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

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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 km^2 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 ± SD) of food stores with an identified hoarder was 63.2 ± 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 km^2 (range 0.4–6.0 km^2; 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 (± SD) 0.05 (± 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

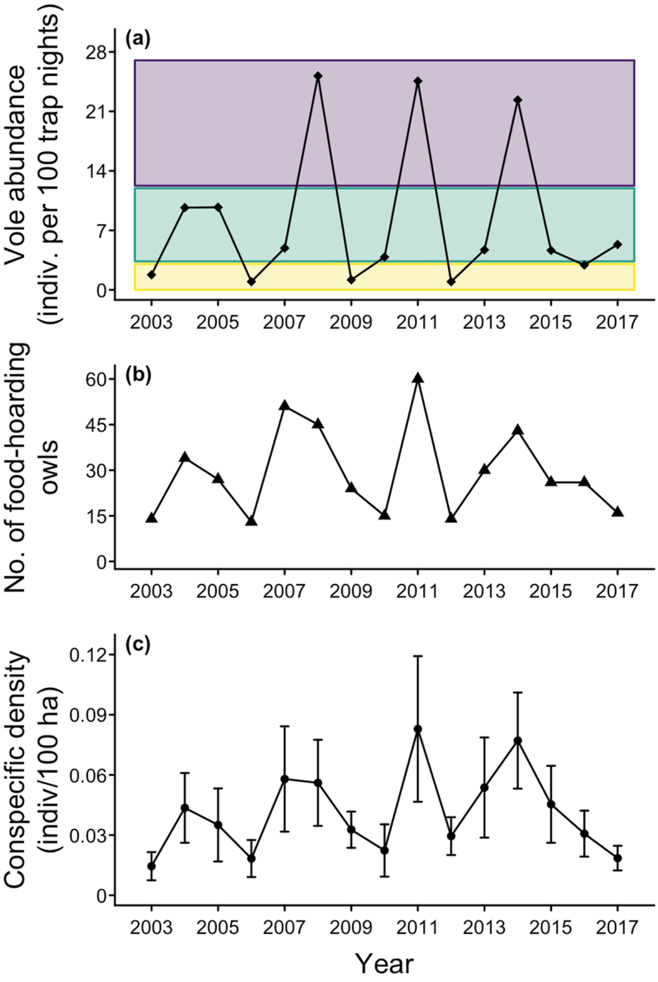

Fig. 1. Among-year variation in (a) autumn vole abundance (number of individuals captured per 100 trap nights), (b) number of food-hoarding individuals and (c) mean (and standard deviation) conspecific density in the 6000 m radius around the food stores of a focal individual in the study area during 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. Colour figure is available in the online version of the article at https://doi.org/10.51812/of.130326.

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 ± 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)

