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High population density in bank voles stimulates food hoarding after breeding

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Abstract. The effects of conspecific density (i.e. risk of intraspecific competition) on hoarding behaviour were studied in breeding pairs of bank voles, *Clethrionomys glareolus.* I simulated high population density by using odours of conspecifics, to exclude the direct effects of exploitation or interference competition for food. The pairs of bank voles hoarded only at the end of their breeding season. Hoarding was not correlated with whether the voles had a litter during the experiment or their litter size, but was more likely at the high population density and for pairs with small females. This may indicate that smaller females especially make caches in the autumn, possibly to ensure better winter survival under high population density. I discuss the hoarding behaviour of bank voles in relation to their territorial behaviour and food resources during the breeding season and predictable population changes during winter.

Food hoarding is suggested to be an important adaptive behaviour for many animals (Vander Wall 1990). The major benefits of hoarding are: (1) better survival over periods of food scarcity, for example over winter (Seeley & Visscher 1985; Wauters et al. 1996); and (2) improved reproductive success because cached food can be used during breeding (Strassman 1979; James & Verbeek 1984). In general, the ultimate reason for hoarding is to ensure a continuous and stable food supply for an individual or for its offspring, when food availability varies daily or seasonally, because of predictable or unpredictable changes in the abiotic (e.g. weather) or biotic (e.g. intra- and interspecific competition for food) environment.

Conspecifics may inhibit food hoarding if caches are often stolen by other individuals (Vander Wall 1990). For example, black-capped chickadees, *Parus atricapillus* (Stone & Baker 1989) and laboratory rats, *Rattus norvegicus* (Miller & Postman 1946; Denenberg 1952) cache less in the presence of conspecifics than when alone. However, if individuals are able to protect or hide their caches, food hoarding may become an important element in a competitive strategy. With the help of caches, animals may significantly enhance their survival over the period of high food competition. Indeed, some correlative field studies (Litvinov & Vasil'ev 1973) have supported the hypothesis that high density of conspecifics stimulates food hoarding, but experimental tests are almost totally lacking (Vander Wall 1990).

In the present study, I examined whether the odour of conspecifics (representing a risk of intraspecific competition) affects hoarding behaviour in the bank vole, *Clethrionomys glareolus*. I used odours of conspecifics rather than conspecifics themselves, to exclude the effects of exploitation or interference competition for food. I also studied whether breeding condition or season (possible wintering strategies) and individual characteristics (age and body mass) affected the hoarding behaviour of pairs of voles.

METHODS

Study Site and Experimental Animals

I carried out the study at Konnevesi Research Station, central Finland (62°37′N, 26°20′E) during the summer of 1991. All bank voles were caught in central Finland, where females breed from early May to September. During that time a female may give birth to three to four litters (E. Koskela & T. Mappes, unpublished data). Bank vole females are intra-sexually territorial during the breeding

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Table I. Numbers of experimental individuals according to their age* and treatment in the latter part of the experiment, when voles hoarded

Manipulation	Females		Males		Total pairs
	Young	Old	Young	Old	
Low density (no odours of conspecifics)	14	6	12	8	20
High density (odours of conspecifics)	16	4	11	9	20
Total individuals	30	10	23	17	40

*Young = summer-born, old = over-wintered.

season, when males have larger inter- and intrasexually overlapping home ranges (Mazurkiewicz 1971; Bujalska 1973). The bank vole is a typical larder-hoarding species, commonly storing large amounts of seeds, berries and lichens in its nest both in captivity and in nature (Ashby 1967; Litvinov & Vasil'ev 1973; Pulliainen & Keränen 1979; Hansson 1986; T. Mappes & E. Koskela, unpublished data).

Experimental Design

The present study is part of another experiment (Mappes & Ylönen 1997) on the effects of density of conspecifics and predation risk on breeding tactics of bank vole females. From the 2 × 2 factorial experiment, I selected only two treatment groups (density and control) for the present study of hoarding behaviour.

I used 62 pairs of both over-wintered and summer-born adults. The experiment was carried out twice: during the middle (beginning of July, $N=22$ pairs, all over-wintered individuals) and at the end of the breeding season (end of August, $N=40$ pairs; see Table I), when females give birth for the last time before winter in my study area. Voles were paired randomly with the opposite sex according to their age (log likelihood ratio test: $G_1=0.03$, $P=0.853$); however, the weights of paired voles were significantly correlated ($r=0.47$, $N=35$, $P<0.005$). Pairs of mature, non-breeding voles were each placed in a wire-mesh cage (36 × 21 × 21 cm), which had wire-mesh walls and a plastic base covered by sawdust. There was a plastic nestbox (12 × 12 × 12 cm) with hay as bedding in one corner and food in another corner of the cage. Individuals could see and smell the surrounding environment. The cages were evenly distributed in two large (0.5 ha) outdoor enclosures. The habitat of the enclosures was an old field with homogeneous grass vegetation (described in Mappes et al. 1995a). In both experimental sets, the cages were distributed at least 15 m apart to ensure independence of replicates. Food (sunflower seeds, potatoes, cabbage) and water were available ad libitum during the experiment.

