Food hoarding of an avian predator: sex- and age-related differences under fluctuating food conditions

Giulia Masoero1 · Chiara Morosinotto1,2 · Toni Laaksonen1,3 · Erkki Korpimäki1

Abstract
Hoarding behaviour (storing food for a later use) has evolved to reduce starvation risk when resources are scarce. Different age and sex classes often show differences in foraging due to experience, skills or life history strategy, but such differences in hoarding under spatio-temporally varying environmental conditions have rarely been studied in the wild. We studied hoarding behaviour of Eurasian pygmy owls (Glaucidium passerinum) during 2003–2016 in western Finland, where the abundance of their main prey (voles) fluctuates in three-year population cycles. In 14 years, 1056 food stores were found during the hoarding season (Oct–Dec) and 330 pygmy owls were trapped at these stores. The number of stores per individual did not vary in relation to age, sex or vole abundance. Adults (+ 1-year old) had their stores farther apart than yearlings. Both the number of stores per year and the biomass of stored prey items increased with vole abundance. Females and yearlings had larger and heavier stores than males and adults, respectively. The same individuals stored more food as yearlings than as adults. These sex- and age-differences in hoarding indicate that it is not constrained by experience or skills. It rather seems that less-experienced yearlings rely more on stored food than adults. Females may need more food due to their larger size and need to accumulate energy reserves before reproduction. A detailed knowledge of age- and sex-related differences in hoarding behaviour under fluctuating abundances of main foods is fundamental to better understand a population response to climate change and forest management.

Significance statement
The hoarding behaviour of animals has evolved to cope with the problem of food limitation. On the basis of 14-year data from pygmy owls, we show that the number of stores per year and the biomass of prey items per store increased with vole abundance in the environment. Adults had stores farther apart than yearlings, and females and yearlings stored more prey items and biomass compared to males and adults, respectively. These results indicate that hoarding behaviour responds to the available main prey abundance and varies with traits such as age and sex. Because different age and sex classes might respond differently to variation in food abundance, due to habitat alterations or climate change, a detailed knowledge of hoarding behaviour can be of particular importance to understand changes in body condition, reproductive success and survival of pygmy owls under changing climate and management of boreal forest.

Communication by N. Clayton

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00265-018-2571-x) contains supplementary material, which is available to authorized users.

© Springer-Verlag GmbH Germany, part of Springer Nature 2018

Keywords Age and experience · Sex-specific · Food cache · Starvation risk · Predator-prey interaction · Vole cycle

Introduction
Animal populations are strongly limited by variation in food availability (Newton 1998) through many different pathways affecting survival and reproduction (Lack 1947; Martin 1987; Reznick et al. 2000). Animals have therefore evolved several strategies to store energy in order to face times of food scarcity (Brodin and Clark 2007), which can arise from fluctuations in food availability (e.g. harsh winter), demand (e.g. reproduction)
or both (Roberts 1979; Vander Wall 1990). They can store energy in the body as fat, carbohydrates or proteins (Brodin and Clark 2007), or externally by hoarding (also referred to as caching or storing) food when resources are abundant (Vander Wall 1990; Brodin and Clark 2007). In particular, harsh wintering conditions, such as cold temperatures and deep snow cover, could have led to the evolution of hoarding (Roberts 1979; Smith and Reichman 1984). At high latitudes, cold climate may promote hoarding behaviour both by creating a situation of food scarcity and by favouring the preservation of the food itself (Källander and Smith 1990). Indeed, in the highly seasonal environment of boreal forests in the north, a considerable number of species hoard food (Smith and Reichman 1984; Vander Wall and Smith 1987), and among avian predators (owls, diurnal raptors and shrikes), some forms of food hoarding are fairly common during periods of food scarcity or during the breeding season (Korpimäki 1987; Yosef and Pinshow 1999; Källander and Smith 1990). These species are usually scatter-hoarders, and food items are dispersed in several cavities or placed on tree branches or bushes (Vander Wall 1990). In many species, there are age differences in foraging behaviour and skills that could lead to different responses in periods of food scarcity. In general, young individuals often appear to have lower performance than more mature ones, both as hunters and as breeders (Orians 1969; Wunderle 1991; Daunt et al. 1999; Laaksonen et al. 2002; Rutz et al. 2006). Several hypotheses have been put forward to explain this age-effect (Forslund and Pärt 1995; Martin 1995). First, according to the constraint hypothesis (Curio 1983), the young individuals could be constrained by their inferior foraging skills, as they are usually still learning and practicing (Kear 1962; Marchetti and Price 1989; Wunderle 1991; Limmer and Becker 2009). Second, the young individuals could be restraining their effort, especially in breeding activities, in order not to jeopardise their survival and future breeding success (the restraint hypothesis; Curio 1983). In the context of hoarding, it could however be hypothesised that young individuals actually need to put more effort into hoarding than old ones if they have poorer hunting skills, whereas old individuals could restrain their effort in the hoarding period because they can rely more on their skills and experience during food scarcity. Third, in cross-sectional data, the cohort of young individuals might contain lower quality individuals that the older age groups no longer contain (the differential mortality hypothesis; Curio 1983; Forslund and Pärt 1995).

Sex differences in foraging are also common (e.g. Clarke et al. 1998; Ishikawa and Watanuki 2002), especially in species of owls and diurnal raptors characterised by reverse size dimorphism (RSD, i.e. females larger than males; Hakkarainen and Korpimäki 1991; Krüger 2005). Numerous hypotheses have been put forward to explain RSD, but the ones that received most support were the small male hypothesis (smaller-sized males more efficient hunters) and the intersexual-competition hypothesis (size differences reduce intersexual competition for food; Hakkarainen and Korpimäki 1991; Massemin et al. 2000; Krüger 2005). In addition, owls and diurnal raptors have distinct intersexual duties during the breeding season: females produce and incubate eggs and brood the young, whereas males are responsible for providing their mates and offspring from prior to egg-laying until the nestlings will fledge (Newton 1979; Schönn 1980; Mikkola 1983; Korpimäki and Hakkarainen 2012). Therefore, selection for hunting skills is probably higher for males than females. RSD and inter-sexual breeding duties would therefore lead to sex differences in the hunting behaviour, skills and species of prey captured (Earhart and Johnson 1970; Ishikawa and Watanuki 2002; Keynan and Yosef 2010; Korpimäki and Hakkarainen 2012).

