# Limitation of reproductive success by food availability and litter size in the bank vole, *Clethrionomys glareolus*

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Food limitation has been suggested as one of the most important factors affecting life-history evolution in terrestrial vertebrates. However, this inference is based mainly on evidence from birds, and reproductive trade-offs may differ among groups with different forms of parental care. To study whether the costs of enlarged litters (decreased mass of offspring) would appear when food is not limiting, we performed outdoor enclosure experiments in which we manipulated simultaneously the litter size (control versus +two pups) and food availability (control versus food-supplemented) of female bank voles, *Clethrionomys glareolus*. The weaning success of females increased significantly in response to supplementary food. When females were provided with extra food, no differences were observed in the body masses of weanlings of control and enlarged litters. Further, food-supplemented females grew to larger sizes during nursing than unsupplemented females. Our experiment suggests that energetic requirements during nursing constrain the number of offspring that can be successfully raised in a particular breeding attempt. The results also indicate that unlimiting food resources may increase future reproductive potential of females, because they can use more energy for somatic growth.

**Keywords:** constraints; food supplementation; litter size manipulation; mammals; reproductive effort; reproductive success

## 1. INTRODUCTION

Lack's (1947) hypothesis, that clutch size in altricial birds is ultimately adjusted to the feeding capacity of the parents, has been tested in numerous studies (reviewed in Murphy & Haukioja (1986) and VanderWerf (1992)). Although Lack's original argument has received some conflicting evidence, and has been refined over the years (e.g. Högstedt 1980; Boyce & Perrins 1987; Nur 1988), limiting food resources has been widely accepted as one of the most important factors affecting life-history evolution in birds (reviewed in Martin (1987) and Boutin (1990)). Lack (1948) urged researchers to test his hypothesis also in free-ranging mammals, but such experiments have been few. Mammals differ from birds in the form of parental care, and hence the reproductive trade-offs may differ between the groups.

The general result from brood size manipulations performed in birds (reviewed in Lindén & Møller (1989) and Roff (1992)), and from an experiment in mammals (Mappes *et al.* 1995), is that brood enlargements do not increase the number of high-quality offspring parents can raise to independence. By supplementing food exclusively during the nestling period, it would be possible to study whether or not this is due to limited feeding capacity of parents (i.e. their ability to provide sufficient food for pups). This kind of evidence is surprisingly scarce, but in general the results demonstrate improved reproductive success (e.g. fledging success, offspring number and/or mass) of food-supplemented parents compared with control nests (Arcese & Smith 1988; Simons & Martin 1990; Richner 1992; Wiehn & Korpimäki 1997; Siikamäki 1998).

The relationship between food resources and reproduction has also been widely studied in mammals (reviewed in Boutin (1990), O'Donoghue & Krebs (1992), Doonan & Slade (1995) and Wauters & Lens (1995)). However, these studies have mostly emphasized the effects of food addition at the population level. Duquette & Millar (1995) examined the influence of food addition on reproduction of individual tropical mouse *Peromyscus mexicanus* females. They found that food-supplemented females had better weaning success than unsupplemented ones, whereas weanling mass was not affected by extra food. This experiment was conducted in unfenced grids and food was provided throughout the reproductive phase. However, there are no field experiments on mammals where the effects of food limitation on reproductive trade-offs of individual females have been studied while simultaneously controlling confounding factors (e.g. changes in densities of adult individuals due to immigration, emigration or increased reproduction, individual state or predation).

We used the bank vole as a study species to examine whether female reproductive success (size, number and proportion of weaned offspring per litter) is food-limited.

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Further, we examined if food availability during nursing affects the body size and future breeding performance of the females. To do this, brood size (control versus +2 pups) and female food resources (control versus supplemented) were simultaneously manipulated in large outdoor enclosures during nursing.

## 2. METHODS

### (a) *Study site and study species*

The study was conducted at Konnevesi, central Finland $(62°37' N, 26°20' E)$ using eight $0.25$ ha $(1 ha = 10^4 m^2)$ outdoor enclosures situated in an old field. Two separate replicates were carried out: the first in June–July and the second in July–August 1997. To monitor individuals, 25 multiple-capture live traps were distributed in each enclosure in a $5 \times 5$ array with 10 m between the trap stations. Each trap was covered by a galvanized sheet-metal chimney that served as a rainproof place for feeders (see below). Fences prevented the access of small mustelid predators to the enclosures and ensured zero emigration and immigration. For a more detailed description of the habitat and the design of the enclosures, see Koskela *et al*. (1997). The bank vole is well suited for the study, because it does not recognize its pups from foreign ones (Mappes *et al*. 1995). In our study area, the litter size of bank voles ranged from one to ten (usually four to eight), and the breeding season lasted from late April to September (T. Mappes and E. Koskela, unpublished data). The bank voles used in the study were wild-caught from nearby forests in May–June. All females had given birth at least once before the experiment. In the first replicate all females were over-wintered, in the second replicate some of the females were year-born.