I simulated high population density of voles by spraying the vegetation surrounding the cages with the odour of captive bank voles. Each time the odours of at least two individuals, both mature females and males, were used. These odours were produced as weak solutions of water and captive animals' faeces and urine. I sprayed 5 ml of this solution around each cage once a day. In addition, there was a free-living bank vole population of 80 individuals in the density treatment enclosures. This is the maximum density observed by Mappes et al. (1995b) in these enclosures. The control treatment (no conspecific odour) was subjected to the same disturbance with the exception that I sprayed distilled water. There were no free-living bank voles in the enclosure surrounding the control cages.

The manipulations of each replicate lasted for 3 weeks during which I checked the possible caches three times at 1-week intervals. Because of this procedure, I could not determine which sex hoarded and the results refer to hoarding by pairs rather than individuals. Voles hoarded sunflower seeds mostly on their nestboxes and all caches consisted of at least 100 seeds. At the end of the study, all the voles were killed humanely using carbon dioxide, since it was necessary to age the animals from their molar teeth and take skeletal measures for another study (unpublished data).

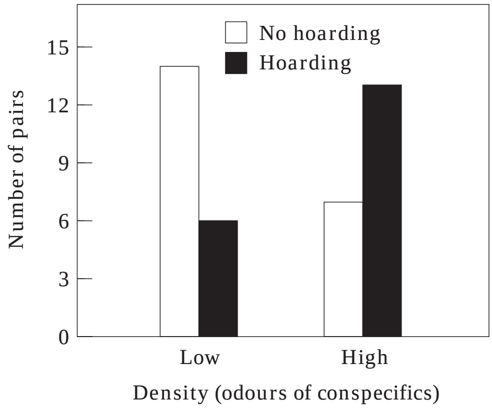

Figure 1. Hoarding of bank vole pairs in simulated (with conspecific odours) high density and low density populations ($G_1 = 5.02$, $P = 0.025$).

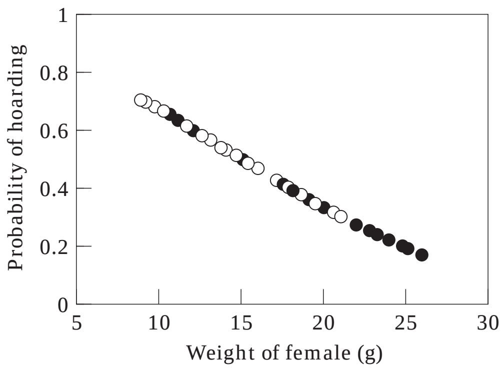

Figure 2. Probability of hoarding by a pair in relation to the initial weight of the female (logistic regression, log likelihood ratio test: $G_1 = 4.21$, $P = 0.040$). Probability is predicted by the logistic regression model: logit $\pi(\text{weight}) = -0.14 \pm 0.07$ (SE) × weight + 2.17 ± 1.23 (SE). ○: Pairs that hoarded; ●: those that did not hoard.

For the present study, I weighed the voles and counted the embryos.

RESULTS

None of the 22 bank vole pairs hoarded food during the middle of the breeding season, whereas at the end of the season, hoarding was more common: 19 out of the 40 pairs (47.5%) hoarded (log likelihood ratio test: $G_1 = 21.06$, $P < 0.001$). In the following analysis of hoarding behaviour, I refer only to data from the latter part of the experiment.

Conspecific odours significantly increased the proportion of pairs hoarding: 65% of pairs ($N = 20$) hoarded in the odour treatment compared to 30% ($N = 20$) in the control treatment (Fig. 1). Neither the female's ($G_1 = 0.30$, $P = 0.582$) nor male's ($G_1 = 0.35$, $P = 0.553$) age affected hoarding behaviour of the pair. The initial body mass of females and males did not differ between the treatments ($t_{37} = 0.90$, $P = 0.377$; $t_{34} = 0.38$, $P = 0.704$, respectively). Hoarding was not related to whether the voles had a litter ($G_1 = 1.01$, $P = 0.315$) or litter size ($G_1 = 1.35$, $P = 0.245$). The odours of conspecific voles did not affect whether the voles had a litter ($G_1 = 0.11$, $P = 0.738$).