We studied age and sex differences in hoarding behaviour of the Eurasian pygmy owl (Glaucidium passerinum; hereafter pygmy owl), a small avian predator that inhabits boreal-alpine forests of the Western Palearctic (Schönn 1980; Mikkola 1983; Terraube et al. 2017), and the only European avian predator that stores large quantities of food in cavities for winter (Mikkola 1983; Solheim 1984a; Schulenburg and Wiesner 1986; Terraube et al. 2017). In boreal environments, the wide periodical fluctuations in the abundances of small mammal populations govern the population densities and reproductive success of predators, including the pygmy owl (Korpimäki and Hakkarainen 1991; Korpimäki and Norrdahl 1991; Korpimäki 1992; Newton 2002; Korpimäki et al. 2005; Lehikoinen et al. 2011b). Most of the potential avian prey of pygmy owls migrate south for the winter while snow cover can hide small mammals. Deep snow layer effectively prevents small-sized owls to hunt voles below snow (Mikkola 1983; Halonen et al. 2007). Stored food can thus be critical for the wintering pygmy owls when fresh food is unavailable. The food hoarding behaviour of pygmy owls in terms of store contents has been described in several studies (e.g. Mikkola 1983; Solheim 1984a; Halonen et al. 2007; Terraube et al. 2017), but little is known about differences in hoarding behaviour in relation to age and sex of the individual. Using a 14-year data, we examined (i) the number of and distance between food stores of the same owl, (ii) among-year variation in the number and biomass of the prey items stored, as well as (iii) sex- and age-class related differences in the hoarding behaviour and food store characteristics under varying abundance of their main prey (voles). The constraint and restraint hypotheses predict that young individuals would have fewer and/or smaller stores than adults, and that store size would increase with age within individuals. The latter would be simultaneously evidence against the differential mortality hypothesis, which does not predict within-individual change.
Second, we predicted that the larger females would store more food than males because they need a larger amount of food to survive the winter and to accumulate energy reserves for reproduction. However, it could also be that females would have smaller stores than males if the males are more efficient hunters (as suggested by the small male hypothesis). Finally, young individuals and females might be less able to cope especially with food scarcity, so we expect differences in hoarding between the age and sex classes to be larger when the food is scarce in the environment.

To our knowledge, the few previous studies on this topic have focused on the among-year variation of the content of the stores, and no other study has considered whether there are sex- and age-related variations under cyclic fluctuations of main food abundance. Since different age and sex classes might have different responses to variation in food abundance, improving the current knowledge of hoarding behaviour of pygmy owls can be of great importance to understand how they may cope with changing wintering climate and habitat alterations due to management of boreal forests.

**Materials and methods**

**Study area**

The data were collected during 2003–2016 in the vicinity of Kauhava, western Finland (63°N, 23°E). The study area covers approximately 1000 km² and consists mainly of managed forests and agricultural land. The management of the forested habitats has created a mosaic of clear-cut areas and 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. 2017). A total of 305 areas of forests (hereafter “forest-sites”): mean ± SD 211 ± 64 forest-sites per year during 2003–2016) were provided with nest-boxes for pygmy owls during the study years, but the number of forest-sites available per year was not constant because each year some of the forest-sites were clear-cut, and the boxes were either relocated to the nearest forest-site or removed. In most cases, we set-up two nest boxes per forest-site (mean ± SD 95 ± 5% sites per year). The two nest boxes were set mainly in spruce trees at the height of 1–2 m, on average 88.5 m apart (range 22–310 m), to allow pygmy owls to have at least one box available throughout the year, since Siberian flying squirrels (Pteromys volans) also prefer to reproduce and roost in these boxes throughout the year (Morosinotto et al. 2017). Each nest box had an entrance hole with a diameter of 45 mm, preventing other owl and diurnal raptor species from entering and storing or stealing prey items (Solheim 1984a; Morosinotto et al. 2017).

**Study species**

The pygmy owl is diurnal with activity peaks at dusk and dawn and predominantly inhabits boreal and alpine forests of Eurasia (Mikkola 1970, 1983; Schönn 1980; Mikkola 1983; Kullberg 1995). It nests in natural tree cavities, or artificial nest boxes, preferring usually old and mature coniferous forests (Strom and Sonerud 2001; Halonen et al. 2007; Barbaro et al. 2016; Morosinotto et al. 2017). The pygmy owl is well-adapted to the cold and individuals usually establish winter territories, with occasional irruptive migrations at times of food depletion (Lindberg 1966; Schönn 1980; Mikkola 1983; Lehikoinen et al. 2011a). In Northern Europe, the prey items stored for the winter consist mainly of bank voles (Myodes glareolus), voles of the genus Microtus (Microtus voles, e.g. the field vole Microtus agrestis, and the sibling vole M. rossiaemeridionalis), shrews (the common shrew Sorex araneus, the pygmy shrew Sorex minutus), mice (the Eurasian harvest mouse Micromys minutus, the house mouse Mus musculus) and small birds, usually passerines, with body mass < 60 g (Kellomäki 1977; Halonen et al. 2007; EK and GM unpublished data). Overall, diet composition of pygmy owls is related to prey availability and can therefore differ according to geographic area and season (Kellomäki 1977; Schönn 1980; Mikkola 1983; Ekman 1986; Schulenberg and Wiesner 1986; Šotnár et al. 2015). During late autumn and early winter, pygmy owls hoard prey items in natural cavities and nest-boxes (Scherzinger 1970; Schönn 1980; Solheim 1984a; Suhonen et al. 2007; Terraube et al. 2017). In the study area, the species occupies the boxes both for breeding in spring and for food hoarding in autumn and winter. It has to be noted that pygmy owls can make more than one food-store and that a single box can be visited by more than one pygmy owl (see “Results” section of this study).

**Monitoring of food stores and trapping of pygmy owls**

The boxes were inspected for the presence of stored prey items twice during the autumn, from late October to mid-December. Prey items were usually stored as whole, and thus species identification was possible in most cases. Prey items in food stores were also marked by toe-clipping (birds) or tail-clipping (mammals) to avoid double counting. The total number and mass of prey items was calculated by summing up the fresh prey items counted in the two visits done from late October to mid-December. If the weight of each prey item was not recorded, but the number and species were (10.9% of the total prey items), the relative average weight of the species for that year was used. In a few cases in which only the number of prey items was recorded, but species and the weight of each prey item were not identified, which can happen when the
prey items get rotten or frozen, the store was excluded from the analysis (7.5% of the total prey items).

From 2003 to 2016 during the hoarding season, pygmy owls were captured, measured and ringed for individual identification. The vast majority of owls (80.47%) were captured with nest box traps (a replica of the box equipped with a swing door), seven individuals with a telescopic fishing pole with a loop at the top, and one individual by hand inside the box. The captured owls were sexed and aged, their wing and tail length were measured and they were weighed with a Pesola spring balance. Sex was assessed on the basis of the known sexual dimorphism of the species (Mikkola 1983), and based on measurements of owls in the study area during breeding season, when females can be distinguished by males being the only ones incubating and having a brood patch (wing length: females mean 106 mm, 5th–95th percentiles 103–110 mm; males mean 99 mm, 5th–95th percentiles 96–102 mm; tail length: females mean 65 mm, 5th–95th percentiles 61–69 mm; males mean 60 mm, 5th–95th percentiles 55–65 mm; body mass: females mean 77 g, 5th–95th percentiles 69–87 g; males mean 60 g, 5th–95th percentiles 55–65 g; EK, unpublished data). When the sex of the owl was not possible to identify with certainty because of overlap in the range of wing length, tail length and body mass between large males and small females, the individuals were excluded from the analyses of inter-sexual differences (N = 17 individuals).

