

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

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18 vole cycle

19

20 **Abstract**

21 Hoarding behaviour (storing food for a later use) has evolved to reduce starvation risk when
22 resources are scarce. Different age and sex classes often show differences in foraging due to

23 experience, skills or life history strategy, but such differences in hoarding under spatio-temporally
24 varying environmental conditions have rarely been studied in the wild. We studied hoarding
25 behaviour of Eurasian pygmy owls (*Glaucidium passerinum*) during 2003-16 in western Finland,
26 where the abundance of their main prey (voles) fluctuates in three-year population cycles. In 14
27 years, 1093 food stores were found during the hoarding season (Oct-Dec) and 337 pygmy owls
28 were trapped at these stores. The number of stores per individual did not vary in relation to age, sex
29 or vole abundance. Adults (+1-year old) had their stores farther apart than yearlings. Both the
30 number of stores per year and the biomass of stored prey items increased with vole abundance.
31 Females and yearlings had larger and heavier stores than males and adults, respectively. The same
32 individuals stored more food as yearlings than as adults. These sex- and age-differences in hoarding
33 indicate that it is not constrained by experience or skills. It rather seems that less-experienced
34 yearlings rely more on stored food than adults. Females may need more food due to their larger size
35 and need to accumulate energy reserves before reproduction. A detailed knowledge of age- and sex-
36 related differences in hoarding behaviour under fluctuating abundances of main foods is
37 fundamental to better understand a population response to climate change and forest management.

38

39 **Significance statement**

40 The hoarding behaviour of animals has evolved to cope with the problem of food limitation. On the
41 basis of 14-year data from pygmy owls we show that the number of stores per year and the biomass
42 of prey items per store increased with vole abundance in the environment. Adults had stores farther
43 apart than yearlings, and females and yearlings stored more prey items and biomass compared to
44 males and adults, respectively. These results indicate that hoarding behaviour responds to the
45 available main prey abundance and varies with traits such as age and sex. Because different age and
46 sex classes might respond differently to variation in food abundance, due to habitat alterations or
47 climate change, a detailed knowledge of hoarding behaviour can be of particular importance to

48 understand changes in body condition, reproductive success and survival of pygmy owls under
49 changing climate and management of boreal forest.

50

51

52 **Introduction**

53 Animal populations are strongly limited by variation in food availability (Newton 1998) through
54 many different pathways affecting survival and reproduction (Lack 1947; Martin 1987; Reznick et
55 al. 2000). Animals have therefore evolved several strategies to store energy in order to face times of
56 food scarcity (Brodin and Clark 2007), which can arise from fluctuations in food availability (e.g.
57 harsh winter), demand (e.g. reproduction), or both (Roberts 1979; Vander Wall 1990). They can
58 store energy in the body as fat, carbohydrates or proteins (Brodin and Clark 2007), or externally by
59 hoarding (also referred to as caching or storing) food when resources are abundant (Vander Wall
60 1990; Brodin and Clark 2007). In particular, harsh wintering conditions, such as cold temperatures
61 and deep snow cover, could have led to the evolution of hoarding (Roberts 1979; Smith and
62 Reichman 1984). At high latitudes, cold climate may promote hoarding behaviour both by creating
63 a situation of food scarcity and by favouring the preservation of the food itself (Källander and
64 Smith 1990). Indeed, in the highly seasonal environment of boreal forests in the north, a
65 considerable number of species hoard food (Smith and Reichman 1984; Vander Wall and Smith
66 1987), and among avian predators (owls, diurnal raptors and shrikes), some forms of food hoarding
67 are fairly common during periods of food scarcity or during the breeding season (Korpimäki 1987;
68 Yosef and Pinshow 1989; Källander and Smith 1990). These species are usually scatter-hoarders,
69 and food items are dispersed in several cavities or placed on tree branches or bushes (Vander Wall
70 1990).

71 In many species, there are age differences in foraging behaviour and skills that could lead to
72 different responses in periods of food scarcity. In general, young individuals often appear to have

73 lower performance than more mature ones, both as hunters and as breeders (Orians 1969; Wunderle
74 1991; Daunt et al. 1999; Laaksonen et al. 2002; Rutz et al. 2006). Several hypotheses have been put
75 forward to explain this age-effect (Forslund and Pärt 1995; Martin 1995). First, according to the
76 *constraint* hypothesis (Curio 1983), the young individuals could be constrained by their inferior
77 foraging skills, as they are usually still learning and practicing (Kear 1962; Marchetti and Price
78 1989; Wunderle 1991; Limmer and Becker 2009). Second, the young individuals could be
79 refraining their effort, especially in breeding activities, in order not to jeopardize their survival and
80 future breeding success (the *restraint* hypothesis; Curio 1983). In the context of hoarding, it could
81 however be hypothesized that young individuals actually need to put more effort into hoarding than
82 old ones if they have poorer hunting skills, whereas old individuals could restrain their effort in the
83 hoarding period because they can rely more on their skills and experience during food scarcity.
84 Third, in cross-sectional data, the cohort of young individuals might contain lower quality
85 individuals that the older age groups no longer contain (the *differential mortality* hypothesis; Curio
86 1983; Forslund and Pärt 1995).

87 Sex differences in foraging are also common (e.g. Clarke et al. 1998; Ishikawa and
88 Watanuki 2002), especially in species of owls and diurnal raptors characterized by reverse size
89 dimorphism (RSD, i.e. females larger than males; Hakkarainen and Korpimäki 1991; Krüger 2005).
90 Numerous hypotheses have been put forward to explain RSD, but the ones that received most
91 support were the *small male* hypothesis (smaller-sized males more efficient hunters) and the
92 *intersexual-competition* hypothesis (size differences reduce intersexual competition for food;
93 Hakkarainen and Korpimäki 1991; Massemin et al. 2000; Krüger 2005). In addition, owls and
94 diurnal raptors have distinct intersexual duties during the breeding season: females produce and
95 incubate eggs and brood the young, whereas males are responsible for providing their mates and
96 offspring from prior to egg-laying until the nestlings will fledge (Newton 1979; Schönn 1980;
97 Mikkola 1983; Korpimäki and Hakkarainen 2012). Therefore, selection for hunting skills is

98 probably higher for males than females. RSD and inter-sexual breeding duties would therefore lead
99 to sex differences in the hunting behaviour, skills and species of prey captured (Earhart and Johnson
100 1970; Ishikawa and Watanuki 2002; Keynan and Yosef 2010; Korpimäki and Hakkarainen 2012).

