

Interspecific competition limits larders of pygmy owls *Glaucidium passerinum*

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To test whether competitive and predatory interactions limit larder size we erected pygmy owl *Glaucidium passerinum* nest-boxes for hoarding with 45 mm entrance diameter near and far (>2 km) from Tengmalm's owl *Aegolius funereus* nest-boxes with >80 mm entrance diameter during early autumn. We found larders of pygmy owls in similar frequency in both near and far plots (41 vs. 42% of plots), but in near plots the number and biomass of cached prey by pygmy owls were lower. These results suggest that there is competition for food between these two owl species and/or that food caching behaviour of pygmy owls is disturbed by larger Tengmalm's owls.

Interactions among species, such as competition and predation, are fundamental biotic factors determining population densities of animals (Sih et al. 1985, Gurevitch et al. 2000). Frequently the competitive effects are asymmetric, with one of the interacting species being more affected than the other (Connell 1983, Schoener 1983, Persson 1985, Wiens 1989). Predation has more direct fitness effects than competition (Lima and Dill 1990), and has also been considered to have at least similar or even larger effects on animal communities than competition (Sih et al. 1985, Gurevitch et al. 2000). In vertebrate predators, intra-guild predation is usually size-determined with larger species preying on smaller one (Korpimäki and Norrdahl 1989a, Polis and Holt 1992, Hakkarainen and Korpimäki 1996, Palomares and Caro 1999). In these conditions, the smaller species may enhance coexistence with its predator by resource partitioning and spatial avoidance (Korpimäki and Norrdahl 1989a, Polis et al. 1989, Hakkarainen and Korpimäki 1996, Sergio et al. 2003). There also is experimental evidence that competitive and predatory interactions among birds of prey can reduce the reproductive success of smaller species involved (Hakkarainen and Korpimäki

1996, Krüger 2002), but experimental studies on competitive and predatory interactions between two bird of prey species during non-breeding season are missing.

This study was aimed to examine whether competitive and predatory interactions by larger owl species affect the size of larders of pygmy owls *Glaucidium passerinum* during winter. Pygmy and Tengmalm's owls *Aegolius funereus* coexist in North and Central European coniferous forests (Schönn 1980, Korpimäki 1981, Mikkola 1983). These two owl species are the only common birds of prey which prey on small mammals and passerine birds in our study region in winter and they have broadly overlapping diets (e.g. Kellomäki 1977, Korpimäki 1981, 1988a, Mikkola 1983, Suhonen 1993, Kullberg 1995). Pygmy owls cache small mammals and birds in holes and nest-boxes during late autumn and winter (Kellomäki 1977, Solheim 1984, Ekman 1986, Suhonen 1993, Halonen et al. 2007). Larder contents vary greatly with the availability of voles (Kellomäki 1977, Solheim 1984, Suhonen 1993, but see Ekman 1986). Adult male Tengmalm's owls occupy their territories throughout the year after the first breeding attempt, apparently guarding their nest-holes against

competitors (Korpimäki 1988b, 1993). Tengmalm's owls can sometimes even kill pygmy owls (Schönn 1980, Mikkola 1983).

Materials and methods

The study was carried out during the two winters 1990–1991 and 1991–1992 in the Kauhava region (63°N, 23°E), western Finland. This area consists of coniferous forests with high proportions of agricultural land and some peatland bogs (Korpimäki 1981, 1987, 1988b, Hakkarainen et al. 2003). During the first winter we established nine near and seven far plots, and during the second winter ten near and ten far plots. During the second winter, both the near and far plots were relocated more than 2 km from the near and far plots of first winter to avoid that the same owl individuals would have used the same nest-boxes for caching in two winters. In each near and far plots, we provided two boxes for pygmy owls as larder sites. The boxes had an entrance hole (45 mm in diameter) that was too small to be used by any other birds of prey (Solheim 1984). Distance between these two boxes within a plot was 50 to 100 m and the distance between two different plots was >1 km. In the near plots, the pygmy owl nest-boxes were erected within 100 m of a Tengmalm's owl nest-box, which had an entrance >80 mm in diameter. Wintering Tengmalm's owls use these nest-boxes for roosting (Korpimäki 1981). The near plots were located within a large (1,300 km²) long-term study area of Tengmalm's owls where the density of nest-boxes with large-entrance (>80 mm) was 0.5–1.0 per km² (Korpimäki 1981, 1988a,b, Hakkarainen et al. 2003). The percentage of nest-boxes inhabited by Tengmalm's owls during the breeding season was 23% in spring 1991 and 33% in spring 1992 (Korpimäki 1994). The density of wintering Tengmalm's owls was high, because the majority of males stay in their breeding territory over the winter (Korpimäki 1988b, 1993). The far plots were >2 km from the nearest Tengmalm's owl nest-box or natural cavity with large entrance, and therefore density of wintering Tengmalm's owls probably was lower than in near plots.