Age was estimated according to wing moult (Cramp 1985; Lagerström and Syrjänen 1990) and individuals were divided in two classes: individuals at their hatching year (hereafter ‘yearlings’) and older individuals (hereafter ‘adults’). The rest of the identities of storing owls (18%) were obtained mainly using Passive Integrated Transponder tags (PIT). From 2011, the owls were marked with a PIT tag, a small electromagnetic microchip implanted subcutaneously. They are the key element of the application of a technology used for individual identification in animals, the radio frequency identification (RFID; Gibbons and Andrews 2004). Data on encounters of individual owls were collected by placing the antenna of the reader around the entrance hole of the nest box. The antenna was then kept in place for at least 2 weeks or until the reader recorded the identity of a hoarding owl. We refer to the owl that was first captured entering the store, or the owl that on the basis of the reader data entered the store most often, as the “hoarder” of the store. Therefore, the reader data helped identify with more certainty the owl that hoarded the food store, since pygmy owls can make multiple stores and several individuals can sometimes visit the same store (see “Results” section). Data related to the identity of the hoarder were therefore provided both by the trapping and by the data collected with the PIT-tag method. Age and sex of the individual were assessed with the focal animals in the field, whereas to minimise observer bias blinded methods were used when all the other behavioural data were recorded and/or analysed.

**Vole abundance**

The abundance of small mammals (voles, shrews and mice) was estimated biannually by snap trapping in early May and mid-September. In two locations 14 km apart within the study area, 50–100 metal mouse snap-traps were set-up to cover 0.5 to 1.0 ha and the four main habitat types i.e. agricultural and abandoned fields, and forests dominated by spruce or pine (Korpimäki et al. 2005). The traps (baited with mixed-grain bread) were placed in runways of small mammals and checked daily for 3 to 4 days. The regional synchrony of vole population cycles and thus indices of small mammals extends 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. To obtain a vole abundance index for the analyses, the results from the four-night trapping sessions done in spring (May) and autumn (September) for both the bank voles and Microtus voles (voles species only) were pooled and standardised as number of animals captured per 100 trap nights.

**Statistical analyses**

To analyse the hoarding behaviour of pygmy owls in relation to the fluctuation in vole abundance and to age and sex of the owl, generalised linear models (GLMs) and generalised linear mixed models (GLMMs) were fitted using maximum likelihood (Laplace approximation). Only the cases in which it was possible to identify the hoarder of the store were used in the analyses involving age and sex of the owl.

The total number of hoarding owls and the number of forest-sites occupied with a food store were analysed in relation to vole population abundance in autumn (called ‘vole index’ in the models), and year to detect temporal trends. A GLM with a Poisson likelihood family was fitted for the number of owls, while for the number of occupied sites a GLM for proportional data as in Zuur et al. (2009) with a quasibinomial likelihood family was constructed. For this analysis, the response variable was a binomial variable consisting of a two-column data frame: the number of forest-sites with at least one active store and the number of empty forest-sites (different from a simple proportion because it allows to specify the actual count).

We analysed whether the number of stores hoarded by an owl and the mean distances between them were affected by the abundance of voles in autumn or whether there were any differences in relation to sex and age of the individual. The distances between every store of each individual (with at least two stores) during a particular year, were calculated from the coordinates of the boxes using the function ‘gDistance’ in the
package GIStools (R package v. 0.7-4; Brunsdon and Chen 2014). From the obtained dataset, minimum, maximum and mean values for every owl and year were extracted. The number of stores of each individual and their mean distance were tested in relation to the abundance index of vole populations, age and sex of the owl, using GLMMs with ‘individual identity’ of the owl (the numeric code of the owl metal ring) as a random effect. The ‘individual identity’ was used to control for possible repeated measures of the same individual, both in different boxes in the same year (e.g. if an individual had multiple stores) or between multiple years.

To analyse the impact of vole abundance and pygmy owl sex and age on the number and biomass of the prey items in the food store, we used a dataset that included only the cases in which the store hoarder was identified. Explanatory variables included autumn vole abundance and age and sex of the owl, and their two-way interactions. Due to the fact that males and females differ in body size, we also tested for an effect of wing length. The wing length standardised by sex was used together with the other variables, but it was never significant (see description of the models and results in Supplementary Material S1). As response variables, we used the total number and the total mass of prey items in the stores, using the content of the single store as a measure and not the sum of the stores hoarded by an individual. This decision was made due to the fact that the content of the single store could be measured exactly while it was not possible to know if the owl had other unknown stores (i.e. in natural cavities or in a box without an identified hoarder). Since the count data for the total number of prey items were over-dispersed, it was decided to use negative binomial likelihood family (Zuur et al. 2009; Lindén and Mäntyniemi 2011). The total mass of prey items was log10-transformed to fit the normal distribution. ‘Individual identity’ of the owl and ‘site/box’ (‘box’ nested in ‘site’, i.e. the forest-site where each nest box pair was set) were used as random effect in all the models. ‘Site/box’ was included as random effect to take into account spatial and temporal pseudo-replications, since most forest-sites had two available nest boxes and were used multiple times during the 14-year data set. Overall, 69% of the sites (over 50% of the boxes) were used as food stores more than once during the study period. Models were run both with and without the statistically significant outlier observation identified by the Grubbs test for outliers (total number: G = 8.20, U = 0.89, p < 0.001; total mass: G = 9.94, U = 0.84, p < 0.001); there were no differences and the full dataset was used. The models without the outlier observation are presented in the Supplementary Material S2. In both analyses, we started with a full model (all the explanatory variables and the two-way interactions) and obtained a model with all significant variables through backward stepwise selection (significance evaluated with the function ‘Anova’ in the R package car v. 2.1–6).

Models were usually constructed through the ‘lmer’ and the ‘glmer’ functions in the package lme4 (R package v. 1.1-13; Bates et al. 2015), in conjunction with package lmerTest (R package v. 2.0-33; Kuznetsova et al. 2016). Whereas the package glmmADMB (R package v. 0.8.3.3) was used in case of negative binomial models (Fournier et al. 2012; Skaug et al. 2016). Least square means (i.e. marginal means) were obtained through the package lsmeans (R package v. 2.27-2; Lenth 2016). All statistical tests and calculations were performed using R v. 3.4.0 (R Core Team 2017).

Data availability The datasets analysed during the current study are available in the Harvard Dataverse repository, https://dataverse.harvard.edu/dataset.xhtml?persistentId=doi:10.7910/DVN/IF3SQN.

Results

Number of food stores in relation to main food abundance

The data collected during the study period (2003–2016) is summarised in Table 1. On average, 32% of the forest-sites had at least one store, with variation from a minimum of 15% in 2006 to a maximum of 47% stores in 2011 (Fig. 1). The proportion of forest-sites with a food store and the number of hoarding pygmy owls captured did not show any long-term temporal trend during 2003–2016 (Table 2a, Fig. 1), but significantly increased with the abundance of voles in the environment (Fig. 2).