101 We studied age and sex differences in hoarding behaviour of the Eurasian pygmy owl
102 (*Glaucidium passerinum*; hereafter pygmy owl), a small avian predator that inhabits boreo-alpine
103 forests of the Western Palearctic (Schönn 1980; Mikkola 1983; Barbaro et al. 2016). The pygmy
104 owl is a sexually size dimorphic species (Schönn 1980; Mikkola 1983; Terraube et al. 2017), and
105 the only European avian predator that stores large quantities of food in cavities for winter (Mikkola
106 1983; Solheim 1984a; Schulenburg and Wiesner 1986; Terraube et al. 2017). In boreal
107 environments, the wide periodical fluctuations in the abundances of small mammal populations
108 govern the population densities and reproductive success of predators, including the pygmy owl
109 (Korpimäki and Hakkarainen 1991; Korpimäki and Norrdahl 1991; Korpimäki 1992; Newton 2002;
110 Korpimäki et al. 2005; Lehikoinen et al. 2011b). Most of the potential avian prey of pygmy owls
111 migrate south for the winter while snow cover can hide small mammals. Deep snow layer
112 effectively prevents small-sized owls to hunt voles below snow (Mikkola 1983; Halonen et al.
113 2007). Stored food can thus be critical for the wintering pygmy owls when fresh food is
114 unavailable. The food hoarding behaviour of pygmy owls in terms of store contents has been
115 described in several studies (e.g. Mikkola 1983; Solheim 1984a; Halonen et al. 2007; Terraube et al.
116 2017), but little is known about differences in hoarding behaviour in relation to age and sex of the
117 individual. Using a 14-year data, we examined (i) number of and distance between food stores of
118 the same owl, (ii) among-year variation in the number and biomass of the prey items stored, as well
119 as (iii) sex- and age-class related differences in the hoarding behaviour and food store
120 characteristics under varying abundance of their main prey (voles). The *constraint* and *restraint*
121 hypotheses predict that young individuals would have fewer and/or smaller stores than adults, and
122 that store size would increase with age within individuals. The latter would be simultaneously

123 evidence against the *differential mortality* hypothesis, which does not predict within-individual
124 change. Second, we predicted that the larger females would store more food than males because
125 they need a larger amount of food to survive the winter and to accumulate energy reserves for
126 reproduction. However, it could also be that females would have smaller stores than males if the
127 males are more efficient hunters (as suggested by the *small male* hypothesis). Finally, young
128 individuals and females might be less able to cope especially with food scarcity, so we expect
129 differences in hoarding between the age and sex classes to be larger when the food is scarce in the
130 environment.

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

138

139

140 **Materials and Methods**

141

142 *Study area*

143 The data were collected during 2003-2016 in the vicinity of Kauhava, western Finland (63°N,
144 23°E). The study area covers approximately 1000 km² and consists mainly of managed forests and
145 agricultural land. The management of the forested habitats has created a mosaic of clear-cut areas
146 and different-aged forests where the main tree species are Scots pine (*Pinus sylvestris*), Norway

147 spruce (*Picea abies*) and in smaller proportions some deciduous trees (Hakkarainen et al. 2003;
148 Morosinotto et al. 2017). A total of 305 areas of forests (hereafter “forest-sites”; mean \pm SD: 211 \pm
149 64 forest-sites per year during 2003-16) were provided with nest-boxes for pygmy owls during the
150 study years, but the number of forest-sites available per year was not constant because each year
151 some of the forest-sites were clear-cut, and the boxes were either relocated to the nearest forest-site
152 or removed. In most cases, we set up two nest boxes per forest-site (mean \pm SD: 95 \pm 5 % sites per
153 year). The two nest boxes were set mainly in spruce trees at the height of 1-2 m, on average 88.5 m
154 apart (range 22-310 m), to allow pygmy owls to have at least one box available throughout the year,
155 since Siberian flying squirrels (*Pteromys volans*) also prefer to reproduce and roost in these boxes
156 throughout the year (Morosinotto et al. 2017). Each nest box had an entrance hole with a diameter
157 of 45 mm, preventing other owl and diurnal raptor species from entering and storing or stealing
158 prey items (Solheim 1984a; Morosinotto et al. 2017).

159

160 *Study species*

161 The pygmy owl is diurnal with activity peaks at dusk and dawn and predominantly inhabits boreal
162 and alpine forests of Eurasia (Mikkola 1970; Schönn 1980; Mikkola 1983; Kullberg 1995). It nests
163 in natural tree cavities, or artificial nest boxes, preferring usually old and mature coniferous forests
164 (Strom and Sonerud 2001; Halonen et al. 2007; Barbaro et al. 2016; Morosinotto et al. 2017). The
165 pygmy owl is well adapted to the cold and individuals usually establish winter territories, with
166 occasional irruptive migrations at times of food depletion (Lindberg 1966; Schönn 1980; Mikkola
167 1983; Lehikoinen et al. 2011a). In Northern Europe, the prey items stored for the winter consist
168 mainly of bank voles (*Myodes glareolus*), voles of the genus *Microtus* (*Microtus* voles, e.g. the field
169 vole *Microtus agrestis*, and the sibling vole *M. rossiaemerdionalis*), shrews (the common shrew
170 *Sorex araneus*, the pygmy shrew *Sorex minutus*), mice (the Eurasian harvest mouse *Micromys*
171 *minutus*, the house mouse *Mus musculus*) and small birds, usually passerines, with body mass <60 g

172 (Kellomäki 1977; Halonen et al. 2007; EK and GM unpublished data). Overall, diet composition of
173 pygmy owls is related to prey availability and can therefore differ according to geographic area and
174 season (Kellomäki 1977; Schönn 1980; Mikkola 1983; Ekman 1986; Schulenburg and Wiesner
175 1986; Šotnár et al. 2015). During late autumn and early winter, pygmy owls hoard prey items in
176 natural cavities and nest-boxes (Scherzinger 1970; Schönn 1980; Solheim 1984a; Suhonen et al.
177 2007; Terraube et al. 2017). In the study area, the species occupies the boxes both for breeding in
178 spring and for food hoarding in autumn and winter. It has to be noted that pygmy owls can make
179 more than one food-store and that a single box can be visited by more than one pygmy owl (see
180 Results of this study).

181

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

183 The boxes were inspected for the presence of stored prey items twice during the autumn, from late
184 October to mid-December. Prey items were usually stored as whole, and thus species identification
185 was possible in most cases. Prey items in food stores were also marked by toe-clipping (birds) or
186 tail-clipping (mammals) to avoid double counting. The total number and mass of prey items were
187 calculated by summing up the fresh prey items counted in the two visits done from late October to
188 mid-December. If the weight of each prey item was not recorded, but the number and species were
189 (10.9% of the total prey items), the relative average weight of the species for that year was used. In
190 a few cases in which only the number of prey items was recorded, but species and the weight of
191 each prey item were not identified, which can happen when the prey items get rotten or frozen, the
192 store was excluded from the analysis (7.5% of the total prey items).