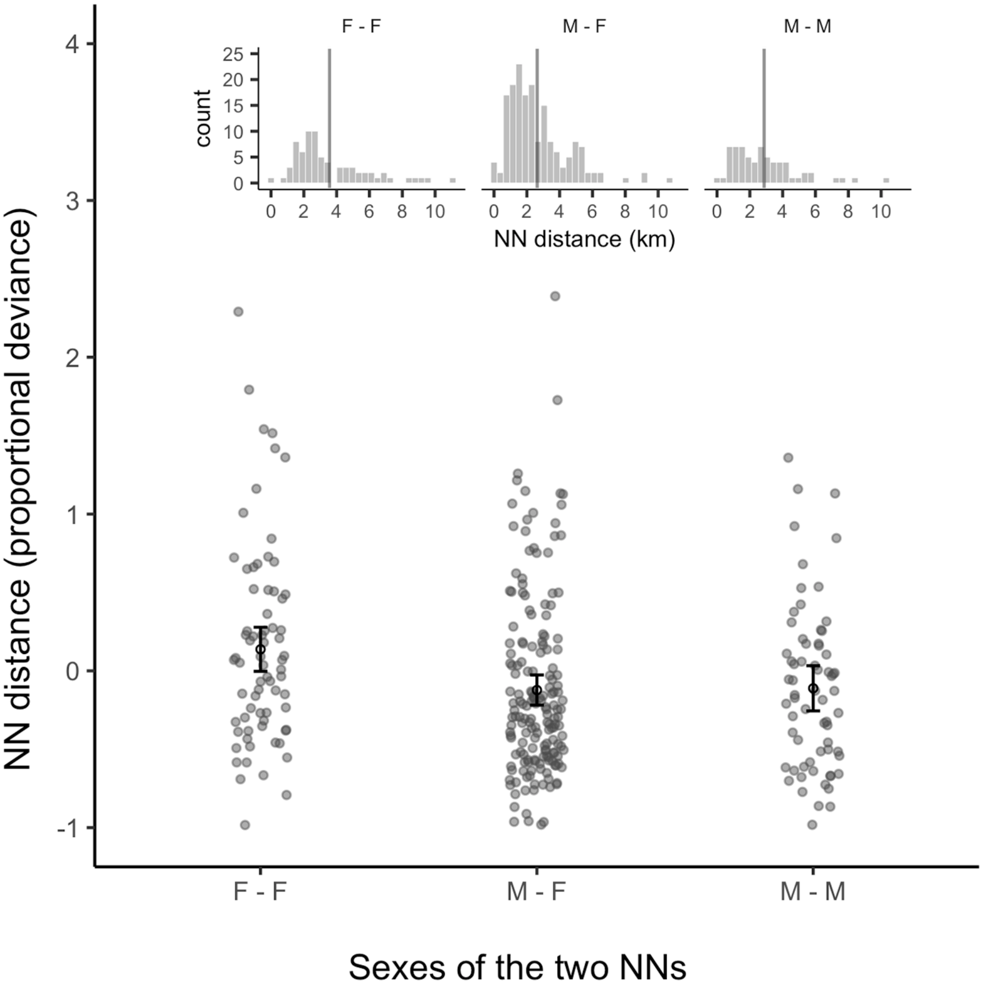

Fig. 2. Predicted values (and 95% CI) of the proportional deviance for the distance between nearest neighbours (NN) in relation to the sexes of the NNs (see Table 1). Observed values are represented with jittered semi-transparent dots, with darker colours meaning a higher number of observations. The 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 that 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		
NNs - ages			0.29	0.8658
	Ad – Ad	0 ± 0		
	1y – Ad	–0.003 ± 0.086		
	1y – 1y	0.079 ± 0.093		
NNs - sexes			10.64	**0.0049**
	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

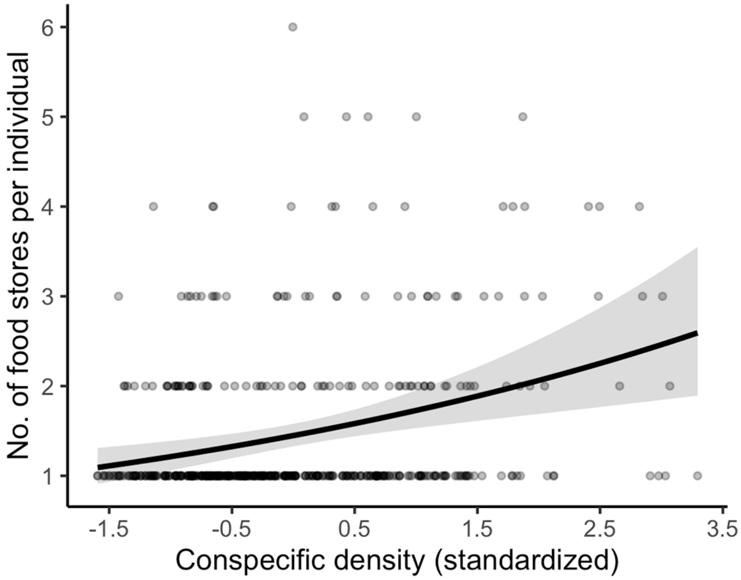

Fig. 3. Predicted values (and 95% CI) of the total number of food stores per individual in relation to conspecific density in a 6000 m radius based on the models in Table 2. Observed values are represented with semi-transparent dots, with darker colours meaning a higher number of observations.