Number of and distance between food stores of individual owls

The hoarder of the store was identified and sexed in 57.5% cases (see Table 1 for details on numbers of stores and owls observed). The owls were either captured inside or in the vicinity of the store or recorded with the PIT-tag reader during the food-hoarding season within the 14 study-years. Of all the captured and sexed owls, 46% were males, 54% were yearlings and 23% were captured or recorded during multiple hoarding seasons. The use of the PIT-tag reader, combined with the trapping, increased the number of identified hoarders from an average of 50.3% per year (± 5.4 SE, from 2003 to 2010, only trapping) to an average of 65.2% per year (± 3.4 SE, from 2011 to 2016, combined methods). The PIT-tag reader recorded data for 156 stores in 6 years (2011–2016), of which in only 20 cases two different individuals visited the same food store. In nine of these cases, the hoarder was easy to identify due to the far higher number of visits to the store by the hoarder. In the remaining 11 cases, it was not possible to identify the hoarder and they were therefore removed from the
analyses. Overall in 48% of the cases, the owl had only one store per storing season (299 stores of 607) whereas in the remaining cases an owl had multiple food stores (range 2–6 stores per owl). The GLMMs indicated no relationship between number of stores by the individual and autumn vole abundance, and no obvious differences in the number of stores between sexes (LSM ± SE: males 1.47 ± 0.08, females 1.46 ± 0.08; see Table 2b) or age classes (LSM ± SE: yearling 1.51 ± 0.08, adults 1.43 ± 0.09; see Table 2b).

Of the 38 cases in which food stores were found in two boxes located in the same forest-site, the two stores were hoarded by different individuals only in ten cases, whereas in the remaining 28 cases the two stores were hoarded by the same owl. The average (± SE) distance between two stores of the same individual was 1470 ± 942 m with the maximum distance recorded 4990 m. There was no obvious association of the autumn vole abundance with the mean distance between stores (Table 2c). The mean distance between stores did not vary between sexes (LSM ± SE: males 1616 ± 119 m, females 1585 ± 124 m; see Table 2c), whereas yearling owls had significantly shorter distance between their stores than adults (LSM ± SE: yearling 1428 ± 105 m, adults 1773 ± 134 m; see Table 2c). A frequency distribution plot of the mean distance between stores of the same individual shows that yearlings had their stores less spread than adults, and both mean and median values were lower than in adults (Fig. 3).

### Number and biomass of prey items

Mammals were stored in a higher frequency than birds (93.6 vs 6.4% of prey items). The autumn vole abundance, and age and sex of the hoarder were all significant predictors of the total number and of the total mass of prey items in a food store (Table 3). In particular, males appeared to store fewer prey items than females (LSM ± SE: males 16.7 ± 3.1 items, females 21.8 ± 3.5 items), and to have lighter stores (LSM ± SE: males 146.4 ± 10.5 g, females 197.6 ± 13.8 g; Table 3, Fig. 4). Also, yearlings stored overall more items than older individuals, but the increase of the number of stored food items in relation to the vole abundance was steeper for adults than for yearlings (LSM ± SE: yearlings 22.3 ± 4.8 and adults 16.3 ± 2.3; Table 3, Fig. 4a). This difference in relation to the vole abundance was not present when analysing the total mass of prey items (none of the interaction was significant), and food stores of both age groups appeared to increase in the same way with the vole abundance in current autumn (LSM ± SE: yearlings 198.5 ± 13.3 g and adults 145.6 ± 10.9 g; Table 3, Fig. 4b). Following these results on the two age classes, we analysed within-individual differences in relation to age. The average store content of the same individual as a yearling and later on as an adult was compared with a paired t-test, and yearling owls were found to have larger and heavier stores than adults (total number of prey items: mean ± SE: yearlings 27.6 ± 3.2 and adults 16.5 ± 2.1, t = 2.96, df = 49, p = 0.002; total mass of prey items: mean ± SE: yearlings 416.9 ± 47 g and adults 244 ± 35.5 g; t = 2.93, df = 49, p = 0.003; N = 50 individuals).
Our main findings were as follows. First, yearling owls and females had overall larger and heavier food-stores than adult owls and males, respectively. These results suggest that food hoarding is not limited by hunting experience or skills as predicted by the constraint-hypothesis, and instead support the hypothesis that yearlings might invest more in hoarding than adults during autumn because they might not be able to rely on daily hunting success during winter. Females, on the other hand, might need larger stores due to their larger size and to maintain and improve body condition for the breeding season. Second, both the number of stores per year, and the number and biomass of prey items in food stores of pygmy owls increased with autumn vole abundance in the field. In years when vole abundance was high, owls of all age and sex classes stored more food than in years of low vole abundance. However, the relationship was stronger in adult than in young individuals. In years of low vole abundance, adult individuals had smaller stores than the young ones, which again shows that lack of experience is not constraining hoarding but on the contrary inducing a higher investment in hoarding.

### Annual variation in the number of hoarding owls and food stores

Fluctuation in vole abundance was the main driver of annual variation in the number of hoarding pygmy owls and of food-stores, with more pygmy owls and food stores when vole densities were high. Some of the main life history traits of pygmy owls were already linked to the availability of the main prey species (voles). For example, breeding densities of pygmy owls are higher and number of food stores larger in good than in poor vole years (Solheim 1984a, b; Ekman 1986; Suhonen et al. 2007; Terraube et al. 2017), and food scarcity may induce irruptive migrations in the autumn (Lehikoinen et al. 2011a). Our results show that also the number of food-hoarding owls that remained in the area during winter is related to vole abundance. Periods of food scarcity may result in lower numbers of breeding owls and in lower reproductive effort and induce larger migrations away from the area.

### Table 2

Model results for the analyses on number and distribution of the stores during 2003–2016. a) GLM of the variation in total number of forest-sites with at least one food store and b) in the number of hoarding owls in relation to autumn vole abundance (“vole index”) and time (year). Note that the estimates are at logit-scale. c) GLMM of the total number of stores per owl in relation to the autumn vole abundance (“vole index”), age (1-yr = yearlings, Ad = adults), and sex (M = males, F = females) of the owl. Individual identity was used as a random effect. d) GLMM of the mean distance (meters) between the stores of one individual in relation to the autumn vole abundance (“vole index”), and to age (1-yr = yearlings, Ad = adults) and sex (M = males, F = females) of the owl. Individual identity of the owl was used as a random effect. Significant variables are printed in italics. N = sample size of the response variable.