193 From 2003 to 2016 during the hoarding season, pygmy owls were captured, measured and
194 ringed for individual identification. The vast majority of owls (80.47%) were captured with nest
195 box traps (a replica of the box equipped with swing door), seven individuals with a telescopic
196 fishing pole with a loop at the top, and one individual by hand inside the box. The captured owls

197 were sexed and aged, their wing and tail length were measured and they were weighed with a
198 Pesola spring balance. Sex was assessed on the basis of the known sexual dimorphism of the
199 species (Mikkola 1983), and based on measurements of owls in the study area during breeding
200 season, when females can be distinguished by males being the only ones incubating and having a
201 brood patch (wing length: females mean 106 mm, 5th-95th percentiles 103-110 mm; males mean 99
202 mm, 5th-95th percentiles 96-102 mm; tail length: females mean 65 mm, 5th-95th percentiles 61-69
203 mm; males mean 60 mm, 5th-95th percentiles 55-65 mm; body mass: females mean 77 g, 5th-95th
204 percentiles 69-87 g; males mean 60 g, 5th-95th percentiles 55-65 g; EK, unpublished data). When the
205 sex of the owl was not possible to identify with certainty because of overlap in the range of wing
206 length, tail length and body mass between large males and small females, the individuals were
207 excluded from the analyses of inter-sexual differences (N = 17 individuals). Age was estimated
208 according to wing moult (Cramp 1985; Lagerström and Syrjänen 1990) and individuals were
209 divided in two classes: individuals at their hatching year (hereafter ‘yearlings’) and older
210 individuals (hereafter ‘adults’). The rest of the identities of storing owls (18%) were obtained
211 mainly using Passive Integrated Transponder tags (PIT). From 2011, the owls were marked with a
212 PIT tag, a small electromagnetic microchip implanted subcutaneously. They are the key element of
213 the application of a technology used for individual identification in animals, the Radio Frequency
214 Identification (RFID; Gibbons and Andrews 2004). Data on encounters of individual owls were
215 collected by placing the antenna of the reader around the entrance hole of the nest box. The antenna
216 was positioned when the food store was found, but we did not succeed in capturing the owl with the
217 nest-box trap. The antenna was then kept in place at least for two weeks or until the reader recorded
218 the identity of a hoarding owl. We refer to the owl that was first captured entering the store, or the
219 owl that on the basis of the reader data entered the store most often, as the “hoarder” of the store.
220 Therefore, the reader data helped identifying with more certainty the owl that hoarded the food
221 store, since pygmy owls can make multiple stores and several individuals can sometimes visit the
222 same store (see Results). Data related to the identity of the hoarder were therefore provided both by

223 the trapping and by the data collected with the PIT-tag method. Age and sex of the individual were
224 assessed with the focal animals in the field, whereas to minimize observer bias blinded methods
225 were used when all the other behavioural data were recorded and/or analysed.

226

227 *Vole abundance*

228 The abundance of small mammals (voles, shrews and mice) was estimated biannually by snap
229 trapping in early May and mid-September. In two locations 14 km apart within the study area, 50-
230 100 metal mouse snap-traps were set up to cover 0.5 to 1.0 ha and the four main habitat types; i.e.
231 agricultural and abandoned fields, and forests dominated by spruce or pine (Korpimäki et al. 2005).
232 The traps (baited with mixed-grain bread) were placed in runways of small mammals and checked
233 daily for three-to-four days. The regional synchrony of vole population cycles and thus indices of
234 small mammals extends up to 80 km (Huitu et al. 2003; Korpimäki et al. 2005), therefore the
235 validity of this index could be extended to the whole study area. To obtain a vole abundance index
236 for the analyses, the results from the four-night trapping sessions done in spring (May) and autumn
237 (September) for both the bank voles and *Microtus* voles (voles species only) were pooled and
238 standardised as number of animals captured per 100 trap nights.

239

240 *Statistical analyses*

241 To analyse the hoarding behaviour of pygmy owls in relation to the fluctuation in vole abundance
242 and to age and sex of the owl, Generalised Linear Models (GLMs) and Generalised Linear Mixed
243 Models (GLMMs) were fitted using maximum likelihood (Laplace approximation). Only the cases
244 in which it was possible to identify the hoarder of the store were used in the analyses involving age
245 and sex of the owl.

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

254 We analysed whether the number of stores hoarded by an owl and the mean distances
255 between them were affected by the abundance of voles in autumn or whether there were any
256 differences in relation to sex and age of the individual. The distances between every store of each
257 individual (with at least 2 stores) during a particular year, were calculated from the coordinates of
258 the boxes using the function ‘gDistance’ in the package *GIStools* (R package v. 0.7-4; Brunsdon
259 and Chen 2014). From the obtained dataset, minimum, maximum and mean values for every owl
260 and year were extracted. The number of stores of each individual and their mean distance were
261 tested in relation to the abundance index of vole populations, age and sex of the owl, using GLMMs
262 with ‘individual identity’ of the owl (the numeric code of the owl metal ring) as a random effect.
263 The ‘individual identity’ was used to control for possible repeated measures of the same individual,
264 both in different boxes in the same year (e.g. if an individual had multiple stores) or between
265 multiple years.

266 To analyse the impact of vole abundance and pygmy owl sex and age on the number and
267 biomass of the prey items in the food store, we used a dataset that included only the cases in which
268 the store hoarder was identified. Explanatory variables included autumn vole abundance and age
269 and sex of the owl, and their two-way interactions. Due to fact that males and females differ in body
270 size, we also tested for an effect of wing length. The wing length standardised by sex was used

271 together with the other variables, but it was never significant (see description of the models and
272 results in Supplementary Material S1). As response variables, we used the total number and the
273 total mass of prey items in the stores, using the content of the single store as a measure and not the
274 sum of the stores hoarded by an individual. This decision was made due to the fact that the content
275 of the single store could be measured exactly while it was not possible to know if the owl had other
276 unknown stores (i.e. in natural cavities or in a box without an identified hoarder). Since the count
277 data for the total number of prey items were over-dispersed, it was decided to use negative binomial
278 likelihood family (Zuur et al. 2009; Lindén and Mäntyniemi 2011). The total mass of prey items
279 was \log_{10} -transformed to fit the normal distribution. ‘Individual identity’ of the owl and ‘site/box’
280 (‘box’ nested in ‘site’, i.e. the forest-site where each nest box pair was set) were used as random
281 effect in all the models. “Site/box’ was included as random effect to take into account spatial and
282 temporal pseudo-replication, since most forest-sites had two available nest boxes and were used
283 multiple times during the 14-year data set. Overall, 69% of the sites (over 50% of the boxes) were
284 used as food stores more than once during the study period. Models were run both with and without
285 the statistically significant outlier observation identified by the Grubbs test for outliers (total
286 number: $G = 8.20$, $U = 0.89$, $P < 0.001$; total mass: $G = 9.94$, $U = 0.84$, $P < 0.001$); there were no
287 differences and the full dataset was used. The models without the outlier observation are presented
288 in the Supplementary Material S2. In both analyses, we started with a full model (all the
289 explanatory variables and the two-way interactions) and obtained a model with all significant
290 variables through backward stepwise selection (significance evaluated with the function ‘Anova’ in
291 the R package *car* v. 2.1-6).

292 Models were usually constructed through the ‘lmer’ and the ‘glmer’ functions in the
293 package *lme4* (R package v. 1.1-13; Bates et al. 2015), in conjunction with package *lmerTest* (R
294 package v. 2.0-33; Kuznetsova et al. 2016). Whereas the package *glmmADMB* (R package v.
295 0.8.3.3) was used in case of negative binomial models (Fournier et al. 2012; Skaug et al. 2016).

296 Least square means (i.e. marginal means) were obtained through the package *lsmeans* (R package v.
297 2.27-2; Lenth 2016). All statistical tests and calculations were performed using R v. 3.4.0 (R Core
298 Team 2017).