Initial body mass of females predicted the pair's hoarding significantly (Fig. 2) so that females in pairs that hoarded were lighter ($\bar{X} \pm$ SE = 14.7 ± 0.9 g) than those in pairs that did not (17.8 ± 1.2 g). In contrast, initial body mass of males did not affect the probability of hoarding ($\beta \pm$ SE = −0.08 ± 0.07; $G_1 = 1.70$, $P = 0.192$). The relative mass of the pair (weight of male per weight of female) was not related to hoarding ($G_1 = 2.06$, $P = 0.152$).

DISCUSSION

Hoarding Tactics During Breeding

Many animals hoard food during their breeding season, allowing them to improve their condition during breeding (i.e. compensate for the energetic costs of reproduction) or to have extra food for their offspring. These benefits seem obvious in some invertebrate species (Strassman 1979) and in some species of birds (James & Verbeek 1984) and mammals (Kawamichi 1980; Wauters et al. 1996). In the present study bank voles hoarded only during the latter part of the breeding season. This clear seasonality in hoarding is probably controlled by photoperiod as has been documented in birds (Shettleworth et al. 1995) and other small mammals (Masuda & Oishi 1988). Furthermore, the food hoarding of bank voles did not correlate with whether they had a litter or with litter size. These results suggest that food hoarding is beneficial only for winter survival and is not so important for the reproductive success of bank voles.

In general, food hoarding is typically associated with food scarcity or with an increase in food demand. Daily energy requirements are 18–25% higher among pregnant mammals and 66–188% higher among lactating mammals compared with non-breeding individuals (Gittleman & Thompson 1988). This increase in energy demand can be a sufficient cause of food hoarding in breeding female hamsters, *Cricetus cricetus* (Miceli & Malsbury 1982; Lisk et al. 1983) and Norway rats (Calhoun 1963). However, little is known about the benefits of hoarding in connection with social behaviour or food availability among these species. Breeding female bank voles are strictly territorial towards other females, with large exclusive areas within their home ranges (Bujalska 1973; Koskela et al. 1997). Defending a territory provides exclusive access to food resources (Ostfeld 1985), which should decrease the benefits of hoarding. On the other hand, territoriality may enhance the benefits of larder hoarding because pilfering is less likely. Moreover, bank vole females are only territorial against other females and so they do not protect their food supply from males or other species using the same food.

Food hoarding may not be favoured when food availability is continuous and stable. In Fennoscandia, bank voles eat a variety of items from leaves, stems and plant seeds to fungi, berries and invertebrates (Hansson 1971, 1979). Most of these food resources are highly renewable during the breeding season of bank voles from May to September. Therefore the costs of food hoarding probably exceed the benefits for bank vole females when breeding.

Density-dependent Hoarding Tactics Before Winter

Conspecifics may inhibit or stimulate food hoarding depending on the social system of the animals (Vander Wall 1990). If the risk of stealing caches is high, hoarding activity should decrease, which has been shown among chickadees (Stone & Baker 1989) and Norway rats (Miller & Postman 1946; Denenberg 1952). So if conspecifics are present, an individual must hide or protect its caches. If hiding or protecting is possible, a hoarding individual may have a competitive advantage over non-hoarding conspecifics. However, there is still little evidence for this hypothesis. As far as I know, only two experiments (in birds: Bednekoff & Balda 1996 and in mammals: Sanchez & Reichman 1987) agree with my finding that a high density of conspecifics may trigger hoarding behaviour. My results also indicate that the body mass of females correlates negatively with the probability of the pair caching, whereas the weights of males do not affect hoarding. However, as I could not be sure which sex hoarded, the hypothesis that caching is more common among female bank voles, especially lighter ones, needs further experiments. It would also be interesting to study whether the difference within or between sexes is connected with their territorial behaviour in the breeding season, with dispersal in autumn or with social behaviour during winter. Reproductively active female bank voles are clearly more philopatric than males (e.g. Kozakiewicz 1976). If females still differ in their dispersal behaviour during autumn and winter, it would be more beneficial for females to store large larder caches in their stable home ranges. Furthermore, neither the previous experiment (Sanchez & Reichman 1987) nor the present study could test whether the hoarding individuals are able to hide or protect their caches, and how important the caches are for survival of hoarding individuals under high intraspecific competition.

In our study area in central Finland, population densities of bank voles usually increase to very high levels (over 100 individuals per ha) about every third autumn and then they crash (to one to two individuals per ha) during late winter and early spring (Hansson & Henttonen 1985). Under these cyclic changes, high autumn density predicts quite well very high intraspecific competition during early and mid winter. This high predictability may favour long-term food hoarding during autumn. With the help of caches, subordinate individuals of low body mass may thus improve their survival over winter to the next breeding season.

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