| Response variable | Explanatory variable | Estimate ± SE | Statistic | P |
|-------------------|-----------------------|---------------|-----------|---|
| a) No. of forest-sites with a store (N=14) | Intercept | 89.091 ± 49.595 | | |
| | Vole index | 0.042 ± 0.010 | 17.16 | 0.0016 |
| | Year | −0.045 ± 0.025 | 3.33 | 0.0954 |
| b) No. of hoarding pygmy owls (N=14) | Intercept | −11.777 ± 54.148 | | |
| | Vole index | 0.035 ± 0.011 | 10.22 | 0.0085 |
| | Year | 0.007 ± 0.027 | 0.07 | 0.7896 |
| c) No. of stores per owl (N=412) | Intercept | 0.326 ± 0.086 | | |
| | Vole index | 0.002 ± 0.004 | 0.52 | 0.6034 |
| | Age | 1-yr | 0.060 ± 0.083 | 0.72 | 0.4718 |
| | | Ad | 0 ± 0 | | |
| | Sex | M | 0.006 ± 0.082 | 0.08 | 0.9400 |
| | | F | 0 ± 0 | | |
| d) Mean distance between stores (N=117) | Intercept | 1792.928 ± 170.606 | | |
| | Vole index | −2.875 ± 8.130 | −0.35 | 0.7249 |
| | Age | 1-yr | −344.606 ± 167.251 | −2.06 | 0.0428 |
| | | Ad | 0 ± 0 | | |
| | Sex | M | 29.567 ± 170.452 | 0.17 | 0.8627 |
| | | F | 0 ± 0 | | |
therefore inducing a decrease in number of owls that are still present in autumn and that will hoard food for the winter.

**Number of and distance between food stores of individual owls**

Pygmy owls are larder hoarders (one or few large stores, while scatter hoarders hoard many small stores), but they often distribute prey items in multiple stores. In our study area, about half of the owls hoarded food in more than one known box. This behaviour has probably evolved to cope with two problems (Vander Wall 1990). First, having more than one store would mean losing only part of the stored prey items in case of discovery by cache-robbing conspecifics and small mustelids (the stoat *Mustela erminea* and the least weasel *M. nivalis*) that can also enter the boxes and natural cavities with the 45-mm diameter of entrance hole (i.e. pygmy owl nest-boxes and cavities excavated by great-spotted woodpeckers *Dendrocopos major*). Second, if the winter territory is wide, by caching in multiple sites, possibly closer to the prey catching place, the costs of carrying prey items would be lower than the cost of always going back to the same central place. Contrary to expectations, autumn vole abundance did not modify the number of food-stores per owl, nor did the age and sex of the owls. Only in relatively few cases the owls hoarded food in the two boxes of the same forest-site, again probably to reduce the probability of losing both stores to robbers (Vander Wall 1990). Unfortunately, our data do not provide sole information on the presence and frequency of inter- or intra-specific cache robbers, nor on the amount of food possibly stolen.

When the same individual hoarded food in more than one box, boxes were usually in neighbouring forest-sites, and with an average distance of 1.5 km, which is close to the average distance between forest-sites in our study area (1429 ± 721 km; see Morosinotto et al. 2017). The distance between stores of the same individual did not change according to autumn vole abundance and no difference was found between sexes. However, we found that yearling owls usually had stores closer to each other than adults. Less experienced yearlings might be less able to widen their home range, possibly because of competition for high-quality food storing sites with abundant food patches. Another possibility is that adult individuals might have learnt that it is more convenient to spread food stores further away from each other and they might also be better at coping with the higher cost of spacing the caches. If considering strictly the range size, previous studies on age-related differences show contrasting results and are usually focused on breeding individuals. In some cases, adult individuals had larger home ranges than sub-adults or yearlings (Ralph and Pearson 1971; Harestad and

![Fig. 2](https://example.com/fig2.png) **Fig. 2** a. The probability and 95% confidence intervals (grey) of a forest-site with two nest boxes to contain at least one food store and b. the variation in the total number of hoarding pygmy owls in relation to autumn vole abundance (“vole index”) in the study area during 2003–2016 (*N* = 14)

![Fig. 3](https://example.com/fig3.png) **Fig. 3** Frequency distributions of the mean distance (meters) between the stores of one individual aggregated every 200 m and divided between a yearlings (*N* = 69) and b adults (*N* = 48). Mean (solid line) and median (dotted line) values are 1423 m and 1441 m for yearlings, and 1733 m and 1673 m for adults
Bunnell 1979), whereas, in others they were larger in immatures or young breeders (Rohner 1997; Penteriani et al. 2013). However, very little is known about winter territories in relation to age. Due to the correlative nature of the long-term dataset collected here it was not possible to investigate the link between experience and the spatial distribution of food-stores, but these preliminary results are a first attempt to address the issue of store spreading in relation to age or experience.

**Age differences under fluctuating food availability**

Regarding age difference on store composition, our results are in contrast with the prediction of the *constraint hypothesis* that yearling owls would have smaller and lighter stores than adults. In particular, yearlings stored a higher number of prey items in years of vole scarcity compared to adults, whereas when vole abundance was high, the number was similar between age groups. This was caused by the steep increment in the number of prey stored by adults when there was a higher abundance of voles in the environment. On the contrary, total prey biomass was always larger in stores hoarded by yearlings and the increment according to vole abundance was similar between age groups. Moreover, the same individuals had larger and heavier stores as juveniles than as adults.

Not much is known about age-specific patterns in food hoarding. Age-related differences in hoarding behaviour are often related to its ontogeny and limited to the first weeks of life of the individual (Vander Wall 1990), i.e. pouch filling and emptying in golden hamsters (Etienne et al. 1982), impaling of prey in shrikes (Yosef and Pinshow 2005) and handling and storing seeds in marsh tits (Clayton 1992). In our case, the hoarding differences between the two age groups are shown when the behaviour has already developed and might therefore reflect differences in hunting performances. In general, young individuals are less experienced than adults and have been shown to have lower performances, both as hunters and as breeders (Orians 1969; Wunderle 1991; Daunt et al. 1999; Laaksonen et al. 2002; Rutz et al. 2006). These results suggest an unexpected better performance by young individuals, but might also hide an improvement in hunting abilities with age, and therefore, a lower dependence on the hoarded food. Adult owls at the start of winter have already lived at least through