299

300 ***Data availability***

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

303

304

305 **Results**

306

307 *Number of food stores in relation to main food abundance*

308 The data collected during the study period (2003-2016) is summarized in Table 1. On average, 32%
309 of the forest-sites had at least one store, with variation from a minimum of 15% in 2006 to a
310 maximum of 47% stores in 2011 (Fig. 1). The proportion of forest-sites with a food store and the
311 number of hoarding pygmy owls captured did not show any long-term temporal trend during 2003-
312 2016 (Table 2a, Fig. 1), but significantly increased with the abundance of voles in the environment
313 (Fig. 2).

314

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

316 The hoarder of the store was identified and sexed in 57.5% cases (see Table 1 for details on
317 numbers of stores and owls observed). The owls were either captured inside or in the vicinity of the
318 store or recorded with the PIT-tag reader during the food-hoarding season within the 14 study-

319 years. Of all the captured and sexed owls, 46% were males, 54% were yearlings and 23% were
320 captured or recorded during multiple hoarding seasons. The use of the PIT-tag reader, combined
321 with the trapping, increased the number of identified hoarders from an average of 50.3% per year (\pm
322 5.4 SE, from 2003 to 2010, only trapping) to an average of 65.2% per year (\pm 3.4 SE, from 2011 to
323 2016, combined methods). The PIT-tag reader recorded data for 156 stores in 6 years (2011-2016),
324 of which in only 20 cases two different individuals visited the same food store. In 9 of these cases,
325 the hoarder was easy to identify due to the far higher number of visits to the store by the hoarder. In
326 the remaining 11 cases, it was not possible to identify the hoarder and they were therefore removed
327 from the analyses. Overall in 48% of the cases, the owl had only one store per storing season (299
328 stores of 607) whereas in the remaining cases an owl had multiple food stores (range 2-6 stores per
329 owl). The GLMMs indicated no relationship between number of stores by the individual and
330 autumn vole abundance, and no obvious differences in the number of stores between sexes (least
331 square means, LSM, \pm SE: males 1.47 ± 0.08 , females 1.46 ± 0.08 ; see Table 2b) or age classes
332 (LSM \pm SE: yearling 1.51 ± 0.08 , adults 1.43 ± 0.09 ; see Table 2b).

333 Of the 38 cases in which food stores were found in two boxes located in the same forest-site,
334 the two stores were hoarded by different individuals only in ten cases, whereas in the remaining 28
335 cases the two stores were hoarded by the same owl. The average (\pm SE) distance between two stores
336 of the same individual was 1470 ± 942 m with the maximum distance recorded 4990 m. There was
337 no obvious association of the autumn vole abundance with the mean distance between stores (Table
338 2c). The mean distance between stores did not vary between sexes (LSM \pm SE: males 1616 ± 119
339 m, females 1585 ± 124 m; see Table 2c), whereas yearling owls had significantly shorter distance
340 between their stores than adults (LSM \pm SE: yearling 1428 ± 105 m, adults 1773 ± 134 m; see
341 Table 2c). A frequency distribution plot of the mean distance between stores of the same individual
342 shows that yearlings had their stores less spread than adults, and both mean and median values were
343 lower than in adults (Fig. 3).

344

345 *Number and biomass of prey items*

346 Mammals were stored in a higher frequency than birds (93.6% vs 6.4% of prey items). The autumn
347 vole abundance, and age and sex of the hoarder were all significant predictors of the total number
348 and of the total mass of prey items in a food store (Table 3). In particular, males appeared to store
349 fewer prey items than females (LSM \pm SE: males 16.7 ± 3.1 items, females 21.8 ± 3.5 items), and to
350 have lighter stores (LSM \pm SE: males 146.4 ± 10.5 g, females 197.6 ± 13.8 g; Table 3, Fig. 4). Also,
351 yearlings stored overall more items than older individuals, but the increase of the number of stored
352 food items in relation to the vole abundance was steeper for adults than for yearlings (LSM \pm SE:
353 yearlings 22.3 ± 4.8 and adults 16.3 ± 2.3 ; Table 3, Fig. 4a). This difference in relation to the vole
354 abundance was not present when analysing the total mass of prey items (none of the interaction was
355 significant), and food stores of both age groups appeared to increase in the same way with the vole
356 abundance in current autumn (LSM \pm SE: yearlings 198.5 ± 13.3 g and adults 145.6 ± 10.9 g; Table
357 3, Fig. 4b). Following these results on the two age classes, we analysed within-individual
358 differences in relation to age. The average store content of the same individual as a yearling and
359 later on as an adult was compared with a paired t-test, and yearling owls were found to have larger
360 and heavier stores than adults (total number of prey items: mean \pm SE: yearlings 27.6 ± 3.2 and
361 adults 16.5 ± 2.1 , $t = 2.96$, $df = 49$, $P = 0.002$; total mass of prey items: mean \pm SE: yearlings 416.9
362 ± 47 g and adults 244 ± 35.5 g; $t = 2.93$, $df = 49$, $P = 0.003$; $N = 50$ individuals).

363

364

365 **Discussion**

366

367 Our main findings were as follows. First, yearling owls and females had overall larger and heavier
368 food-stores than adult owls and males, respectively. These results suggest that food hoarding is not
369 limited by hunting experience or skills as predicted by the *constraint-hypothesis*, and instead
370 support the hypothesis that yearlings might invest more in hoarding than adults during autumn
371 because they might not be able to rely on daily hunting success during winter. Females, on the other
372 hand, might need larger stores due to their larger size and to maintain and improve body condition
373 for the breeding season. Second, both the number of stores per year, and the number and biomass of
374 prey items in food stores of pygmy owls increased with autumn vole abundance in the field. In
375 years when vole abundance was high, owls of all age and sex classes stored more food than in years
376 of low vole abundance. However, the relationship was stronger in adult than in young individuals.
377 In years of low vole abundance, adult individuals had smaller stores than the young ones, which
378 again shows that lack of experience is not constraining hoarding but on the contrary inducing a
379 higher investment in hoarding.

380

381 *Annual variation in the number of hoarding owls and food stores*

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

391 away from the area, therefore inducing a decrease in number of owls that are still present in autumn
392 and that will hoard food for the winter.

393

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

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

410 When the same individual hoarded food in more than one box, boxes were usually in
411 neighbouring forest-sites, and with an average distance of 1.5 km, which is close to the average
412 distance between forest-sites in our study area (1429 ± 721 km; see Morosinotto et al. 2017). The
413 distance between stores of the same individual did not change according to autumn vole abundance
414 and no difference was found between sexes. However, we found that yearling owls usually had
415 stores closer to each other than adults. Less experienced yearlings might be less able to widen their

416 home range, possibly because of competition for high-quality food storing sites with abundant food
417 patches. Another possibility is that adult individuals might have learnt that it is more convenient to
418 spread food stores further away from each other and they might also be better at coping with the
419 higher cost of spacing the caches. If considering strictly the range size, previous studies on age-
420 related differences show contrasting results and are usually focused on breeding individuals. In
421 some cases, adult individuals had larger home ranges than sub-adults or yearlings (Ralph and
422 Pearson 1971; Harestad and Bunnell 1979), whereas, in others they were larger in immatures or
423 young breeders (Rohner 1997; Penteriani et al. 2013). However, very little is known about winter
424 territories in relation to age. Due to the correlative nature of the long-term dataset collected here it
425 was not possible to investigate the link between experience and the spatial distribution of food-
426 stores, but these preliminary results are a first attempt to address the issue of store spreading in
427 relation to age or experience.

