1–3.0 animals captured per 100 trap nights), “intermediate” (3.1–12.0) and “high” (>12.0) abundance (Fig. 1a).

2.2. Owl density

Pygmy Owl density was calculated at a 6000 m radius around a single food store of a focal Pygmy Owl. If the individual had more than one food store, a convex hull, which formed the smallest area that included the buffers around the individual food stores and the area between them, was created. This convex hull reflected the area that an owl individual would have to fly across to move between nest-box sites. The results on a previous study on the same population shows that ca. three-fourths (299 owls out of 412) of the owls had only one store per storing season, whereas the rest had two to six food stores (Masoero *et al.* 2018). The value of 6000 m was chosen based on previous research since the home range size was estimated to be around 2.3 km² (range 0.4–6.0 km²; Strøm & Sonerud 2001). The average distance between two stores of the same individual is known to be 1.5 km and the maximum distance is 5.0 km (Masoero *et al.* 2018). Thus, the chosen 6000 m radius is likely to include all the food stores of an individual. The density values were computed using the function ‘density’ in the package spatstat (R package v. 1.59-0; Baddeley *et al.* 2015), which computes a kernel smoothed intensity function from a pattern of points. Mean density values within buffers and convex hulls were extracted using the function ‘extract’ in the package raster

(R package v. 2.5-8; Hijmans & van Etten 2012). The distance between an individual and its nearest neighbour during a particular year was calculated from the coordinates of the boxes using the function ‘gDistance’ in the package GIStools (R package v. 0.7-4; Brunsdon & Chen 2014).

2.3. Statistical analyses

To be able to detect whether distances between individuals depend on sex, age, and food abundance, we need to estimate the proportional deviance between observed and randomly simulated values and then build a Linear Mixed-effects Model (LMM). Observed values were then compared to randomly distributed owls. Given the owls present each year, we generated 10,000 simulated datasets by re-assigning the owls to different food-hoarding boxes and then checking the identity of the new nearest neighbour (NN) and its distance from the focal owl. Using the average of the simulated values for the NN distance (simulated distance), we calculated the proportional deviance of the observed values as $(obs-sim)/sim$. Using an LMM, we then investigated whether the proportional deviance of the distance between an owl and its NN was related to the vole abundance level (three levels: “low”, “intermediate”, “high”), to the ages (“1y–Ad”, “1y–1y”, “Ad–Ad”), and sexes (“F–M”, “F–F”, “M–M”) of the two neighbours. Year was used as a random factor to control for environmental conditions in a certain year.

We then tested the effects of competition on the number of food stores hoarded by an individual and the number of prey items stored (as proxies for hoarding success) using Generalised Linear Mixed-effects Models (GLMMs) with a Poisson family. As independent variables in both models, we considered the neighbouring owls’ density (continuous variable), and the categorical variables: vole abundance level, age (“1y” or “Ad”) and sex (“F” or “M”) of the hoarding owl and of its NN (to understand how characteristics of the NN can affect the hoarder). Continuous variables were standardised ($\mu=0$ and $\sigma^2=1$) using the scale function in R. The identity of the owl and year were used as random factors in the GLMMs to control for multiple stores from the same individual and for environmental conditions

in a certain year. We used the dredge function within the package MuMIn (Bartoń 2023) to apply model selection (model selection tables for the number of food stores hoarded by an individual and the number of prey items stored can be found in Supplementary materials S1 and S2, respectively). The optimal model was selected using Akaike Information Criterion corrected for small sample size (AICc) values. If the difference between the model with the lowest AICc and the second one was smaller than two, we decided to keep the most parsimonious model. We fixed vole index, age, and sex of the hoarder to be kept in all models since their significance for the food-hoarding Pygmy Owls is already known (Masoero *et al.* 2018). The three two-way interactions between neighbour density and vole abundance level, age of the hoarder and age of the NN and between sex of the hoarder and sex of its NN were also tested. All analyses were carried out using R v. 4.1.0 (R Core Team 2022), and all GLMMs were run using the package lme4 (Bates *et al.* 2015).

3. Results

3.1. Conspecific density

Variations in both the number of food-hoarding owls and in the conspecific density generally followed variation in vole abundance (Fig. 1). The number of food-hoarding owls varied from a minimum of 13 (2006) to a maximum of 60 (2011) during the 15 years of the study (Fig 1b) in the study area. Conspecific density in the 6000 m radius around the food stores of a focal individual was on average (\pm SD) 0.05 (\pm 0.03) and ranged between 0.002–0.150, varying among years (Fig 1c).

3.2. Distance to nearest neighbour

Concerning the spatial distribution of Pygmy Owls, we found that the proportional deviance between observed distance of food stores of NNs from the random distances (calculated as $(obs-sim)/sim$) was significantly different according to the sexes of the two NNs. In particular, the

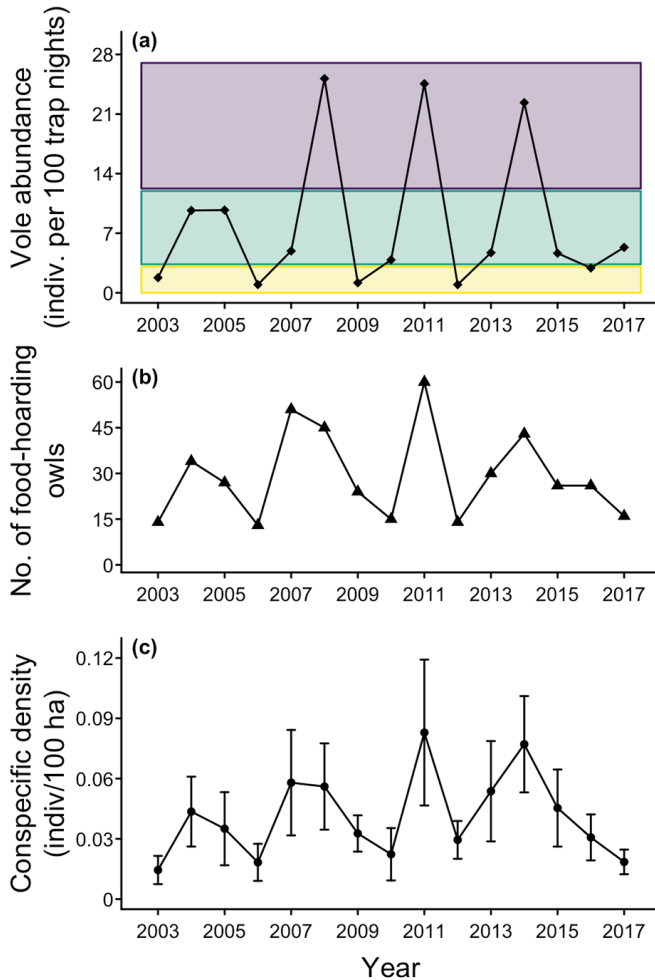


Fig. 1. Among-year variation in (a) autumn vole abundance (number of individuals captured per 100 trap nights), (b) number of food-hoarding individuals and (c) mean (and standard deviation) conspecific density in the 6000 m radius around the food stores of a focal individual in the study area during 2003–2017. In panel (a), the colours represent the subdivision of the vole abundance in 3 levels: low (0–3) in yellow, intermediate (3–12) in green, and high (>12) in purple.

distance between stores of neighbouring owls was similar to what simulated by random (values of proportional deviance ~ 0) if the two owls were both females (Fig. 2; mean linear distance \pm SD: 3.6 ± 2.3 km), whereas stores between male neighbours (2.8 ± 1.8 km) and different sex neighbours (2.7 ± 1.8 km) were closer than simulated by random (proportional deviance < 0) (Table 1, Fig. 2).