| Response variable | Explanatory variable | Estimate ± SE  | df  | Statistic | P      |
|-------------------|----------------------|---------------|-----|-----------|--------|
| **a) Total number of prey items** | Intercept | 2.505 ± 0.107 | z   |           |        |
|                 | Vole index | 0.035 ± 0.006 | 5.07 < 0.0001 |
|                 | Age 1-yr | 0.575 ± 0.136 | 4.24 < 0.0001 |
|                 | Ad      | 0 ± 0         |     |           |        |
|                 | Sex M   | −0.267 ± 0.086 | −3.12 0.0018 |
|                 | F       | 0 ± 0         |     |           |        |
|                 | Vole index×Age 1-yr | −0.022 ± 0.009 | −2.76 0.0149 |
|                 | Ad      | 0 ± 0         |     |           |        |
| **Removed terms** | Vole index×Sex M | −0.003 ± 0.009 | −0.35 0.7300 |
|                 | F       | 0 ± 0         |     |           |        |
| **b) Total mass of prey items** | Intercept | 2.015 ± 0.044 | 308 |           |        |
|                 | Vole index | 0.018 ± 0.002 | 535 7.95 < 0.0001 |
|                 | Age 1-yr | 0.134 ± 0.043 | 488 3.11 0.0020 |
|                 | Ad      | 0 ± 0         |     |           |        |
|                 | Sex M   | −0.130 ± 0.043 | −3.03 0.0027 |
|                 | F       | 0 ± 0         |     |           |        |
| **Removed terms** | Vole index×Age 1-yr | −0.005 ± 0.005 | −1.13 0.2589 |
|                 | Ad      | 0 ± 0         |     |           |        |
|                 | Vole index×Sex M | 0.001 ± 0.004 | 549 0.24 0.8113 |
|                 | F       | 0 ± 0         |     |           |        |
another winter and a reproductive season, in which they would have likely acquired experience in hunting skills. Moreover, the differential mortality hypothesis states that individuals of lower quality are more prone to die or disperse, leading to an adult-cohort composed mainly by high-quality better performing individuals (e.g. Nol and Smith 1987; Laaksonen et al. 2002). If yearlings are in fact less efficient hunters than adults, they may compensate by hoarding a higher amount of food. We therefore suggest that adult individuals might have to depend less on stored food than yearlings. This hypothesis might be also supported by the fact that the store size of a certain individual decreased with age. It is likely energetically costly to hunt (Williams et al. 2004) and a heavy investment in hoarding might trade off with other functions during the hoarding season. Unfortunately, we were not able to find out whether the differences found in the amount of food stored are due to an improvement in the hunting skills of adults or a restraint in their effort to hoard.

**Sex differences in hoarding behaviour**

Our results are consistent with the prediction that female pygmy owls hoarded larger and heavier stores than males. We suggest that hunting skills might therefore not constrain the amount of food stored by the females, but other behavioural and physical differences among sexes might determine the observed pattern. The size of the owl per se did not affect the size of the food store (Supplementary Material S1), showing that the differences between sexes are not strictly related to size, but possibly to behavioural differences. Females have indeed a larger body mass, and therefore might need a larger amount of food than males, but they would also need to maintain high body condition during the winter and gain weight towards the spring to be ready for the breeding season. In many species, body condition of females in winter influences the subsequent breeding attempt (e.g. Martin 1987; Persson 2005; Waite and Strickland 2006; Derbyshire et al. 2015). Having more food throughout the winter, leading to larger body mass and thus better body condition at the beginning of the breeding season, might have a significant importance on the following reproductive success. On the other hand, adult males have captured prey for the female and the chicks throughout the breeding season acquiring a better hunting experience. According to the small male hypothesis, males of many birds of prey have evolved a smaller size to be more agile and efficient hunters in order to provide enough food for their families (Hakkarainen and Korpimäki 1991; Massemin et al. 2000). Essential behavioural differences between sexes and thus different sex-related selection pressures during the breeding season might explain the differences we found in the hoarding behaviour. Therefore, we suggest that females would need a larger amount of prey during the winter and might thus have to rely more than males on hoarded food, whereas males might be able to rely on better every-day hunting success.

Sex differences in food hoarding have previously been reported in small mammals, with females often storing more food than males, and this behaviour is likely controlled to some extent by sex hormones (Smith and Ross 1950; Nyby et al. 1973; Brenner and Lyle 1975; Formanowicz et al. 1989; Clarke and Kramer 1994; Jenkins 2011). Many hoarding birds are sexually monomorphic, and sex differences might go unnoticed (Vander Wall 1990). Most differences are found during the breeding season, as a ritual for pair bonding males can provide prey items to show to the female their hunting abilities, for example, in southern grey shrikes *Lanius meridionalis* (Keynan and Yosef 2010). In many species, male individuals...
often store prey items to feed the female and chicks during incubation and chick rearing (see examples in Schnell 1958; Vaughan 1961; Brown 1976; Newton 1979; Korpimäki 1987; Schneider and Wilden 1994). In contrast to the breeding season in which hoarding behaviour is shown only by one sex, in autumn and winter both sexes hunt for themselves. Compared to diet analyses from nest sites, the analysis of food stored for the winter thus allows to better explore inter-sexual differences in hoarding behaviour and diet selection.

Conclusions

This study shows how the hoarding behaviour of a predator can depend on food availability, and the age and sex of the hoarder. Natural fluctuation in availability of main prey deeply modified the hoarding behaviour of pygmy owls, because the overall number of stores and the amount of prey stored increased with vole abundance. It also provided us a way to understand inter-individual differences in hoarding behaviour. Sex-related size differences can easily shape food-storing behaviour of an avian predator, with larger females storing more prey per food cache and possibly needing more stored food than males. Adult owls had smaller and lighter stores than yearlings in years of low vole abundance. These results suggest that the amount of food stored by the pygmy owls might not be limited by hunting skills, but rather we hypothesise that more experienced adults are able to rely less on hoarded food and therefore refrain from maximum hoarding effort. Reversed sexual size dimorphism and differences in behaviour, arising from their distinct breeding behaviour, might induce the higher investment of females in hoarding food for the winter. Investigating age and sex patterns in hoarding and foraging behaviour is relevant, since different age and sex classes might respond differently to variation in food abundance due to habitat alterations or climate change, which may thus affect the population structure. A detailed knowledge of hoarding behaviour can therefore be of particular importance to understand changes in over-winter condition and reproductive success of pygmy owls, and ultimately in the whole species community.

Acknowledgments

We thank Rauno Varjonen, Jorma Nurmi, Julien Terraubé, Alexandre Villers, Brigitte Planade, Michel Griesser, Claire Cuginiere, Stefan Siivonen, Léo Poudré, Robert L. Thomson and Ville Vasko for great help with the fieldwork. We are grateful to Fabio Balotari Chieba for the help in the GIS analysis. We also would like to thank the editors and anonymous reviewers for the thorough and constructive work they did to help us improve this manuscript.

Funding information

This project was financially supported by the Academy of Finland (grant nos. 123379, 136717 and 250709 to EK). GM was founded by the University of Turku Graduate School (UTUGS).

Compliance with ethical standards

Ethical approval

All applicable international, national and institutional guidelines for the care and use of animals were followed. This study was executed in accordance with Finnish laws and regulations and under the approval of the Animal Experiment Committee of the State Provincial Office (Etelä-Suomen aluehallintovirasto ESAVI; permit numbers: EASVI-2010-05480/Ym-23, ESAVI/3221/04.10.07/2013).

Conflict of interest

The authors declare no conflict of interest.