428

429 *Age differences under fluctuating food availability*

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

439 Not much is known about age-specific patterns in food hoarding. Age-related differences in
440 hoarding behaviour are often related to its ontogeny and limited to the first weeks of life of the

441 individual (Vander Wall 1990), i.e. pouch filling and emptying in golden hamsters (Etienne et al.
442 1982), impaling of prey in shrikes (Yosef and Pinshow 2005), and handling and storing seeds in
443 marsh tits (Clayton 1992). In our case, the hoarding differences between the two age groups are
444 shown when the behaviour has already developed and might therefore reflect differences in hunting
445 performances. In general, young individuals are less experienced than adults and have been shown
446 to have lower performances, both as hunters and as breeders (Orians 1969; Wunderle 1991; Daunt
447 et al. 1999; Laaksonen et al. 2002; Rutz et al. 2006). These results suggest an unexpected better
448 performance by young individuals, but might also hide an improvement in hunting abilities with
449 age, and therefore, a lower dependence on the hoarded food. Adult owls at the start of winter have
450 already lived at least through another winter and a reproductive season, in which they would have
451 likely acquired experience in hunting skills. Moreover, the *differential mortality* hypothesis states
452 that individuals of lower quality are more prone to die or disperse, leading to an adult-cohort
453 composed mainly by high-quality better performing individuals (e.g. Nol and Smith 1987;
454 Laaksonen et al. 2002). If yearlings are in fact less efficient hunters than adults, they may
455 compensate by hoarding a higher amount of food. We therefore suggest that adult individuals might
456 have to depend less on stored food than yearlings. This hypothesis might be also supported by the
457 fact that the store size of a certain individual decreased with age. It is likely energetically costly to
458 hunt (Williams et al. 2004) and a heavy investment in hoarding might trade off with other functions
459 during the hoarding season. Unfortunately, we were not able to find out whether the differences
460 found in the amount of food stored are due to an improvement in the hunting skills of adults or a
461 restraint in their effort to hoard.

462

463 *Sex differences in hoarding behaviour*

464 Our results are consistent with the prediction that female pygmy owls hoarded larger and heavier
465 stores than males. We suggest that hunting skills might therefore not constrain the amount of food

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

485 Sex differences in food hoarding have previously been reported in small mammals, with
486 females often storing more food than males, and this behaviour is likely controlled to some extent
487 by sex hormones (Smith and Ross 1950; Nyby et al. 1973; Brenner and Lyle 1975; Formanowicz et
488 al. 1989; Clarke and Kramer 1994; Jenkins 2011). Many hoarding birds are sexually monomorphic,
489 and sex differences might go unnoticed (Vander Wall 1990). Most differences are found during the
490 breeding season, as a ritual for pair bonding males can provide prey items to show to the female

491 their hunting abilities, for example, in southern grey shrikes *Lanius meridionalis* (Keynan and
492 Yosef 2010). In many species, male individuals often store prey items to feed the female and chicks
493 during incubation and chick rearing (see examples in Schnell 1958; Vaughan 1961; Brown 1976;
494 Newton 1979; Korpimäki 1987; Schneider and Wilden 1994). In contrast to the breeding season in
495 which hoarding behaviour is shown only by one sex, in autumn and winter both sexes hunt for
496 themselves. Compared to diet analyses from nest sites, the analysis of food stored for the winter
497 thus allows to better explore inter-sexual differences in hoarding behaviour and diet selection.

498

499 *Conclusions*

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

515 behaviour can therefore be of particular importance to understand changes in over-winter condition
516 and reproductive success of pygmy owls, and ultimately in the whole species community.

517

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519

520

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527

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532 Ethical approval

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538 Conflict of interest

539 The authors declare no conflict of interest.

540

541

542 **References**

543

544 Barbaro L, Blache S, Trochard G, Arlaud C, de Lacoste N, Kayser Y (2016) Hierarchical habitat
545 selection by Eurasian Pygmy Owls *Glaucidium passerinum* in old-growth forests of the
546 southern French Prealps. *J Ornithol* 157:333–342. doi: 10.1007/s10336-015-1285-3

547 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J*
548 *Stat Softw* 67:1–48. doi: 10.18637/jss.v067.i01

549 Brenner FJ, Lyle PD (1975) Effect of previous photoperiodic conditions and visual stimulation on
550 food storage and hibernation in the Eastern chipmunk (*Tamias striatus*). *Am Midl Nat* 93:227-
551 234. doi: 10.2307/2424123

552 Brodin A, Clark CW (2007) Energy storage and expenditure. In: Stephens DW, Brown JS,
553 Ydenberg RC (eds) *Foraging: Behavior and Ecology*. The University of Chicago Press,
554 Chicago, pp 221–269

555 Brown L (1976) *Birds of prey: their biology and ecology*. A & W Publishers, New York

556 Brunsdon C, Chen H (2014) *GISTools: Some further GIS capabilities for R*, <http://CRAN.R->

557 project.org/packageGISTools

558 Clarke J, Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S (1998) Sex differences in
559 Adélie penguin foraging strategies. *Polar Biol* 20:248–258. doi: 10.1007/s003000050301

560 Clarke MF, Kramer DL (1994) Scatter-hoarding by a larder-hoarding rodent: intraspecific variation
561 in the hoarding behaviour of the eastern chipmunk, *Tamias striatus*. *Anim Behav* 48:299–308.
562 doi: 10.1006/anbe.1994.1243

563 Clayton NS (1992) The ontogeny of food-storing and retrieval in marsh tits. *Behaviour* 122:11–25

564 Cramp S (ed) (1985) Handbook of the birds of Europe, the Middle East, and North Africa: terns to
565 woodpeckers, vol. 4. Oxford University Press, Oxford

566 Curio E (1983) Why do young birds reproduce less well? *Ibis* 125:400–404. doi: 10.1111/j.1474-
567 919X.1983.tb03130.x

568 Daunt F, Wanless S, Harris MP, Monaghan P (1999) Experimental evidence that age-specific
569 reproductive success is independent of environmental effects. *Proc R Soc Lond B* 266:1489–
570 1493. doi: 10.1098/rspb.1999.0805

571 Derbyshire R, Strickland D, Norris DR (2015) Experimental evidence and 43 years of monitoring
572 data show that food limits reproduction in a food-caching passerine. *Ecology* 96:3005–3015.
573 doi: 10.1890/15-0191.1.sm

574 Earhart CM, Johnson NK (1970) Size dimorphism and food habits of North American owls. *Condor*
575 72:251–264

576 Ekman J (1986) Tree use and predator vulnerability of wintering passerines. *Ornis Scand* 17:261–
577 267

578 Etienne AS, Emmanuelli E, Zinder M (1982) Ontogeny of hoarding in the golden hamster: The
579 development of motor patterns and their sequential coordination. *Dev Psychobiol* 15:33–45.
580 doi: 10.1002/dev.420150107