Near and far plots were situated in managed coniferous forests where deciduous trees and natural cavities were scarce. Therefore, all Tengmalm's owls bred in nest-boxes. On the basis of several criteria, we chose the study plots as similar as possible. We used the proportions of main habitat types measured on landscape maps and also recorded in the field within 500 m of each near and far plots as indicators of similarity. Because voles are the main prey species of pygmy and Tengmalm's owls, small mammal abundance was estimated by snap-trapping in mid-September in four

sample plots in the western and eastern parts of the Tengmalm's owl study area. Sample plots were in each of the main habitat types and were at least 2 km of pygmy owl nest-boxes used in this study (see Korpimäki and Norrdahl 1989b for further details on the methods).

Prey items cached by pygmy owls in boxes of near and far plots were checked on one day once a month from late October to early March. Prey items were identified to the species and were weighed with a Pesola spring balance to the nearest 1.0 g. To avoid counting any stored prey item twice, all items were marked individually, birds with plastic colour rings and small mammals by toe clipping. The number of cached prey items and their biomass were pooled for both nest-boxes in a plot. These pooled data per plot were used as independent observations for statistical testing.

We examined possible differences in numbers of cached prey items and total biomass of cached prey items by two-way ANOVAs. The treatment was introduced as fixed factor and year as random factor. Number of cached prey items and biomass of larder were log₁₀ -transformed in the two-way ANOVA. We did not calculate interaction term in the two-way ANOVAs because sample size was only one in the first winter in experiment plots (Fig. 1). We used the Mann-Whitney U test to find the differences in habitat variables, different prey groups and number of consumed prey items between control and experimental plots. We conducted all analyses in SPSS (version 12.0.1).

Results

Caches of pygmy owls in small-entrance nest-boxes were found in both the far and near plots (41% vs. 42% of plots, respectively; Table 1) with no difference in occurrence ($\chi^2 = 0.003$, $df = 1$, $P = 0.96$). In contrast, pygmy owls did not cache prey items in large-entrance nest-boxes in the near plots. During the first winter, when the vole density was lower (pooled number of *Microtus* and bank voles *Cletrionomys glareolus* 9.9 per 100 trap-nights), only one larder was found in near plot (Fig. 1). In the second winter, when vole numbers had increased to 21.9 individuals per 100 trap-nights, six near plots contained larders (Fig. 1).

In the near plots the larders contained one to nine prey items, except in one plot, where a pygmy owl cached 42 voles in one plot. In each of the far plots, the larders of pygmy owls contained more prey items (two-way ANOVA, $F_{1,12} = 14.10$, $P = 0.003$; Fig. 1). The total biomass of cached prey items in the plots was significantly higher in the far than near plots (mean = 700g, SD = 380g vs. mean 210g, SD = 330g; two-way ANOVA, $F_{1,12} = 10.68$, $P = 0.007$). However, the

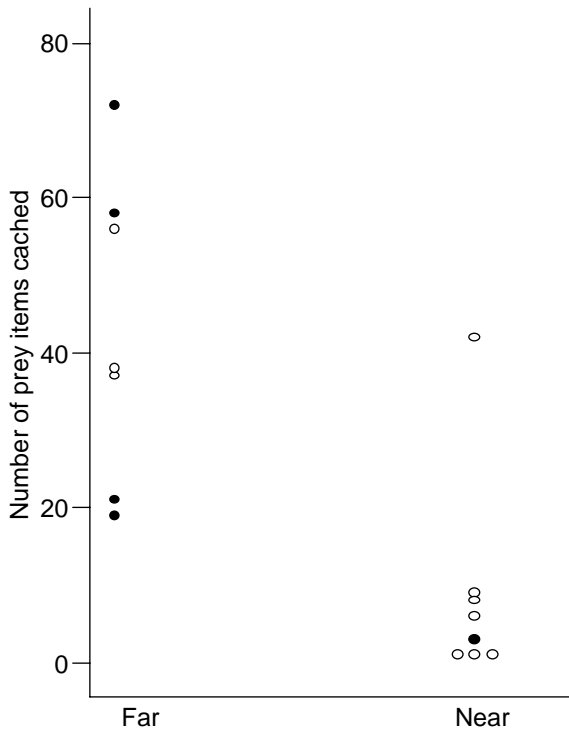


Fig. 1. Number of prey items in larders of pygmy owls in each far from Tengmalm's owl nest-boxes (Far) and in the vicinity of Tengmalm's owl nest-boxes (near) plots. Filled dots denote winter 1990–1991 and open dots denote the winter 1991–1992.

between-year difference was not statistically significant in the number of cached prey items ($F_{1,12} = 0.11$, $P = 0.75$), nor in total biomass ($F_{1,12} = 0.72$, $P = 0.41$).