3.3. Number of stores per individual

The top model for the number of stores per individual included only a significant effect of conspecific density (see Supplementary materials

Table S1 for the model selection table). This means that the number of food stores hoarded by a focal individual increased with increasing density of surrounding Pygmy Owls (Table 2, Fig. 3), but was not affected by level of vole abundance, age, or sex of the hoarding individual.

3.4. Hoarding success

The top model for the total number of prey items stored by an owl (hoarding success) included all the variables and two of the tested two-way interactions (Table 3; see Supplementary materials Table S2). The interaction between conspecific density and level of vole abundance (Fig. 4a)

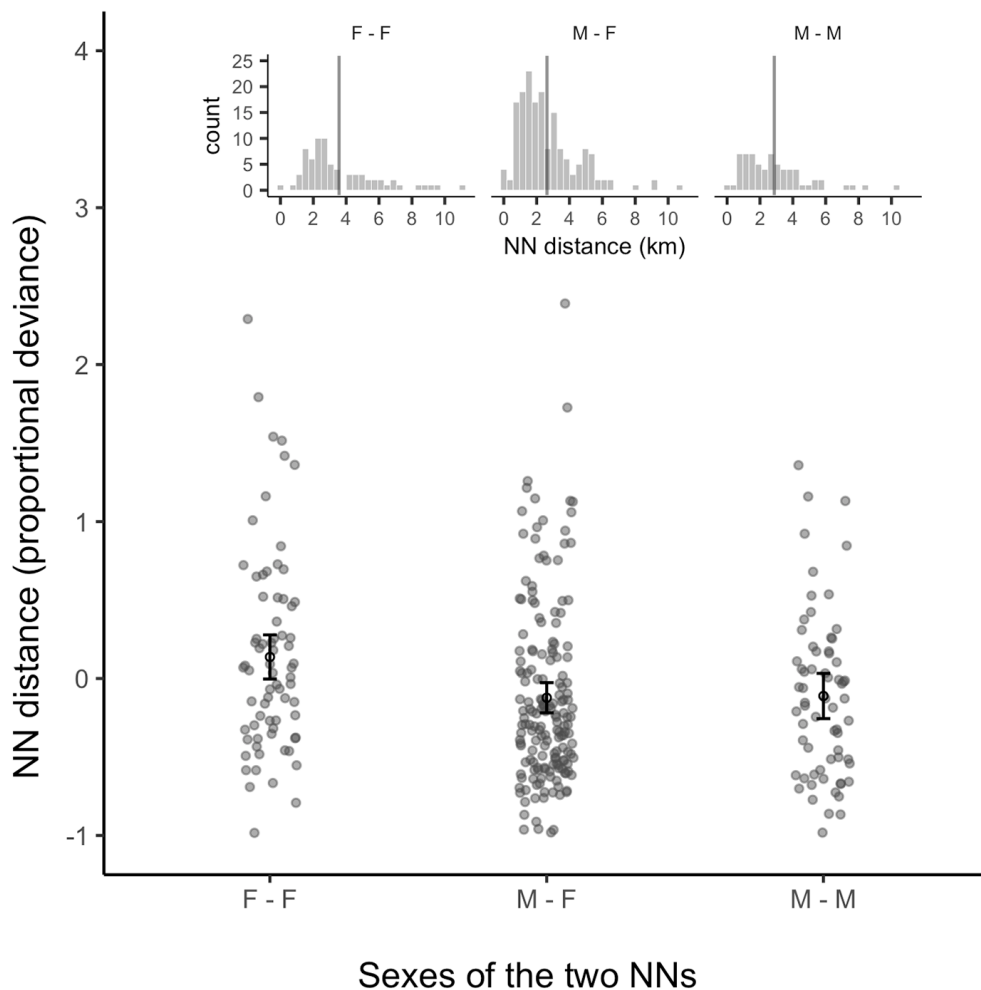


Fig. 2. Predicted values (and 95% CI) of the proportional deviance for the distance between nearest neighbours (NN) in relation to the sexes of the NNs (see Table 1). Observed values are represented with jittered semi-transparent dots, with darker colours meaning a higher number of observations. The histograms on top of the panel represent the distribution of the actual distances between NNs in km (light grey bars), with the mean value for each group represented with a dark grey vertical line. $N=295$ NNs.

indicates that when vole abundance is low, the increasing density of conspecifics is associated with a decreasing amount of food stored. In intermediate and high years of vole abundance, increasing density of conspecifics is associated with, respectively, either no relationship or increased number of food items stored (Table 3). The interaction between the age of the hoarder and the age of its NN was not significant and was not present in the best model. Yearlings showed a tendency to store more prey items than adults (Fig. 4b), and owls

with a yearling NN stored more prey items than owls with an adult NN (Fig. 4c). The interaction between the sex of the hoarder and the sex of the NN indicates that there were some significant differences between groups (Fig. 4d) that were tested using post-hoc Tukey tests. Female hoarders with a female NN hoarded more prey than females with a male NN ($z = -7.20$, $p < 0.0001$), or male hoarders independently of the sex of their NN (with female NN: $z = -4.60$, $p < 0.0001$; with male NN: $z = 5.27$, $p < 0.0001$).

Table 1. LMMs analysing the proportional deviation from random distances between the food stores of two nearest neighbours (NN) according to the level of vole abundance, age, and sex of the NNs. All models included ‘year’ as a random factor. Significant variables ($p < 0.05$) are shown in bold. N=295 NNs.

Explanatory		Estimate ± SE	Chisq	p
Intercept		0.100 ± 0.106		
Vole abundance			1.05	0.5903
	Low	0 ± 0		
	Intermediate	0.056 ± 0.095		
	High	−0.018 ± 0.103	0.29	0.8658
NNs - ages				
	Ad – Ad	0 ± 0	10.64	0.0049
	1y – Ad	−0.003 ± 0.086		
	1y – 1y	0.079 ± 0.093		
NNs - sexes				
	F – F	0 ± 0		
	M – F	−0.260 ± 0.082		
	M – M	−0.249 ± 0.101		

Table 2. GLMMs on the total number of food stores per individual in relation to conspecific density at 6000 m. Explanatory variables also included vole abundance level (Low, Intermediate, High), age (1y = yearlings and Ad = Adults) and sex (M = males and F = females) of the hoarder. All models included year and individual identity of the owl as random factors. Significant variables ($p < 0.05$) are shown in bold. N=428 cases for 327 individuals in 15 years.