References

Barbaro L, Blache S, Trochard G, Arlaud C, de Lacoste N, Kayser Y (2016) Hierarchical habitat selection by Eurasian pygmy owls Glaucomium passerinum in old-growth forests of the southern French Prealps. J Ornithol 157:333–342. https://doi.org/10.1007/s10336-015-1285-3
Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01
Brenner FJ, Lyle PD (1975) Effect of previous photoperiodic conditions and visual stimulation on food storage and hibernation in the eastern chipmunk (Tamias striatus). Am Midl Nat 95:227–234. https://doi.org/10.2307/242123
Brodin A, Clark CW (2007) Energy storage and expenditure. In: Stephens DW, Brown JS, Ydenberg RC (eds) Foraging: behavior and ecology. The University of Chicago Press, Chicago, pp 221–269
Brown L (1976) Birds of prey: their biology and ecology. A & W Publishers, New York
Brunsdon C, Chen H (2014) GISTools: some further GIS capabilities for R, http://CRAN.R-project.org/packageGISTools
Clarke J, Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S (1998) Sex differences in Adélie penguin foraging strategies. Polar Biol 20:248–258. https://doi.org/10.1007/s003000050301
Clarke MF, Kramer DL (1994) Scatter-hoarding by a larder-hoarding rodent: intraspecific variation in the hoarding behaviour of the eastern chipmunk, Tamias striatus. Anim Behav 48:299–308. https://doi.org/10.1006/anbe.1994.1243
Clayton NS (1992) The ontogeny of food-storing and retrieval in marsh tits. Behaviour 122:11–25
Cramp S (ed) (1985) Handbook of the birds of Europe, the Middle East, and North Africa: terns to woodpeckers, vol 4. Oxford University Press, Oxford
Curio E (1983) Why do young birds reproduce less well? Ibis 125:400–404. https://doi.org/10.1111/j.1471-919X.1983.tb03130.x
Daunt F, Wanless S, Harris MP, Monaghan P (1999) Experimental evidence that age-specific reproductive success is independent of environmental effects. Proc R Soc Lond B 266:1489–1493. https://doi.org/10.1098/rspb.1999.0805
Derbyshire R, Strickland D, Norris DR (2015) Experimental evidence and 43 years of monitoring data show that food limits reproduction in a food-caching passerine. Ecology 96:3005–3015. https://doi.org/10.1890/15-0191.1
Earhart CM, Johnson NK (1970) Sise dimorphism and food habits of North American owls, Condor 72:251–264
Ekman J (1986) Tree use and predator vulnerability of wintering passerines. Ornis Scand 17:261–267
Etienne AS, Emmanuelli E, Zinder M (1982) Ontogeny of hoarding in the golden hamster: the development of motor patterns and their sequential coordination. Dev Psychobiol 15:33–45. https://doi.org/10.1002/dev.420150107
Formanowicz DR, Bradley PJ, Brodie ED (1989) Food hoarding by the least shrew (Cryptotis parva): intersexual and prey type effects. Am Midl Nat 122:26–33. https://doi.org/10.2307/2425679

Forsslund P, Pärt T (1995) Age and reproduction in birds - hypotheses and tests. Trends Ecol Evol 10:374–378. https://doi.org/10.1016/S0169-5347(00)89141-7

Fournier DA, Skaug HJ, Anhett H, Acheta D, Jainelli L, Magnusson A, Maumber MN, Nielsen A, Sibert J (2012) AD model builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim Methods Softw 27:233–249. https://doi.org/10.1080/10556788.2011.597854

Gibbons JW, Andrews KM (2004) PIT tagging: simple technology at its best. Bioscience 54:447. https://doi.org/10.1641/0006-3568(2004)054[0447:PTSTAJ]2.0.CO;2

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, Mykrä S, Kurki S, Korpimäki E, Nikula A, Koivunen V (2007) Influence of snow and spatial properties of vole population fluctuations. Oecologia 159:209–220. https://doi.org/10.1007/s00442-005-0717-6

Ishikawa K, Watanuki Y (2002) Sex and individual differences in foraging behavior of Japanese commoners in years of different prey availability. J Ethol 20:49–54. https://doi.org/10.1007/s10164-002-0053-z

Jenkins SH (2011) Sex differences in repeatability of food-hoarding behavior of kangaroo rats. Anim Behav 81:1155–1162. https://doi.org/10.1016/j.anbehav.2011.02.021

Källander H, Smith HG (1990) Food storing in birds: an evolutionary perspective. In: Power DM (ed) Current ornithology. Plenum Press, New York, pp 147–207

Kear J (1962) Food selection in finches with special reference to interspecific differences. P Zool Soc Lond 138:163–204

Kellomäki E (1977) Food of the pygmy owl Glaucidium passerinum in the breeding season. Ornis Fenn 12:49–51. https://doi.org/10.1016/j.beproc.2010.06.005

Korpimäki E (1987) Prey caching of breeding Tengmalm’s owls. J Anim Ecol 61:103–111. https://doi.org/10.2307/5513

Korpimäki E, Hakkarainen H (1991) Fluctuating food abundance determines the lifetime reproductive success of male Tengmalm’s owls. J Anim Ecol 61:552–555

Korpimäki E, Kallmark O (1998) Prey selection and survival in birds. J Anim Ecol 67:51–70. https://doi.org/10.1046/j.0021-8790.2001.00570.x

Korpimäki E, Norrdahl K, Huitu O, Klemola T (2005) Predator-induced synchrony in population oscillations of coexisting small mammal species. Proc R Soc Lond B 272:193–202. https://doi.org/10.1098/rspb.2004.2860

Krugér O (2005) The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. Ecol Evol 19:467–486. https://doi.org/10.1007/s10682-005-0293-9

Kullberg C (1995) Strategy of the pygmy owl while hunting avian and mammalian prey. Ornis Fenn 72:72–78

Kuznetsova A, Brockhoff PB, Christensen RHB (2016) lmerTest: tests in linear mixed effects models, https://cran.r-project.org/web/packages/lmerTest/index.html

Laaksonen T, Korpimäki E, Hakkarainen H (2002) Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm’s owls. J Anim Ecol 71:23–31. https://doi.org/10.1046/j.1461-0266.2001.00570.x

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

Lagerström M, Syrjänen J (1990) Varpuspöllön iän määrittäminen (Summary: Ageing Pygmy Owls). Linumittus 25:291–194

Lehikoinen A, Hokkanen T, Lokki H (2011a) Young and female-biased irruptions in pygmy owls Glaucidium passerinum in southern Finland. J Avian Biol 42:564–569. https://doi.org/10.1111/j.1600-048X.2011.05461.x

Lehikoinen A, Ranta E, Pietäiäinen H, Byholm P, Saurola P, Valkama J, Huitu O, Henttonen H, Korpimäki E (2011b) The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. Oecologia 165:349–355. https://doi.org/10.1007/s00442-010-1730-1

Lenth RV (2016) Least-squares means: the R package lsmeans. J Stat Softw 69:1–33. https://doi.org/10.18637/jss.v069.i01

Limmer B, Becker PH (2009) Improvement in chick provisioning with parental experience in a seabird. Anim Behav 77:1095–1101. https://doi.org/10.1016/J.ANBEHAV.2009.01.015