581 Formanowicz DR, Bradley PJ, Brodie ED (1989) Food hoarding by the least shrew (*Cryptotis*
582 *parva*): intersexual and prey type effects. *Am Midl Nat* 122:26–33. doi: 10.2307/2425679

583 Forslund P, Pärt T (1995) Age and reproduction in birds - hypotheses and tests. *Trends Ecol Evol*
584 10:374–378. doi: 10.1016/S0169-5347(00)89141-7

585 Fournier DA, Skaug HJ, Ancheta J, Acheta J, Ianelli J, Magnusson A, Maunder MN, Nielsen A,
586 Sibert J (2012) AD Model Builder: using automatic differentiation for statistical inference of
587 highly parameterized complex nonlinear models. *Optim Methods Softw* 27:233–249. doi:
588 10.1080/10556788.2011.597854

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

591 Hakkarainen H, Korpimäki E (1991) Reversed sexual size dimorphism in Tengmalm's Owl: is
592 small male size adaptive? *Oikos* 61:337–346. doi: 10.2307/3545241

593 Hakkarainen H, Mykrä S, Kurki S, Korpimäki E, Nikula A, Koivunen V (2003) Habitat
594 composition as a determinant of reproductive success of Tengmalm's owls under fluctuating
595 food conditions. *Oikos* 100:162–171. doi: 10.1034/j.1600-0706.2003.11906.x

596 Halonen M, Mappes T, Meri T, Suhonen J (2007) Influence of snow cover on food hoarding in
597 Pygmy Owls *Glaucidium passerinum*. *Ornis Fenn* 84:105–111

598 Harestad AS, Bunnell FL (1979) Home range and body weight - a reevaluation. *Ecol Ecol* 60:389–
599 402

600 Huitu O, Norrdahl K, Korpimäki E (2003) Landscape effects on temporal and spatial properties of
601 vole population fluctuations. *Oecologia* 135:209–220. doi: 10.1007/s00442-002-1171-6

602 Ishikawa K, Watanuki Y (2002) Sex and individual differences in foraging behavior of Japanese
603 cormorants in years of different prey availability. *J Ethol* 20:49–54. doi: 10.1007/s10164-002-
604 0053-z

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

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

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

611 Kellomäki E (1977) Food of the Pygmy Owl *Glaucidium passerinum* in the breeding season. *Ornis*
612 *Fenn* 54:1–29

613 Keynan O, Yosef R (2010) Temporal changes and sexual differences of impaling behavior in
614 Southern Grey Shrike (*Lanius meridionalis*). *Behav Process* 85:47–51. doi:
615 10.1016/j.beproc.2010.06.005

616 Korpimäki E (1987) Prey caching of breeding Tengmalm's Owls *Aegolius funereus* as a buffer
617 against temporary food shortage. *Ibis* 129:499–510. doi: 10.1111/j.1474-919X.1987.tb08237.x

618 Korpimäki E (1992) Fluctuating food abundance determines the lifetime reproductive success of
619 male Tengmalms Owls. *J Anim Ecol* 61:103–111. doi: 10.2307/5513

620 Korpimäki E, Hakkarainen H (1991) Fluctuating food supply affects the clutch size of Tengmalm's
621 owl independent of laying date. *Oecologia* 85:543–552. doi: 10.1007/BF00323767

- 622 Korpimäki E, Hakkarainen H (2012) The boreal owl: ecology, behaviour, and conservation of a
623 forest-dwelling predator. Cambridge University Press, Cambridge
- 624 Korpimäki E, Norrdahl K (1991) Numerical and functional responses of kestrels, short-eared owls,
625 and long-eared owls to vole densities. *Ecology* 72:814–826. doi: 10.2307/1940584
- 626 Korpimäki E, Norrdahl K, Huitu O, Klemola T (2005) Predator-induced synchrony in population
627 oscillations of coexisting small mammal species. *Proc R Soc Lond B* 272:193–202. doi:
628 10.1098/rspb.2004.2860
- 629 Krüger O (2005) The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a
630 comparative study. *Evol Ecol* 19:467–486. doi: 10.1007/s10682-005-0293-9
- 631 Kullberg C (1995) Strategy of the pygmy owl while hunting avian and mammalian prey. *Ornis
632 Fenn* 72:72–78
- 633 Kuznetsova A, Brockhoff PB, Christensen RHB (2016) lmerTest: Tests in Linear Mixed Effects
634 Models, <https://cran.r-project.org/web/packages/lmerTest/index.html>
- 635 Laaksonen T, Korpimäki E, Hakkarainen H (2002) Interactive effects of parental age and
636 environmental variation on the breeding performance of Tengmalm’s owls. *J Anim Ecol*
637 71:23–31. doi: 10.1046/j.0021-8790.2001.00570.x
- 638 Lack D (1947) The significance of clutch-size. *Ibis* 89:302–352
- 639 Lagerström M, Syrjänen J (1990) Varpuspöllön iän määrittäminen (Summary: Ageing Pygmy
640 Owls). *Lintumies* 25:291–194
- 641 Lehtikoinen A, Hokkanen T, Lokki H (2011a) Young and female-biased irruptions in pygmy owls
642 *Glaucidium passerinum* in southern Finland. *J Avian Biol* 42:564–569. doi: 10.1111/j.1600-
643 048X.2011.05461.x

- 644 Lehtikoinen A, Ranta E, Pietiäinen H, Byholm P, Saurola P, Valkama J, Huitu O, Henttonen H,
645 Korpimäki E (2011b) The impact of climate and cyclic food abundance on the timing of
646 breeding and brood size in four boreal owl species. *Oecologia* 165:349–355. doi:
647 10.1007/s00442-010-1730-1
- 648 Lenth R V. (2016) Least-squares means: the R package lsmeans. *J Stat Softw* 69:1–33. doi:
649 10.18637/jss.v069.i01
- 650 Limmer B, Becker PH (2009) Improvement in chick provisioning with parental experience in a
651 seabird. *Anim Behav* 77:1095–1101. doi: 10.1016/J.ANBEHAV.2009.01.015
- 652 Lindberg P (1966) Irruption of the pygmy owl (*Glaucidium passerinum*) into southern Scandinavia
653 1963-1964. *Vår Fågelvärld* 25:106–142
- 654 Lindén A, Mäntyniemi S (2011) Using the negative binomial distribution to model overdispersion
655 in ecological count data. *Ecology* 92:1414–1421. doi: 10.2307/23035094
- 656 Marchetti K, Price T (1989) Differences in the foraging of juvenile and adult birds: the importance
657 of developmental constraints. *Biol Rev* 64:51–70. doi: 10.1111/j.1469-185X.1989.tb00638.x
- 658 Martin K (1995) Patterns and mechanisms for age-dependant reproduction and survival in birds.
659 *Am Zool* 35:340–348
- 660 Martin TE (1987) Food as a limit on breeding birds: a life-history perspective. *Annu Rev Ecol Syst*
661 18:453–487. doi: 10.1146/annurev.es.18.110187.002321
- 662 Massemin S, Korpimäki E, Wiehn J (2000) Reversed sexual size dimorphism in raptors: evaluation
663 of the hypotheses in kestrels breeding in a temporally changing environment. *Oecologia*
664 124:26–32
- 665 Mikkola H (1970) On the activity and food of the Pygmy Owl *Glaucidium passerinum* during