Explanatory		Estimate ± SE	Chisq	p
Intercept		0.471 ± 0.119		
Conspecific density		0.181 ± 0.048	14.09	0.0002
Vole abundance	Low	0 ± 0	1.43	0.4883
	Intermediate	−0.091 ± 0.124		
	High	−0.181 ± 0.152		
Hoarder age	Ad	0 ± 0	0.07	0.7894
	1y	0.022 ± 0.084		
Hoarder sex	F	0 ± 0	0	0.9999
	M	0 ± 0.081		

4. Discussion

We expected Pygmy Owls to avoid neighbours with similar hunting strategies (same sex or same age) to reduce exploitative intraspecific competition. In accordance with this expectation, the observed distance between stores of nearest neighbours was larger when the neighbours were both females. According to proportional deviance, male-male and male-female pairs seemed to be closer to each other than expected by random. Despite this spatial distribution, food stores were mostly larger when the hoarder was a female and especially so when the nearest neighbour was also female. In contrast, we found no age-specific

spatial distribution but having yearlings as neighbours led to overall higher hoarding success, suggesting a benefit from having neighbours with modest hunting experience. The number of prey items stored by an owl depended on vole abundance as well as conspecific density, suggesting high costs of exploitative competition when food is scarce. However, in high years of vole abundance, increasing conspecific density resulted in a larger number of stored prey items, probably indicating an overall positive effect of food abundance on population densities. As expected, the number of stores hoarded by an owl increased with increasing conspecific densities to decentralize stored prey items to avoid potential

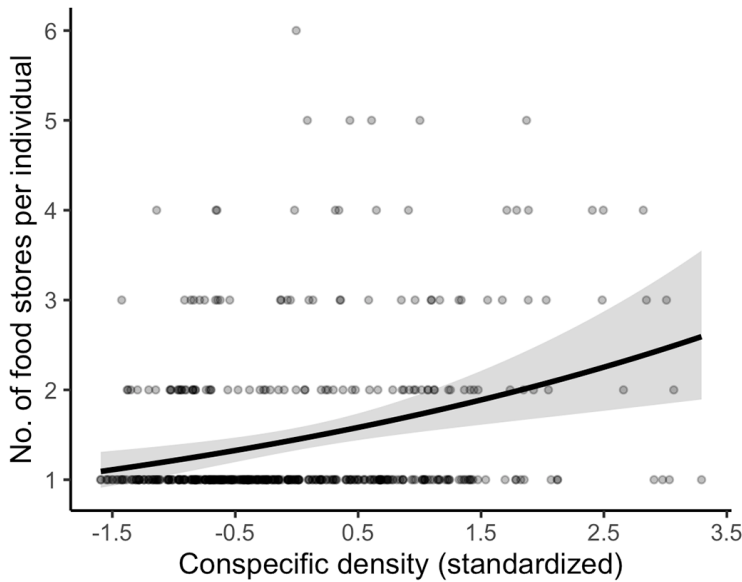


Fig. 3. Predicted values (and 95% CI) of the total number of food stores per individual in relation to conspecific density in a 6000 m radius based on the models in Table 2. Observed values are represented with semi-transparent dots, with darker colours meaning a higher number of observations.

Table 3. GLMMs analysing the variation in hoarding success (as total number of prey items stored by one individual) in relation to conspecific density in a 6000 m radius from its store(s), vole abundance level (Low, Intermediate, High), age (1y = yearlings and Ad = adults) and sex (M = males and F = females) of the hoarder and of the nearest neighbour (NN). The symbol "X" denotes an interaction. All models included year and owl identity as random factors. Significant variables ($p < 0.05$) are shown in bold. $N = 428$ cases for 327 individuals in 15 years.

Explanatory		Estimate \pm SE	Chisq	p
Intercept		1.694 \pm 0.246		
Conspecific density X Vole abundance	Low	0 \pm 0	53.22	<0.0001
	Intermediate	1.101 \pm 0.168		
	High	1.225 \pm 0.169		
Conspecific density		-1.041 \pm 0.178	14.64	0.0001
Vole abundance	Low	0 \pm 0	5.69	0.0581
	Intermediate	1.443 \pm 0.272		
	High	1.593 \pm 0.334		
Hoarder age	1yr	0.084 \pm 0.045	3.52	0.0605
	Ad	0 \pm 0		
NN age	1y	0.237 \pm 0.050	22.16	<0.0001
	Ad	0 \pm 0		
Hoarder sex X NN sex	M–M	0.430 \pm 0.093	21.35	<0.0001
	others	0 \pm 0		
Hoarder sex	M	-0.526 \pm 0.114	8.81	0.0030
	F	0 \pm 0		
NN sex	M	-0.521 \pm 0.072	33.05	<0.0001
	F	0 \pm 0		

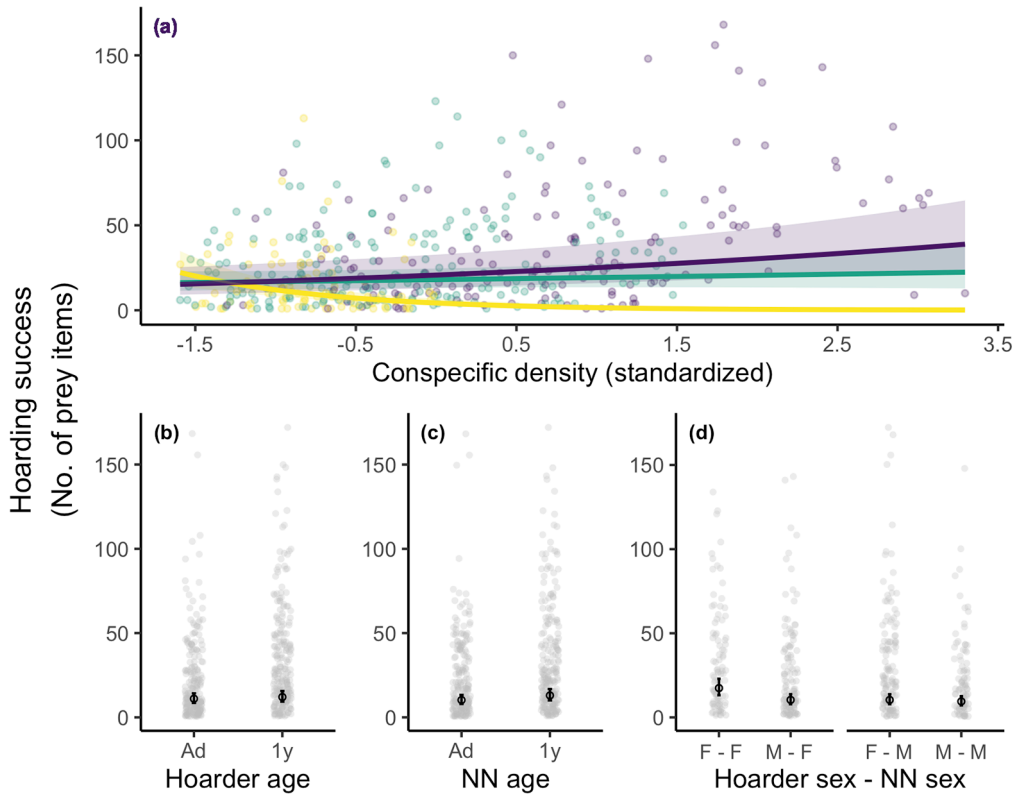


Fig. 4. Predicted values (and 95% CI) of total number of prey items stored (hoarding success) in all the food stores of one individual Pygmy Owl in relation to (a) the conspecific density in a 6000 m radius, (b) age of the hoarder, (c) of its NN, and (d) the interaction sex of the hoarder and of its NN. Predicted values are based on the models in Table 3. In plot (a), the three lines represent the different levels of vole abundance: low in yellow, intermediate in green, high in purple. Observed values are represented with dots, with darker colours meaning a higher number of observations.

pilfering and interference competition. These results suggest that high conspecific density overall inflames interference competition when food availability is low and leads to sex-specific spatial distribution.