### (b) *Study design*

To get enough pregnant bank vole females for the study $(n = 64)$, females were paired at the same time both in the enclosures and in the laboratory. The females that were paired in enclosures were removed to the laboratory before parturitions. Females were inspected twice a day, and those giving birth within 2 d were chosen for the experiment. As soon as pups were found, they were counted, weighed, marked, and their sex was determined (by the length of anogenital distance). The proportions of females mated in the enclosures $(n = 41)$ or in the laboratory $(n = 23)$ were assigned equally to different treatment groups (food treatment, $\chi^2 = 0.61$, $p > 0.4$; litter treatment, $\chi^2 = 0.07$, $p > 0.7$). Furthermore, the body mass, size (measured as width of head) or initial litter size did not differ between females mated in enclosure or laboratory (two-sample *t*-tests, $p > 0.2$ for all the three variables).

The uterine environment and mother's quality may significantly influence the behaviour and life history of individuals (reviewed in vom Saal (1981) and Clark & Calef (1995)), and so cross-fosterings were performed to randomize prenatal maternal effects on performance of pups. Litters were manipulated and cross-fosterings performed within 2 d of parturition. All pups in a litter were changed in the cross-fosterings. According to a previous experiment, the growth and survival of bank vole pups do not differ between the female's own pups and foreign pups (Mappes *et al*. 1995).

To manipulate food resources during nursing we had two treatments: supplemented, where food was provided *ad libitum* at every trap station, and control, where no supplemental food was available in the enclosures. The bank voles' normal food in the enclosure habitat consists mainly of forbs and seeds (Larsson &

Hansson 1977). Supplemental food was laboratory rodent chow (Labfor R36), and it was provided in wiremesh feeders that prevented food hoarding by the voles. Feeders were set out at the same time when females and pups were released into the enclosures and removed 20 d later. In litter size manipulations, we assigned litters of each original size randomly to two treatment groups: enlarged litters, where two pups were added, and control litters, where the original litter size was not changed. Thus, as a result of the manipulations (in both replicates) we had four food-supplemented enclosures and four unsupplemented enclosures with four females in each, two females nursing a control litter and two an enlarged litter (total $n = 64$). The assignment of enclosures into food and control treatments was reversed between replicates. At the beginning of the experiment there were no significant differences in initial litter sizes, body masses, or sizes of mothers between treatments or enclosures (treatments, two-way ANOVAs, $p > 0.2$ for all; enclosures, Kruskal–Wallis one-way ANOVAs, $p > 0.7$ for all).

After the manipulations were performed in the laboratory, females with litters were transferred in breeding cages to enclosures. Cages were placed near the corners of the enclosures (in rainproof covers), 7.5 m away from the fences. Cages were left open so that the mothers could move pups into the enclosures. This method has been successful in previous studies (Mappes *et al*. 1995). In natural populations, small mammal females with postpartum oestrus are usually pregnant at the same time when lactating (e.g. Bronson 1989). In the first replicate, pregnancy was made possible by introducing three mature males into each enclosure after releasing females. In the second replicate, males were not released into the enclosures; instead, all females were given the opportunity to mate in the laboratory. Mating procedure was different in the second replicate, to enable the estimation of the amount of extra food eaten by nursing females (P. Jonsson, T. Hartikainen, E. Koskela and T. Mappes, unpublished data). There was no difference in the proportion of subsequent pregnancy in mothers between replicates (79% and 80% of females pregnant in first and second replicate, respectively, $\chi^2 = 0.01$, $p = 0.940$).

Before expected parturitions of subsequent litters (*ca*. 20 d after possible matings), females were removed from enclosures, measured, and the number of embryos was determined. Successfully weaned offspring (from manipulated litters) were captured and taken to the laboratory at age 30 d, and they were individually weighed (weaning mass) and measured (width of head).

### (c) *Data analysis*

As parameters of reproductive success, we used the proportion (arcsin square-root transformed) and number of weaned young per litter, and the size (body mass and head width) of weaned offspring. The effect of manipulations on growth of mothers was examined by measuring the head width of females before and after the study. Head width was more appropriate for this purpose than weight because it is not directly affected by pregnancy. Head width also correlates well with structural size (T. Mappes and E. Koskela, unpublished data).