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

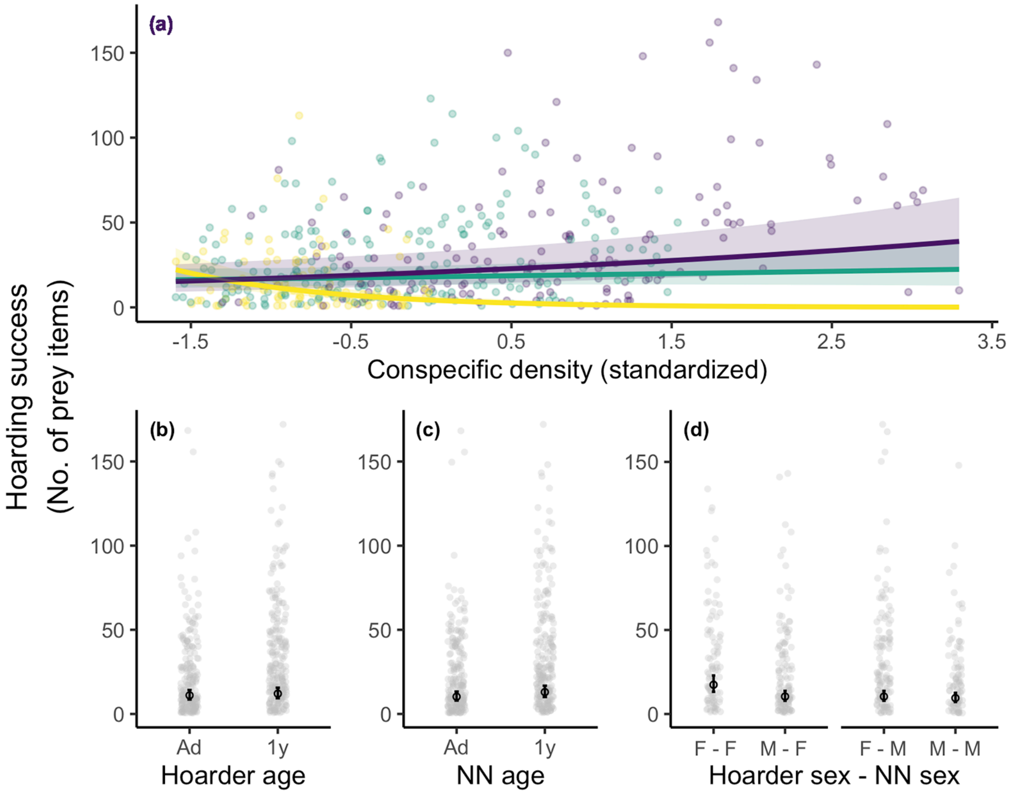

Fig. 4. Predicted values (and 95% CI) of total number of prey items stored (hoarding success) in all the food stores of one individual Pygmy Owl in relation to (a) the conspecific density in a 6000 m radius, (b) age of the hoarder, (c) of its NN, and (d) the interaction sex of the hoarder and of its 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. Colour figure is available in the online version of the article at https://doi.org/10.51812/of.130326.

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 (Donázar *et al.* 1999, Smallegange & van der Meer 2006, Breed *at 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 talvilevittäytymistä 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 tiheyteen.

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 varastopaikoille 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 saalisyhteisöön.

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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 (https://doi.org/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.

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Online supplementary material

Supplementary material available in the online version (https://doi.org/10.51812/of.130326) includes Tables S1–S2 with information on model selection.