4.1. Sex-specific competition

Pygmy Owls showed sex-specific spatial distribution. Females had overall larger distances to same-sex neighbours compared to male-male neighbours or neighbours of the opposite sex, which were instead closer to each other than expected at random. Close distances between the stores of male-male and opposite-sex neighbours

were associated which led to higher conspecific density, but their different hoarding strategies and diverse diet could reduce the costs of exploitative competition. Males can hunt a large array of prey including small birds along with small mammals while females mostly hunt voles (Masoero *et al.* 2020). Therefore, the intrasexual exploitative competition among males, or between sexes, may be reduced since individuals may specialize on different prey groups. Interference competition and especially conspecific aggression could also be reduced if the neighbours are of opposite sex, or both are males. Female Pygmy Owls are larger and likely need more food than males and indeed store larger food hoards (Masoero *et al.* 2018). The energy requirement of an individual increases

together with body size (Schmidt-Nielsen & Knut 1984), and therefore leads to a consequent increase in space used (Jetz *et al.* 2004). Indeed, females are known to be more aggressive toward conspecifics at least during the breeding season (Mikusek 2019). During the hoarding season their aggressive behaviour could lead females to occupy wider territories, and thus to have stores further away from each other. These results suggest that there is an asymmetry in the competitive abilities of males and females. This supports previous studies which show that individuals of the larger sex (females in our case) exert stronger competition by acquiring resources at the expense of others (Oddie 2000, Bedhomme *et al.* 2003), and they can respond more strongly than males to the presence of a competing female (Iglesias-Carrasco *et al.* 2020).

The sex-specific spatial distribution that we observed here is thus probably a combined result of exploitative and interference competition. The role of interference competition is suggested by the fact that the hoarding success of female owls with a same-sex neighbour was higher than owls with different-sex neighbours or male owls. The larger territories of females with same-sex neighbours, being in average 1 km further apart from their neighbours compared to individuals with opposite-sex neighbours or male-male neighbours (see results), probably derive from the high intrasexual aggression. These large territories could be beneficial not only to reduce interference competition but also as they reduce exploitative competition due to higher prey availability. On the other hand, being closer than expected to a neighbour with different hoarding strategy could also be beneficial in terms of reduced interference competition, while the diverse diet can help to reduce the costs of living at closer distance and thus alleviate exploitative competition. Different individuals thus seem to adopt different strategies to cope with the cost of aggressive interactions (interference competition) and the cost of exploitative completion at high densities, thus resulting in a sex-specific spatial distribution of stores.

Overall, our findings indicate that Pygmy Owls show sex-specific responses to competitor sex, supporting previous studies showing that under resource limitation, the larger sex is at a disadvantage due to the costs of producing and maintaining

a large body (Wikelski & Thom 2000, Benito & González-Solís 2007). Our results also confirm the importance of considering not only the age and sex characteristics of the focal owl but also of their competitors when evaluating competition (Bonisoli-Alquati *et al.* 2011, Iglesias-Carrasco *et al.* 2020). We also suggest that Pygmy Owls might avoid same-sex nearest neighbours to further release the intrasexual interference competition and resource depression (sensu Charnov *et al.* 1976). In general, interference competition can be exhausting by reducing food availability and the energy allocated in competition is then unavailable for other functions (Jaeger *et al.* 1983, Cresswell 1997), which in turn can lead to reduced fitness (Eccard & Ylönen 2002). Therefore, intraspecific competition and resource depression are probably among the main drivers in regulating wintering population of Pygmy Owls, as suggested for other predators (e.g., Cubaynes *et al.* 2014), and behavioural mechanisms releasing this competition can thus be highly beneficial. In addition, interspecific competition with other predators subsisting small mammals may also be important, because Pygmy Owls are able to store less food in the presence of larger Tengmalm's Owls (*Aegolius funereus*; Suhonen *et al.* 2007).

4.2. Conspecific density and resource abundance

The number of stores hoarded by an owl increased with increasing conspecific densities. Allocating prey in several food stores can reduce transportation distance and, thus, energetic costs. Distributing prey items to multiple store-sites instead of one (shifting from larder-hoarding towards scatter-hoarding) can help to reduce the overall loss to potential pilfering when the conspecific density is high (Vander Wall & Jenkins 2003). Pygmy Owls can visit each other's food stores (Masoero *et al.* 2018) and multiple food stores likely reduce pilfering from conspecifics or other small predators, such as small mustelids (*Mustela* sp.), which also increase in numbers during years of vole abundance (Korpimäki *et al.* 1991). When food is abundant, the variance in competitive abilities might be higher, because also more inexperienced or inferior competitors may be able to survive in the population and be

more prone to conduct pilfering, as shown in other food-hoarding species (e.g., American red squirrels *Tamiasciurus hudsonicus*; Donald & Boutin 2011). A high density of competitors will increase both exploitative and interference competition and having several hunting grounds might dilute this effect. It has been found that animals can adjust their behavioural patterns according to the assessed population density (Dantzer *et al.* 2012), so it can be suggested that showing activity in multiple store locations could also be a way for Pygmy Owls to strengthen their territory ownership, which can, in turn, reduce the confrontations from intruders.

In low vole abundance years, conspecific density decreased the total prey number stored by an owl, showing high costs of competition. This is in line with previous studies showing that when resources are scarce, intraspecific exploitative competition is stronger (e.g., Amundsen 2007, Morosinotto *et al.* 2017a). Hoarding success increased with conspecific density in high vole years in early winter, which is consistent with an earlier finding that Pygmy Owls avoided breeding close to each other but less so when food was plentiful (Morosinotto *et al.* 2017a). When voles are abundant, also the number of Pygmy Owls over-wintering in the area is high (Masoero *et al.* 2020) but, due to the good food availability, the intraspecific competition *per se* appeared to be relaxed. This shows the crucial role of the high-amplitude vole cycles for the predator community in northern areas. Voles are keystone herbivores in boreal landscapes and the main food source for a whole predator community, consisting of several avian and mammalian predators (e.g., Korpimäki 1987, Korpimäki *et al.* 1991). Accordingly, Dhondt (2012) highlights the importance of resource availability for intraspecific competition. It is often difficult to disentangle the effects of food availability and population density when they are highly intertwined (Dantzer *et al.* 2012). For example, and consistently with our results, in breeding Eagle Owls (*Bubo bubo*) the population growth rate is positive in low conspecific abundance, whereas it tends to be negative when conspecific abundance is high (Fernandez-de-Simon *et al.* 2014). Population growth was also positively related to the density of Eagle Owls'

main prey (rabbits *Oryctolagus cuniculus*), when considering Eagle Owl conspecific abundance (Fernandez-de-Simon *et al.* 2014). Especially in systems with drastically varying food supply from year to year, the focus of the competition can fluctuate between food (when food is scarce) and space, like roosting sites during winter, when food is not the limiting factor.