In every prey group, the mean number of cached prey items was higher in the far plots than in the near plots, but the difference was statistically significant for bank voles and shrews (*Sorex* spp.) only (Table 1). Also,

the number of cached prey items consumed during winter was slightly larger in the far plots than in the near plots (mean = 20.0, SD = 12.0 vs. mean = 5.1, SD = 10.3; $U = 11.5$, $P = 0.054$).

We measured the percent cover of five main habitat types in near and far plots: pine *Pinus sylvestris* dominated forests (mean (SD) percent cover in near plots 59% (11, number of plots 19) and in far plots 52% (17, $n = 17$)), spruce *Picea abies* dominated forests (8% (7) vs. 8% (12)), peatland bogs (mostly pine-dominated bogs 16% (10) vs. 20% (14)), agricultural fields [16% (10) vs. 16% (12)], and lakes (2% (5) vs. 4% (9)). There were no obvious differences in the habitat composition variables between near and far plots (Mann-Whitney U-tests, two-tailed $P > 0.25$ for each habitat type).

Discussion

Larders of pygmy owls were smaller in the plots with Tengmalm's owl boxes than in those without. Therefore, our results support the prediction of the interspecific food competition hypothesis (Korpimäki 1987). Moreover, our results were in disagreement with the prediction of Oksanen's (1983) hypothesis that food stores of pygmy owls should be larger in near than far plots.

We found that small-entrance nest-boxes near large-entrance ones contained lower numbers of cached prey items than small-entrance nest-boxes far from large-entrance ones. Therefore, we can exclude the possibility that avoidance of cache-robbing in large-entrance nest-boxes would be the only reason for lower cache sizes in the plots with Tengmalm's owl boxes. Solheim (1984) found that pygmy owls preferred small-entrance nest-boxes for caching. He suggested that pygmy owls avoided cache-robbers, such as Tengmalm's owls and pine martens *Martes martes*. However, he could not rule

Table 1. The mean number of prey items lardered in nest-boxes by pygmy owls in near plots with Tengmalm's owl boxes and far plots without Tengmalm's owl boxes. Pooled data from winters 1990–1991 and 1991–1992. U represents Mann-Whitney U-test, comparing the plots with low or high density of Tengmalm's owls and P is the probability level (two-tailed).

Prey species	Far		Near		Test	
	Mean	SD	Mean	SD	U	P
<i>Microtus voles*</i>	16.9	16.1	6.8	13.3	14	0.12
Bank vole <i>Clethrionomys glareolus</i>	10.1	4.8	1.8	1.7	4.5	0.0015
Harvest mouse <i>Micromys minutus</i>	7.6	14.2	0.0	0.0	12	0.073
Shrews (<i>Sorex</i> spp.)	7.6	13.3	0.1	0.4	5.5	0.011
Birds	0.7	1.1	0.3	0.5	22	0.52
Number of plots with caches	7		8			
Total number of plots	17		19			

*The field vole *Microtus agrestis* and the sibling vole *M. rossiaemerionalis*.

out the possibility that competition for food from other predators would have been the reason, why pygmy owls cached lower prey numbers (usually one prey item) in large-entrance nest-boxes than small-entrance ones.

We suggest that pygmy owls made smaller larders in the near than in the far plots because of food competition by Tengmalm's owls (see also Korpimäki, 1987). Tengmalm's owls hunt in dense vole patches and are able to depress vole densities (Korpimäki and Norrdahl 1989b), in particular with other vole-eating avian and mammalian predators (Korpimäki et al. 2005). This may lower hunting success of pygmy owls and thus make them less able to larder. Alternatively, pygmy owls had to reduce foraging or to avoid best food patches when foraging under the Tengmalm's owl predation risk and this resulted in smaller larders. However, we found similar numbers of larders of pygmy owls in both near and far plots, and only the larder size was different. This supports the interpretation that pygmy owls can co-exist with larger owls, but the larder size is smaller because of higher competition for the non-renewable food resource during winter.

In this study, food competition between pygmy owls and the larger Tengmalm's owls seemed to be more important than predation risk in reducing food cache size of smaller allospecifics in late autumn and winter. Whether the competition for food with Tengmalm's owls and/or Tengmalm's owl predation risk lowers the reproductive success and survival of pygmy owls will be a challenge for future studies.

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