- 666 breeding. *Ornis Fenn* 47:10–14
- 667 Mikkola H (1983) *Owls of Europe*. T. and A. D. Poyser, New York
- 668 Morosinotto C, Villers A, Thomson RL, Varjonen R, Korpimäki E (2017) Competitors and
669 predators alter settlement patterns and reproductive success of an intraguild prey. *Ecol Monogr*
670 87:4–20. doi: 10.1002/ecm.1238
- 671 Newton I (1979) *Population Ecology of Raptors*. T. & A.D. Poyser Ltd., Berkhamstead, UK
- 672 Newton I (1998) *Population Limitation in Birds*. Academic Press, London, UK
- 673 Newton I (2002) Population ecology in Holarctic owls. In: Newton I, Kavanagh R, Olsen J, Taylor I
674 (eds) *Ecology and conservation of owls*. CSIRO publishing, Collingwood, VIC, pp 3–29
- 675 Nol E, Smith JNM (1987) Effects of age and breeding experience on seasonal reproductive success
676 in the song sparrow. *J Anim Ecol* 56:301–313. doi: 10.2307/4816
- 677 Nyby J, Wallace P, Owen K, Thiessen DD (1973) An influence of hormones on hoarding behavior
678 in the Mongolian gerbil (*Meriones unguiculatus*). *Horm Behav* 4:283–288. doi: 10.1016/0018-
679 506X(73)90027-5
- 680 Orians GH (1969) Age and hunting success in the brown pelican (*Pelecanus occidentalis*). *Anim*
681 *Behav* 17:316–319
- 682 Penteriani V, Rutz C, Kenward R (2013) Hunting behaviour and breeding performance of northern
683 goshawks *Accipiter gentilis*, in relation to resource availability, sex, age and morphology.
684 *Naturwissenschaften* 100:935–942. doi: 10.1007/s00114-013-1093-7
- 685 Persson J (2005) Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food
686 availability. *Can J Zool* 83:1453–1459. doi: 10.1139/z05-143

- 687 R Core Team (2017) R: A language and environment for statistical computing. R Foundation for
688 Statistical Computing, Vienna, Austria, <http://www.R-project.org>
- 689 Ralph CJ, Pearson CA (1971) Correlation of age, size of territory, plumage, and breeding success in
690 white-crowned sparrows. *Condor* 73:77–80
- 691 Reznick D, Nunney L, Tessier A (2000) Big houses, big cars, superfleas and the costs of
692 reproduction. *Trends Ecol Evol* 15:421–425. doi: 10.1016/S0169-5347(00)01941-8
- 693 Roberts RC (1979) The evolution of avian food-storing behavior. *Am Nat* 114:418–438
- 694 Rohner C (1997) Non-territorial ‘floaters’ in great horned owls: space use during a cyclic peak of
695 snowshoe hares. *Anim Behav* 53:901–912. doi: 10.1006/ANBE.1996.0381
- 696 Rutz C, Whittingham MJ, Newton I (2006) Age-dependent diet choice in an avian top predator.
697 *Proc R Soc Lond B* 273:579–586. doi: 10.1098/rspb.2005.3353
- 698 Scherzinger W (1970) Zum Aktionssystem des Sperlingskauzes (*Glaucidium passerinum*, L.).
699 *Zoologica* 41:1-130
- 700 Schneider R, Wilden I (1994) Choice of prey and feeding activity of urban Peregrine Falcons *Falco*
701 *peregrinus* during the breeding season. In: Meyburg B-U, Chancellor RD (eds) *Raptor*
702 *Conservation Today*. The Pica Press, Berlin, pp 203-209
- 703 Schnell JH (1958) Nesting behavior and food habits of Goshawks in the Sierra Nevada of
704 California. *Condor* 60:377–403. doi: 10.2307/1365696
- 705 Schönn S (1980) *Der Sperlingskauz*. Die Neue Brehm-Bücherei, Ziemsen Verlag, Wittenberg
- 706 Schulenburg J, Wiesner J (1986) Zur Winternahrung des Sperlinkgskauzes (*Glaucidium*
707 *passerinum*) in zwei unterschiedlichen Gebieten der DDR. *Acta Ornithoecol* 1:167–183

- 708 Skaug H, Fournier D, Bolker B, Magnusson A, Nielsen A (2016) Generalized linear mixed models
709 using “AD Model Builder.”, <https://rdrr.io/rforge/glmmADMB/>
- 710 Smith CC, Reichman OJ (1984) The evolution of food caching by birds and mammals. *Annu Rev*
711 *Ecol Syst* 15:329–351
- 712 Smith WI, Ross S (1950) Hoarding behavior in the golden hamster (*Mesocricetus auratus auratus*).
713 *Pedagog Semin J Gen* 77:211–215. doi: 10.1080/08856559.1950.10533549
- 714 Solheim R (1984a) Caching behaviour, prey choice and surplus killing by Pygmy Owls *Glaucidium*
715 *passerinum* during winter, a functional response of a generalist predator. *Ann Zool Fenn*
716 21:301–308
- 717 Solheim R (1984b) Breeding biology of the Pygmy Owl *Glaucidium passerinum* in two
718 biogeographical zones in southeastern Norway. *Ann Zool Fenn* 21:295–300
- 719 Šotnár K, Pačenovský S, Obuch J (2015) On the food of the Eurasian pygmy owl (*Glaucidium*
720 *passerinum*) in Slovakia. *Slovak Raptor J* 9:115–126. doi: 10.1515/stj-2015-0009
- 721 Strom H, Sonerud GA (2001) Home range and habitat selection in the Pygmy Owl *Glaucidium*
722 *passerinum*. *Ornis Fenn* 78:145–158
- 723 Suhonen J, Halonen M, Mappes T, Korpimäki E (2007) Interspecific competition limits larders of
724 pygmy owls *Glaucidium passerinum*. *J Avian Biol* 38:630–634. doi: 10.1111/j.2007.0908-
725 8857.03960.x
- 726 Terraube J, Villers A, Poudré L, Varjonen R, Korpimäki E (2017) Increased autumn rainfall
727 disrupts predator-prey interactions in fragmented boreal forests. *Glob Change Biol* 23:1361–
728 1373. doi: 10.1111/gcb.13408
- 729 Vander Wall SB (1990) *Food Hoarding in Animals*. The University of Chicago Press, Chicago