4.3. Age-specific effects

Pygmy Owls did not seem to spatially avoid individuals according to age, because the age of the nearest neighbour only slightly affected hoarding success. Hoarders with a yearling neighbour had larger food stores than hoarders with an adult neighbour, but independently from the hoarder's age. Young competitors likely lack the same experience in hunting as adults have, as shown in numerous other species (Marchetti & Price 1989, Wunderle 1991), and they are usually at a disadvantage when having to compete with adult individuals (Donazar *et al.* 1999, Smallegange & van der Meer 2006, Breed *et al.* 2013). Among food-hoarding species as well, young individuals face a higher risk of pilfering than adult individuals due to their lower experience (Beck *et al.* 2020). Furthermore, adults appear to be able to hunt a wider variety of prey (Masoero *et al.* 2020) and therefore might suffer less from competition. As adult owls cache also more small birds, they could be more mobbed. Intra and interspecific collaborative mobbing/antipredator behaviours from prey (Bshary & Noë 1997, Templeton *et al.* 2005, Dutour *et al.* 2016) may interfere with the hunting of many predators in the same forest patch and induce depression of food resources (*sensu* Charnov *et al.* 1976). Individuals may therefore be favoured by competing with a young neighbour and avoid food depletion by an adult neighbour due to intense mobbing of small birds.

4.4. Concluding remarks

Our results highlight the importance of intraspecific competition during a non-breeding season. We found that in food-hoarding predators high wintertime conspecific densities can lead

to a lowered food-storing success, which can, in turn, decline the chances for over-winter survival or reduce breeding success in the following year. Therefore, in harsh winter conditions, sex-specific spatial segregation in species with sex-dependent hunting differences could have evolved to reduce the costs of interference competition rather than exploitative competition. Having the right neighbour can help to reduce the severity of intraspecific competition locally, as sexes are known to have differences in diet and hunting behaviour (Mills *et al.* 2019, Masoero *et al.* 2020). When predators are in question, the outcome of their interactions will also indirectly impact prey populations (Ritchie & Johnson 2009), because prey will modify their habitat choice according to the spatial distribution of predators (Korpimäki *et al.* 1996, Morosinotto *et al.* 2010, Byholm *et al.* 2012). As male Pygmy Owls hunt more birds than females do, the sex-specific spatial settlement patterns of wintering Pygmy Owls can further modify the habitat selection of their main and alternative prey, voles, and small passerine birds, respectively. Since harsh winter months are critical for the abundance and condition of small birds in boreal forests (*e.g.*, Morosinotto *et al.* 2017b), even small-scale habitat decisions made by predators can have severe consequences on a wintering animal. Thus, understanding how conspecific predators interact and how this can impact their spatial distribution and hunting success is crucial to investigate predator effects at a landscape scale.

Lajinsisäinen tiheys ohjaa varpuspöllön sukupuolikohtaista alueellista talvilevittytymistä ja ravinnonkeräämiskäyttäytymistä

Useimmat tutkimukset lajinsisäisestä kilpailusta on tehty pesimäkaudella. Pohjoisilla leveysasteilla lajinsisäisen kilpailun kuitenkin odotetaan olevan erityisen voimakasta pesimäkauden ulkopuolella, kun sääolosuhteet ovat ankarat ja resursseja on tarjolla rajallisesti. Tässä tutkimuksessa tarkastelimme talvehtivien varpuspöllöjen (*Glaucidium passerinum*) ravinnonkeräämiskäyttäytymistä 15 vuoden ajalta. Lisäksi analysoimme sekä sukupuoli- että ikäkohtaista alueellista levittäytymistä suhteessa

vaihtelevaan pääsaaliin (myyrien) runsauteen ja lajinsisäiseen tiheeseen.

Huonoina myyrävuosina korkeampi lajinsisäinen tiheys vähensi varpuspöllöjen varastoiman saaliin kokonaismäärää, mikä voi johtua epäsuoran resurssikilpailun korkeista kustannuksista. Etäisyydet ruokavarastojen välillä olivat pidempiä silloin, kun lähimmät naapurit olivat naaraita, mikä viittaa alueellisen käyttäytymisen liittyvän sukupuolikohtaiseen kilpailuun. Naarasvarpuspöllöjen varastot sisälsivät kuitenkin enemmän saalista erityisesti silloin, kun lähin naapuri oli samaa sukupuolta. Yksilöt varastoivat enemmän saalista varpuspöllöpopulaation tiheyden kasvaessa. Saaliiden jakaminen useille varstopaikoille yhden sijasta voi auttaa vähentämään mahdollisia varkauksia pöllöpopulaation tiheyden ollessa suuri.

Nämä tulokset yhdistettyinä viittaavat siihen, että suuri lajinsisäinen tiheys kärjistää sukupuolisidonnaista suoraa häirintäkilpailua (eikä pelkästään epäsuoraa resurssikilpailua), mikä puolestaan voi johtaa havaitsemaamme sukupuolikohtaiseen alueelliseen levittäytymiseen. Ravinnonkeräämis- ja häirintäkäyttäytymisen perusteella sukupuolikohtainen alueellinen levittäytyminen voi olla keino vähentää lajinsisäisen kilpailun voimakkuutta paikallisesti. Sillä voi olla myös kerrannaisvaikutuksia saalisyyhteisöön.

Acknowledgements. We thank Jorma Nurmi, Rauno Varjonen, Kari Hongisto, Julien Terraube, Alexandre Villers, Brigitte Planade, Michel Griesser, Claire Cuginiere, Stefan Siivonen, Léo Poudré, Robert L. Thomson and Ville Vasko for great help with the fieldwork. Thanks to Andrea Santangeli for the statistical discussions.

Competing interests and funding. The study was financially supported by the Academy of Finland (grant nos. 123379, 136717 and 250709 to EKor). EKoi was financially supported by the Finnish Cultural Foundation's South Ostrobothnia Regional Fund and GM by the University of Turku Graduate School (UTUGS). The authors declare no conflict of interest.

Author contributions statement. EKoi, CM, GM and EKor conceived the ideas and designed methodology; EKor, GM and CM collected the data;

GM and ELT analysed the data; EKoi, GM and CM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement. The data (DOI 10.17605/OSF.IO/ACWKS) is available at the following link: <https://osf.io/acwks/>.

Please note that the location data are not included to avoid endangering the nesting sites of the Pygmy Owls.

Ethical approval. Trapping and ringing of Pygmy Owls were executed under the ringing licence (no. 524 to EKor) by Ringing Centre of the Finnish Museum of the Natural History. Pit-tags were used in accordance with Finnish and EU Laws and regulations and under the approval of the Animal Experiment Committee of the State Provincial Office (Etelä-Suomen aluehallintovirasto ESAVI; permit numbers: ESAVI-2010-05480/Ym-23, ESAVI/3221/04.10.07/2013, ESAVI/3021/04.10.07/2017). Ethical approval from ethics committee for involving animals in this study was not required. All applicable international, national and/or institutional guidelines for the use of animals were followed and all methodologies adopted in this manuscript were in line with Finnish law, including snap trapping of small rodents.