Lindberg P (1966) Irruption of the pygmy owl (Glaucidium passerinum) into southern Scandinavia 1963-1964. Vär Fågelmäst 25:106–142

Lindén A, Mäntyniemi S (2011) Using the negative binomial distribution to model overdispersion in ecological count data. Ecology 92:1414–1421. https://doi.org/10.18637/jss.v069.i01

Marchetti K, Price T (1989) Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. Biol Rev 64:51–70. https://doi.org/10.1017/S0006815X.1989.00638.x

Martin K (1995) Patterns and mechanisms for age-dependant reproduction and survival in birds. Am Zool 35:340–348

Martin TE (1987) Food as a limit on breeding birds: a life-history perspective. Annu Rev Ecol Syst 18:453–487. https://doi.org/10.1146/annurev.es.18.110187.002321

Massimini S, Korpimäki E, Wiehn J (2000) Reversed sexual size dimorphism in Raptors: evaluation of the hypotheses in kestrels breeding in a temporarily changing environment. Oecologia 124:26–32

Mikkola H (1970) On the activity and food of the pygmy owl Glaucidium passerinum during breeding. Ornis Fenn 49:50–51. https://doi.org/10.1002/ecm.1238

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

Morosinotto C, Villers A, Thomson RL, Varjonen R, Korpimäki E (2017) Competitors and predators alter settlement patterns and reproductive success of an intraguild prey. Ecol Monogr 87:4

Newton I (1979) Population ecology of raptors. T. & A.D. Poyser Ltd., Berkhamstead

Newton I (1998) Population limitation in birds. Academic Press, London

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

Nol E, Smith JNM (1987) Effects of age and breeding experience on seasonal reproductive success in the song sparrow. J Anim Ecol 56:301–313. https://doi.org/10.2307/4816

Nyby J, Wallace P, Owen K, Thiessen DD (1973) An influence of hormones on hoarding behavior in the Mongolian gerbil (Meriones unguiculatus). Horm Behav 4:283–288. https://doi.org/10.1016/0018-500X(73)90027-5

Springer
Orians GH (1969) Age and hunting success in the brown pelican (Pelecanus occidentalis). Anim Behav 17:316–319
Penteriani V, Rutz C, Kenward R (2013) Hunting behaviour and breeding performance of northern goshawks Accipiter gentilis, in relation to resource availability, sex, age and morphology. Naturwissenschaften 100:935–942. https://doi.org/10.1007/s00114-013-1093-7
Persson J (2005) Female wolverine (Gulo gulo) reproduction: reproductive costs and winter food availability. Can J Zool 83:1453–1459. https://doi.org/10.1139/z05-205-143
Core Team R (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna http://www.R-project.org
Ralph CJ, Pearson CA (1971) Correlation of age, size of territory, plumage, and breeding success in white-crowned sparrows. Condor 73:77–80
Reznick D, Nunney L, Tessier A (2000) Big houses, big cars, superfleas and the costs of reproduction. Trends Ecol Evol 15:418–425, https://doi.org/10.1016/S0169-5347(00)01941-8
Scherzinger W (1970) Zum Aktions system des Sperlingskauzes. J Avian Biol 38:630–634. https://doi.org/10.1111/j.2007.0908-8857.03960.x
Solheim R (1984a) Caching behaviour, prey choice and surplus killing by pygmy owls Glaucidium passerinum during winter, a functional response of a generalist predator. Ann Zool Fenn 21:301–308
Solheim R (1984b) Breeding biology of the pygmy owl Glaucidium passerinum in two biogeographical zones in southeastern Norway. Ann Zool Fenn 21:295–300
Strümpell K (1999) On the food of the Eurasian pygmy owl (Glaucidium passerinum) in Switzerland. Slovak Raptor J 9:115–126. https://doi.org/10.1515/srj-2015-0009
Strom H, Sonerud GA (2001) Home range and habitat selection in the pygmy owl Glaucidium passerinum. Ornis Fenn 78:145–158
Suhonen J, Halonen M, Mapses T, Korpimäki E (2007) Interspecific competition limits larders of pygmy owls Glaucidium passerinum. J Avian Biol 38:630–634. https://doi.org/10.1111/j.2007.0908-8857.03960.x
Terrabke J, Villers A, Poudré L, Varjonen K, Korpimäki E (2017) Increased autumn rainfall disrupts predator-prey interactions in fragmented boreal forests. Glob Change Biol 23:1361–1373. https://doi.org/10.1111/gcb.13408
Vander Wall SB (1990) Food hoarding in animals. The University of Chicago Press, Chicago
Vander Wall SB, Smith KG (1987) Cache-protecting behavior of food-hoarding animals. In: Kamil AC, Krebs JR, Pulliam HR (eds) Foraging behavior. Springer US, Boston, MA, pp 611–644
Vaughan R (1961) Falco eleonorae. Ibis 103:114–128. https://doi.org/10.1111/j.1474-919X.1961.tb02424.x
Walter TA, Strickland D (2006) Climate change and the demographic demise of a hoarding bird living on the edge. Proc R Soc Lond B 273:2809–2813. https://doi.org/10.1098/rspb.2006.3667
Williams T, Fuijman L, Horning M, Davis R (2004) The cost of foraging by a marine predator, the Weddell seal Leptonychotes weddellii: pricing by the stroke. J Exp Biol 207:973–982
Wunderle JM Jr (1991) Age-specific foraging proficiency in birds. In: Kamil AC, Krebs JR, Pulliam HR (eds) Foraging behavior. Springer US, Boston, MA, pp 611–644
Vander Wall SB, Smith KG (1987) Cache-protecting behavior of food-hoarding animals. In: Kamil AC, Krebs JR, Pulliam HR (eds) Foraging behavior. Springer US, Boston, MA, pp 611–644
Vaughan R (1961) Falco eleonorae. Ibis 103:114–128. https://doi.org/10.1111/j.1474-919X.1961.tb02424.x
Walter TA, Strickland D (2006) Climate change and the demographic demise of a hoarding bird living on the edge. Proc R Soc Lond B 273:2809–2813. https://doi.org/10.1098/rspb.2006.3667
Williams T, Fuijman L, Horning M, Davis R (2004) The cost of foraging by a marine predator, the Weddell seal Leptonychotes weddellii: pricing by the stroke. J Exp Biol 207:973–982
Wunderle JM Jr (1991) Age-specific foraging proficiency in birds. In: Power DM (ed) Current ornithology, vol 8. Plenum Publishing Corporation, New York, pp 273–324
Yosef R, Pinshow B (1989) Cache size in shrikes influences female mate choice and reproductive success. Auk 106:418–421
Yosef R, Pinshow B (2005) Impaling in true shrikes (Laniidae): a behavioral and ontogenetic perspective. Behav Process 69:363–367. https://doi.org/10.1016/j.beproc.2005.02.023
Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York