- 730 Vander Wall SB, Smith KG (1987) Cache-protecting behavior of food-hoarding animals. In: Kamil
731 AC, Krebs JR, Pulliam HR (eds) Foraging Behavior. Springer US, Boston, MA, pp 611–644
- 732 Vaughan R (1961) *Falco eleonora*. Ibis 103:114–128. doi: 10.1111/j.1474-919X.1961.tb02424.x
- 733 Waite TA, Strickland D (2006) Climate change and the demographic demise of a hoarding bird
734 living on the edge. Proc R Soc Lond B 273:2809–2813. doi: 10.1098/rspb.2006.3667
- 735 Williams T, Fuiman L, Horning M, Davis R (2004) The cost of foraging by a marine predator, the
736 Weddell seal *Leptonychotes weddellii*: pricing by the stroke. J Exp Biol 207:973-982
- 737 Wunderle JM Jr (1991) Age-specific foraging proficiency in birds. In: Power DM (ed) Current
738 ornithology, vol. 8. Plenum Publishing Corporation, New York, pp 273–324
- 739 Yosef R, Pinshow B (1989) Cache size in shrikes influences female mate choice and reproductive
740 success. Auk 106:418–421
- 741 Yosef R, Pinshow B (2005) Impaling in true shrikes (*Laniidae*): A behavioral and ontogenetic
742 perspective. Behav Process 69:363–367. doi: 10.1016/j.beproc.2005.02.023
- 743 Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and
744 extensions in ecology with R. Springer, New York

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748 **Tables**

749

750 **Table 1** Summary of the examined forest-sites and nest-boxes, and of the pygmy owl food hoarding
 751 data in 2003–2016. The total no. is the total number recorded (sum) over the 14 years, the mean
 752 corresponds to the yearly mean calculated using the total value for every year, while the range
 753 corresponds to the minimum and maximum values observed during the 14 years. 1-yr = yearlings,
 754 Ad = adults, M = males and F = females

Variable	Total no.	Mean per year (range)
No. of forest-sites	305	211 (124-255)
No. of nest-boxes	633	423 (246-519)
No. of food stores	1056	75 (31-137)
No. of food stores with identified hoarder	607; 1-yr 330; Ad 277	43 (15-90)
No. of owls captured	330; M 145; F 171; unsexed 14	31 (14-60)
No. of prey items found	19048	1270 (136-3474); per store/year: 19 (1-205)
No. of prey items found in stores with identified hoarder	12595	899 (86-2598); per store/year 21 (1-205)
Mass of prey items found in stores with identified hoarder (g)	193292	13807 (1286-46226); per store/year: 318 (3-4129)

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757 **Table 2** Model results for the analyses on number and distribution of the stores during 2003-2016.
758 a) GLM of the variation in total number of forest-sites with at least one food store and b) in the
759 number of hoarding owls in relation to autumn vole abundance (“vole index”) and time (year). Note
760 that the estimates are at logit-scale. c) GLMM of the total number of stores per owl in relation to the
761 autumn vole abundance (“vole index”), age (1-yr = yearlings, Ad = adults) and sex (M = males, F =
762 females) of the owl. Individual identity was used as a random effect. Note that the estimates are at
763 log-scale. d) GLMM of the mean distance (meters) between the stores of one individual in relation
764 to the autumn vole abundance (vole index), and to age (1-yr = yearlings, Ad = adults) and sex (M =
765 males, F = females) of the owl. Individual identity of the owl was used as a random effect. N =
766 sample size of the response variable

Response variable	Explanatory variable	Estimate ± SE	Statistic	P	
<i>a) No. of forest-sites with a store (N = 14)</i>			<i>F</i>		
	Intercept	89.091 ± 49.595			
	Vole index	0.042 ± 0.010	17.16	0.0016	
	Year	-0.045 ± 0.025	3.33	0.0954	
<i>b) No. of hoarding pygmy owls (N = 14)</i>			<i>F</i>		
	Intercept	-11.777 + 54.148			
	Vole index	0.035 + 0.011	10.22	0.0085	
	Year	0.007 + 0.027	0.07	0.7896	
<i>c) No. of stores per owl (N = 412)</i>			<i>z</i>		
	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		
<i>d)</i>	<i>Mean distance between stores (N = 117)</i>				<i>t</i>
		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		

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768

769 **Table 3** GLMMs analysing the variation of a) the total number and b) the total mass of prey items
770 per single food stores of pygmy owls according to autumn vole abundance (“vole index”), owl age
771 (1-yr = yearlings, Ad = adults) and sex (M = males, F = females) during 2003-2016. Note that the
772 estimates are at log-scale. Individual identity of the owl and of the box nested in the forest-site were
773 used as random effects. N = 607 food stores of 316 individuals, with 12595 prey items

Response variable	Explanatory variable	Estimate ± SE	df	Statistic	P
<i>a) Total number of prey items</i>				<i>z</i>	
	Intercept	2.505 ± 0.107			
	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 X Age				
	1-yr	-0.022 ± 0.009		-2.76	0.0149
	Ad	0 ± 0			
<i>Removed terms</i>					
	Vole index X Sex				
	M	-0.003 ± 0.009		-0.35	0.7300
	F	0 ± 0			
<i>b) Total mass of prey items</i>				<i>t</i>	
	Intercept	2.015 ± 0.044	308		
	Vole index	0.018 ± 0.002	535	7.95	< 0.0001
	Age				
	1-yr	0.13 ± 0.043	0 ± 0	488	3.11
	Ad	0 ± 0			0.0020

Sex	M	-0.130 ± 0.043	220	-3.03	0.0027
	F	0 ± 0			
<i>Removed terms</i>					
Vole index X Age	1-yr	-0.005 ± 0.005	494	-1.13	0.2589
	Ad	0 ± 0			
Vole index X Sex	M	0.001 ± 0.004	549	0.24	0.8113
	F	0 ± 0			

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775

776 **Figure captions**

777 **Fig. 1** Among-year variation in the percentage of forest-sites (with usually two nest boxes in each)
778 containing a pygmy owl food store (solid line), in the number of individuals captured as food
779 hoarders (dashed line) and in the autumn vole abundance (“vole index”, dotted line) in the study
780 area during 2003-2016

781

782 **Fig. 2** a) The probability and 95% confidence intervals (grey) of a forest-site with two nest boxes to
783 contain at least one food store and b) the variation in the total number of hoarding pygmy owls in
784 relation to autumn vole abundance (“vole index”) in the study area during 2003-2016 (N = 14)

785

786 **Fig. 3** Frequency distributions of the mean distance (meters) between the stores of one individual
787 aggregated every 200 m and divided between a) yearlings (N = 69) and b) adults (N = 48). Mean
788 (solid line) and median (dotted line) values are 1423 m and 1441 m for yearlings, and 1733 m and
789 1673 m for adults

790

791 **Fig. 4** Predicted values and 95% confidence intervals of a) the total number (from Table 3 model a)
792 and b) total mass (from Table 3 model b) of prey items per single food store in relation to autumn
793 vole abundance (“vole index”) for yearling (dashed line) and adult (solid line) females (black, with
794 confidence intervals in darker grey) and males (grey, with confidence intervals in lighter grey). The
795 model for total number of prey items shown in Fig. 4a includes an interaction between autumn vole
796 abundance and age (“VxA” in the plot), whereas there was no interaction for the total mass of prey
797 items (Fig. 4b, and see Table 3). N = 607 food stores of 316 individuals, with 12595 prey items