References

- Abramsky, Z., Rosenzweig, M.L. & Subach, A. 2001: The cost of interspecific competition in two gerbil species. — *Journal of Animal Ecology* 70: 561–567. <https://doi.org/10.1046/j.1365-2656.2001.00520.x>
- Amundsen, P.-A., Knudsen, R. & Klemetsen, A. 2007: Intraspecific competition and density dependence of food consumption and growth in Arctic charr. — *Journal of Animal Ecology* 76: 149–158. <https://doi.org/10.1111/j.1365-2656.2006.01179.x>
- Armstrong, D.P., Davidson, R.S., Dimond, W.J., Perrott, J.K., Castro, I., Ewen, J.G., Griffiths, R. & Taylor, J. 2002: Population dynamics of reintroduced forest birds on New Zealand islands. — *Journal of Biogeography* 29: 609–621. <https://doi.org/10.1046/j.1365-2699.2002.00710.x>
- Avgar, T., Betini, G.S. & Fryxell, J.M. 2020: Habitat selection patterns are density-dependent under the Ideal Free Distribution. — *Journal of Animal Ecology* 89: 2777–2787. <https://doi.org/10.1111/1365-2656.13352>
- Baddeley, A., Rubak, E. & Turner, R. 2015: *Spatial Point Patterns: Methodology and Applications with R*. — Chapman and Hall/CRC Press, London. <http://www.crcpress.com/Spatial-Point-Patterns-Methodology-and-Applications-with-R/Baddeley-Rubak-Turner/9781482210200/>
- 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: 333–342. <https://doi.org/10.1007/s10336-015-1285-3>
- Baroni, D., Masoero, G., Korpimäki, E., Morosinotto, C. & Laaksonen, T. 2021: Habitat choice of a secondary cavity user indicates higher avoidance of disturbed habitat during breeding than during food-hoarding. — *Forest Ecology and Management* 483: 118925. <https://doi.org/10.1016/j.foreco.2021.118925>
- Bartoň, K. 2023: MuMIn: Multi-Model Inference. R package version 1.47.5. <https://cran.hafro.is/web/packages/MuMIn/MuMIn.pdf>
- 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: 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Beck, K.B., Loretto, M.-C. & Bugnyar, T. 2020: Effects of site fidelity, group size and age on food-caching behaviour of common ravens, *Corvus corax*. — *Animal Behavior* 164: 51–64. <https://doi.org/10.1016/j.anbehav.2020.03.015>
- Bedhomme, S., Agnew, P., Sidobre, C. & Michalakakis, Y. 2003: Sex-specific reaction norms to intraspecific larval competition in the mosquito *Aedes aegypti*. — *Journal of Evolutionary Biology* 16: 721–730. <https://doi.org/10.1046/j.1420-9101.2003.00576.x>
- Benito, M.M. & González-Solís, J. 2007: Sex ratio, sex-specific chick mortality and sexual size dimorphism in birds. — *Journal of Evolutionary Biology* 20: 1522–1530. <https://doi.org/10.1111/j.1420-9101.2007.01327.x>
- Bonisoli-Alquati, A., Boncoraglio, G., Caprioli, M. & Saino, N. 2011: Birth order, individual sex and sex of competitors determine the outcome of conflict among siblings over parental care. — *Proceedings of the Royal Society B: Biological Sciences* 278: 1273–1279. <https://doi.org/https://doi.org/10.1098/rspb.2010.1741>
- Both, C. 1998: Experimental evidence for density dependence reproduction in great tits. — *Journal of Animal Ecology* 67: 667–674. <https://www.jstor.org/stable/2647286>
- Breed, G.A., Bowen, W.D. & Leonard, M.L. 2013: Behavioral signature of intraspecific competition and density dependence in colony-breeding marine predators. — *Ecology and Evolution* 3: 3838–3854. <https://doi.org/10.1002/ece3.754>
- Brunsdon, C. & Chen, H. 2014: GISTools: Some further GIS capabilities for R. <http://CRAN.R-project.org/>

packageGISTools

- Bshary, R. & Noë, R. 1997: Red colobus and Diana monkeys provide mutual protection against predators. — *Animal Behaviour* 54: 1461–1474. <https://doi.org/10.1006/anbe.1997.0553>
- Bull, E.L. 1990: Ecology of the great gray owl. — US Department of Agriculture, Forest Service, Pacific Northwest Research Station. <https://doi.org/10.2737/PNW-GTR-265>
- 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: 1802–1808. <https://doi.org/10.1890/12-0285.1>
- Calsbeek, R. & Sinervo, B. 2002: An experimental test of the ideal despotic distribution. — *Journal of Animal Ecology* 71: 513–523. <https://doi.org/10.1046/j.1365-2656.2002.00619.x>
- Carrete, M., Sánchez-Zapata, J.A. & Tella, J.L. 2006: Components of breeding performance in two competing species: habitat heterogeneity, individual quality and density-dependence. — *Oikos* 112: 680–690. <https://doi.org/10.1111/j.0030-1299.2006.14528.x>
- Chang, A.M. & Wiebe, K.L. 2016: Body condition in Snowy Owls wintering on the prairies is greater in females and older individuals and may contribute to sex-biased mortality. — *The Auk* 133: 738–746. <https://doi.org/10.1642/AUK-16-60.1>
- Charnov, E.L., Orians, G.H. & Hyatt, K. 1976: Ecological implications of resource depression. — *American Naturalist* 110: 247–259. <https://doi.org/10.1086/283062>
- 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: 1528–1531. <https://doi.org/10.1126/science.292.5521.1528>
- Cresswell, W. 1997: Interference Competition at Low Competitor Densities in Blackbirds *Turdus merula*. — *Journal of Animal Ecology* 66: 461–471. <https://doi.org/10.2307/5941>
- Cubaynes, S., MacNulty, D.R., Stahler, D.R., Quimby, K.A., Smith, D.W. & Coulson, T. 2014: Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). — *Journal of Animal Ecology* 83: 1344–1356. <https://doi.org/10.1111/1365-2656.12238>
- Dann, P. & Norman, F.I. 2006: Population regulation in Little Penguins (*Eudyptula minor*): the role of intraspecific competition for nesting sites and food during breeding. — *Emu - Austral Ornithology* 106: 289–296. <https://doi.org/10.1071/MU06011>
- Dantzer, B., Boutin, S., Humphries, M.M. & McAdam, A.G. 2012: Behavioral responses of territorial red squirrels to natural and experimental variation in population density. — *Behavioral Ecology and Sociobiology* 66: 865–878. <https://doi.org/10.1007/s00265-012-1335-2>
- Denac, D. 2006: Intraspecific Exploitation Competition as Cause for Density Dependent Breeding Success in the White Stork. — *Waterbirds* 29: 391–394. [https://doi.org/10.1675/1524-4695\(2006\)29\[391:IECACF\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2006)29[391:IECACF]2.0.CO;2)
- Dhondt, A.A. 2012: Interspecific competition in birds. — Oxford University Press, Oxford.
- Donald, J.L. & Boutin, S. 2011: Intraspecific cache pilferage by larder-hoarding red squirrels (*Tamiasciurus hudsonicus*). — *Journal of Mammalogy* 92: 1013–1020. <https://doi.org/10.1644/10-MAMM-A-340.1>
- Donazar, J.A., Travaini, A., Ceballos, O., Rodríguez, A., Delibes, M. & Hiraldo, F. 1999: Effects of sex-associated competitive asymmetries on foraging group structure and despotic distribution in Andean condors. — *Behavioral Ecology and Sociobiology* 45: 55–65. <https://doi.org/10.1007/s002650050539>
- Dutour, M., Lena, J.P. & Lengagne, T. 2016: Mobbing behaviour varies according to predator dangerousness and occurrence. — *Animal Behaviour* 119: 119–124. <https://doi.org/10.1016/j.anbehav.2016.06.024>
- Eccard, J.A. & Ylönen, H. 2002: Direct interference or indirect exploitation? An experimental study of fitness costs of interspecific competition in voles. — *Oikos* 99: 580–590. <https://doi.org/10.1034/j.1600-0706.2002.11833.x>
- Faegre, S.K., Nietmann, L., Hannon, P., Ha, J.C. & Ha, R.R. 2020: Age-related differences in diet and foraging behavior of the critically endangered Mariana Crow (*Corvus kubaryi*), with notes on the predation of *Coenobita* hermit crabs. — *Journal of Ornithology* 161: 149–158. <https://doi.org/10.1007/s10336-019-01705-3>
- Fernandez-de-Simon, J., Diaz-Ruiz, F., Cirilli, F., Tortosa, F.S., Villafuerte, R. & Ferreras, P. 2014: Role of prey and intraspecific density dependence on the population growth of an avian top predator. — *Acta Oecologica* 60: 1–6. <https://doi.org/10.1016/j.actao.2014.06.006>
- Ferrer, M. & Donazar, J.A. 1996: Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. — *Ecology* 77: 69–74. <https://doi.org/10.2307/2265655>
- Field, I.C., Bradshaw, C.J.A., van den Hoff, J., Burton, H.R. & Hindell, M.A. 2007: Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche. — *Marine Biology* 150: 1441–1452. <https://doi.org/10.1007/s00227-006-0417-y>
- Fretwell, S.D. 1972: Populations in a seasonal environment. — Princeton University Press, Princeton.
- Forsman, E.D. 1983: Methods and materials for locating and studying spotted owls. — US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. <https://doi.org/10.2737/PNW-GTR-162>
- Garabedian, J.E., Moorman, C.E., Peterson, M.N. & Kilgo, J.C. 2022: Group size mediates effects of intraspecific competition and forest structure on productivity in a

- recovering social woodpecker population. — *Animal Conservation* 25: 438–452. <https://doi.org/10.1111/acv.12757>
- Gurevitch, J., Morrison, J.A. & Hedges, L.V. 2000: The interaction between competition and predation: a meta-analysis of field experiments. — *American Naturalist* 155: 435–453. <https://doi.org/10.1086/303337>
- Hakkarainen, H. & Korpimäki, E. 1991: Reversed sexual size dimorphism in Tengmalm's Owl: is small male size adaptive? — *Oikos* 61: 337–346. <https://doi.org/10.2307/3545241>
- Hakkarainen, H., Korpimäki, E., Koivunen, V. & Ydenberg, R. 2002: Survival of male Tengmalm's owls under temporally varying food conditions. — *Oecologia* 131: 83–88. <https://doi.org/10.1007/s00442-001-0865-5>
- 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: 162–171. <https://doi.org/10.1034/j.1600-0706.2003.11906.x>
- Halonen, M., Mappes, T., Meri, T. & Suhonen, J. 2007: Influence of snow cover on food hoarding in pygmy owls *Glaucidium passerinum*. — *Ornis Fennica* 84: 105–111. <https://ornisfennica.journal.fi/article/view/133686>
- Hijmans, R.J. & van Etten, J. 2012: raster: Geographic analysis and modelling with raster data. R package version 2.5–8. <http://CRAN.R-project.org/package=raster>
- Huitu, O., Norrdahl, K. & Korpimäki, E. 2003: Landscape effects on temporal and spatial properties of vole population fluctuations. — *Oecologia* 135: 209–220. <https://doi.org/10.1007/s00442-002-1171-6>
- Iglesias-Carrasco, M., Brookes, S., Kruuk, L.E.B. & Head, M.L. 2020: The effects of competition on fitness depend on the sex of both competitors. — *Ecology and Evolution* 10: 9808–9826. <https://doi.org/10.1002/ece3.6620>
- 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: 49–54. <https://doi.org/10.1007/s10164-002-0053-z>
- Jaeger, R.G., Nishikawa, K.C.B. & Barnard, D.E. 1983: Foraging tactics of a terrestrial salamander: Costs of territorial defence. — *Animal Behaviour* 31: 191–198. [https://doi.org/10.1016/S0003-3472\(83\)80188-2](https://doi.org/10.1016/S0003-3472(83)80188-2)
- Jetz, W., Carbone, C., Fulford, J. & Brown, J.H. 2004: The Scaling of Animal Space Use. — *Science* 306: 266–268. <https://doi.org/10.1126/science.1102138>
- Kellomäki, E. 1977: Food of the pygmy owl *Glaucidium passerinum* in the breeding season. — *Ornis Fennica* 54: 1–29. <https://ornisfennica.journal.fi/article/view/132921>
- Korpimäki, E. 1987: Dietary shifts, niche relationships and reproductive output of coexisting Kestrels and Long eared Owls. — *Oecologia* (Berlin) 74: 277–285. <https://doi.org/10.1007/BF00379371>
- Korpimäki, E., Norrdahl, K. & Rinta-Jaskari, T. 1991: Responses of stoats and least weasels to fluctuating vole abundances: is the low phase of the vole cycle due to mustelid predation? — *Oecologia* 88: 552–561. <https://doi.org/10.1007/BF00317719>
- Korpimäki, E., Koivunen, V. & Hakkarainen, H. 1996: Microhabitat use and behavior of voles under weasel and raptor predation risk: predator facilitation? — *Behavioral Ecology* 7: 30–34. <https://doi.org/10.1093/beheco/7.1.30>
- 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. <https://doi.org/10.1098/rspb.2004.2860>
- Korpimäki, E. & Hakkarainen, H. 2012: The Boreal owl: ecology, behaviour and conservation of a forest-dwelling predator. — Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511844164>
- Korpimäki, E., Hongisto, K., Masoero, G. & Laaksonen, T. 2020: The difference between generalist and specialist: the effects of wide fluctuations in main food abundance on numbers and reproduction of two co-existing predators. — *Journal of Avian Biology* 51: 1–13. <https://doi.org/https://doi.org/10.1111/jav.02508>
- Krüger, O. 2005: The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. — *Evolutionary Ecology* 19: 467–486. <https://doi.org/10.1007/s10682-005-0293-9>
- Lagerström, M. & Syrjänen, J. 1990: Ageing Pygmy Owls. — *Lintumies* 25: 291–194. (In Finnish with English summary)
- Marchetti, K., & Price, T. 1989: Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. — *Biological Reviews* 64: 51–70. <https://doi.org/10.1111/j.1469-185X.1989.tb00638.x>
- 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. <https://doi.org/10.1007/s004420050021>
- Masoero, G., Morosinotto, C., Laaksonen, T. & Korpimäki, E. 2018: Food hoarding of an avian predator: sex- and age-related differences under fluctuating food conditions. — *Behavioral Ecology and Sociobiology* 72: 159. <https://doi.org/10.1007/s00265-018-2571-x>
- Masoero, G., Laaksonen, T., Morosinotto, C. & Korpimäki, E. 2020: Age and sex differences in numerical responses, dietary shifts, and total responses of a generalist predator to population dynamics of main prey. — *Oecologia* 192: 699–711. <https://doi.org/10.1007/s00442-020-04607-x>
- Mikusek, R. 2019: The role of caches in the Eurasian Pygmy Owl *Glaucidium passerinum* during the breeding season. — *Ornis Polonica* 60: 1–15. http://ornis-polonica.pl/_pdf/OP-60-1-Mikusek.pdf
- Miller, R.S. 1967: Pattern and process in competition. —

- Advances in Ecological Research 4: 1–74.
- 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* 2019: e01979. <https://doi.org/10.1111/jav.01979>
- 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: 327–333. <https://doi.org/10.1111/j.1365-2656.2009.01638.x>
- Morosinotto, C., Villers, A., Thomson, R.L., Varjonen, R. & Korpimäki, E. 2017a: Competitors and predators alter settlement patterns and reproductive success of an intraguild prey. — *Ecological Monographs* 87: 4–20. <https://doi.org/10.1002/ecm.1238>
- Morosinotto, C., Villers, A., Varjonen, R. & Korpimäki, E. 2017b: Food supplementation and predation risk in harsh climate: interactive effects on abundance and body condition of tit species. — *Oikos* 126: 863–873. <https://doi.org/10.1111/oik.03476>
- Oddie, K.R. 2000: Size matters: Competition between male and female great tit offspring. — *Journal of Animal Ecology* 69: 903–912. <https://doi.org/10.1046/j.1365-2656.2000.00438.x>
- Pérez-Camacho, L., García-Salgado, G., Rebollo, S., Martínez-Hestekamp, S. & Fernández-Pereira, J.M. 2015: Higher reproductive success of small males and greater recruitment of large females may explain strong reversed sexual dimorphism (RSD) in the northern goshawk. — *Oecologia* 177: 379–387. <https://doi.org/10.1007/s00442-014-3146-9>
- Pérez-Camacho, L., Martínez-Hestekamp, S., Rebollo, S., García-Salgado, G. & Morales-Castilla, I. 2018: Structural complexity of hunting habitat and territoriality increase the reversed sexual size dimorphism in diurnal raptors. — *Journal of Avian Biology* 49: e01745. <https://doi.org/10.1111/jav.01745>
- Pulliam, H.R. & Danielson, B.J. 1991: Sources, sinks, and habitat selection: a landscape perspective on population dynamics. — *American Naturalist* 137: 50–66. <https://doi.org/10.1086/285139>
- R Core Team 2022: R: A language and environment for statistical computing. — R Foundation for Statistical Computing.
- Reigert, J. & Fuchs, R. 2011: Fidelity to roost sites and diet composition of wintering male urban Common Kestrels *Falco tinnunculus*. — *Acta Ornithologica* 46: 183–189. <https://doi.org/10.3161/000164511X625955>
- Ritchie, E.G. & Johnson, C.N. 2009: Predator interactions, mesopredator release and biodiversity conservation. — *Ecology Letters* 12: 982–998. <https://doi.org/10.1111/j.1461-0248.2009.01347.x>
- Schmidt-Nielsen, K. & Knut, S.N. 1984: Scaling: why is animal size so important? — Cambridge university press, Cambridge.
- Schoener, T.W. 1974: Resource partitioning in ecological communities. — *Science* 185: 27–39. <https://doi.org/10.1126/science.185.4145.27>
- Schoener, T.W. 1983: Field experiments on interspecific competition. — *American Naturalist* 122: 240–285. <https://www.jstor.org/stable/2461233>
- Schönn, S. 1980: Der Sperlingskauz. — Die Neue Brehm-Bücherei, Wittenberg-Luthesstadt. (In German)
- Sih, A., Crowley, P., McPeck, M., Petranka, J. & Strohmeier, K. 1985: Predation, competition and prey communities: a review of field experiments. — *Annual Review of Ecology, Evolution, and Systematics* 16: 269–311. <https://doi.org/10.1146/annurev.es.16.110185.001413>
- Smallegange, I.M. & van der Meer, J. 2006: Interference from a game theoretical perspective: shore crabs suffer most from equal competitors. — *Behavioral Ecology* 18: 215–221. <https://doi.org/10.1093/beheco/arl071>
- Smith, R.D. & Metcalfe, N.B. 1994: Age, Sex and Prior Site Experience Have Independent Effects on the Foraging Success of Wintering Snow Buntings. — *Behaviour* 129: 99–111. <https://doi.org/10.1163/156853994X00370>
- Solheim, R. 1984a: 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. <https://www.jstor.org/stable/23734162>
- Solheim, R. 1984b: Breeding biology of the pygmy owl *Glaucidium passerinum* in two biogeographical zones in southeastern Norway. — *Annales Zoologici Fennici* 21: 295–300. <https://www.jstor.org/stable/23734161>
- Strøm, H. & Sonerud, G.A. 2001: Home range and habitat selection in the pygmy owl *Glaucidium passerinum*. — *Ornis Fennica* 78: 145–158. <https://ornisfennica.journal.fi/article/view/133558>
- Suhonen, J., Halonen, M., Mappes, T. & Korpimäki, E. 2007: Interspecific competition limits larders of pygmy owls. — *Journal of Avian Biology* 38: 630–634. <https://doi.org/10.1111/j.2007.0908-8857.03960.x>
- Svanbäck, R. & Bolnick, D.I. 2007: Intraspecific competition drives increased resource use diversity within a natural population. — *Proceedings of the Royal Society B: Biological Sciences* 274: 839–844. <https://doi.org/10.1098/rspb.2006.0198>
- Svanbäck, R., Eklöv, P., Fransson, R. & Holmgren, K. 2008: Intraspecific competition drives multiple species resource polymorphism in fish communities. — *Oikos* 117: 114–124. <https://doi.org/10.1111/j.2007.0030-1299.16267.x>
- Taylor, I.R. 1994: Barn Owls. Predator-prey relationships and conservation. — Cambridge University Press, Cambridge.
- Templeton, C.N., Greene, E. & Davis, K. 2005: Allometry of Alarm Calls: Black-Capped Chickadees Encode Information About Predator Size. — *Science* 308: 1934. <https://doi.org/10.1126/science.1108841>
- 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: 1361–1373. <https://doi.org/doi.org/10.1111/gcb.13408>
- Valeix, M., Chamaillé-Jammes, S. & Fritz, H. 2007: Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. — *Oecologia* 153: 739–748. <https://doi.org/10.1007/s00442-007-0764-5>
- Vander Wall, S.B. 1990: *Food Hoarding in Animals*. — University of Chicago Press, Chicago. [https://doi.org/10.1016/0169-5347\(90\)90034-B](https://doi.org/10.1016/0169-5347(90)90034-B)
- Vander Wall, S.B. & Jenkins, S.H. 2003: Reciprocal pilferage and the evolution of food-hoarding behaviour. — *Behavioral Ecology* 14: 656–667. <https://doi.org/10.1093/beheco/arg064>
- Wikelski, M. & Thom, C. 2000: Marine iguanas shrink to survive El Niño. — *Nature* 403: 37–38. <https://doi.org/10.1038/47396>
- Wunderle, J.M. Jr 1991: Age-specific foraging proficiency in birds. — In *Current ornithology* vol. 8 (Ed. Power, D.M.): 273–324, Plenum Publishing Corporation, New York.
- Ziv, Y., Abramsky, Z., Kotler, B.P. & Subach, A. 1993: Interference competition and temporal and habitat partitioning in two gerbil species. — *Oikos* 66: 237–246. <https://doi.org/10.2307/3544810>

Online supplementary material

Supplementary material available in the online version includes Tables S1–S2 with information on model selection.