The possible effects (or interactions) of replicate and enclosure on dependent variables were examined using analyses of variance. If any tendency for differences between groups to occur was found $(p < 0.1)$, the factor was included in the analyses with dependent variables. To avoid pseudoreplication, the offspring size and mass at weaning were analysed using ANOVA models where individual offspring of the foster female

were nested within food and litter manipulations (see Zar 1996). The total number of weanlings was 192, and the number per individual mother ranged from zero to nine. To enable successful analyses of weanling mass and size (i.e. no redundancies in the design matrix (SPSS Inc. 1992)), the variation in offspring number per female had to be decreased to a maximum of six young. This was done by randomly removing data on required number of offspring (a total of 12 young) from eight mothers originally having more than six weanlings. The procedure makes it possible to include the within-foster female variation in the analyses. The following abbreviations are used when referring to the four treatment groups: (i) no food added, control litters 'CC'; (ii) no food added, enlarged litters 'CE'; (iii) extra food, control litters 'FC'; and (iv) extra food, enlarged litters 'FE'. Only the mothers that were alive throughout the study ($n=54$) were included in the analyses. When the assumptions of parametric tests were not met, non-parametric tests were used. All the tests were two-tailed. The level of statistical significance was set to $\alpha=0.05$, and probability values between 0.05 and 0.1 were considered only as a tendency for finding a real effect.

## 3. RESULTS

### (a) *Weaning success and number of offspring*

The proportion of weaned offspring per litter (weaning success) increased significantly in response to supplementary feeding, whereas there was no difference between litter manipulation groups (ANOVA: replicate, $F_{1,49}=4.84$, $p=0.033$; food, $F_{1,49}=5.24$, $p=0.026$; litter, $F_{1,49}=1.11$, $p=0.296$; food × litter, $F_{1,49}=0.10$, $p=0.758$; figure 1). After litter size manipulations, the number of offspring was higher in enlarged litters than in control litters, but there was no difference between food treatments (ANOVA: food, $F_{1,60}=0.05$, $p=0.821$; litter, $F_{1,60}=43.65$, $p<0.001$; food × litter, $F_{1,60}=0.47$, $p=0.497$; figure 2). However, there was a slight tendency for number of young at weaning to be greater with supplemental food, whereas there was no difference in litter size between litter manipulation groups (ANOVA: food, $F_{1,50}=3.24$, $p=0.078$; litter, $F_{1,50}=0.33$, $p=0.567$; food × litter, $F_{1,50}=0.26$, $p=0.612$; figure 2).

### (b) *Body mass and size of offspring*

Food supplementation increased both the body mass and size of weaned offspring (table 1 and figure 3*a,b*). Without extra food, the mass and size of offspring in enlarged litters were lower compared with the control litters. Furthermore, a significant litter × food manipulation interaction indicated that when the females were food-supplemented, there were no differences in the body masses of weanlings between control and enlarged litters (table 1 and figure 3*a*).

### (c) *Characteristics of mothers and subsequent breeding*

A total of ten mothers died (disappeared) during the experiment without any obvious difference between four treatment groups (CC 4, CE 2, FC 1, FE 3). In general, the size of the mothers increased during the experiment. When provided with supplemental food, mothers grew significantly more than the unsupplemented ones, whereas litter manipulation did not have any significant effect on growth (ANOVA: replicate, $F_{1,46}=16.83$,
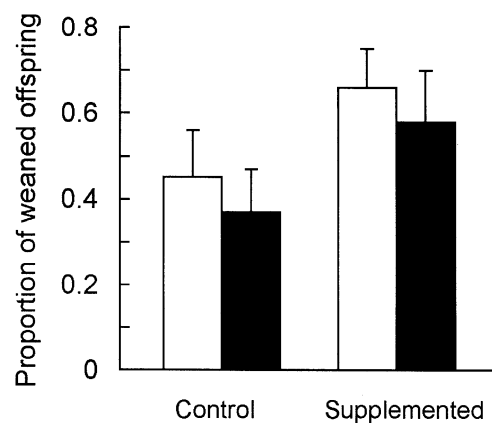


Figure 1. Proportion of weaned offspring per litter (weaning success) in food-supplemented (supplemented) and control (control) females. Control litters = white bars, enlarged litters = black bars. Bars show the mean ± s.e (untransformed values).
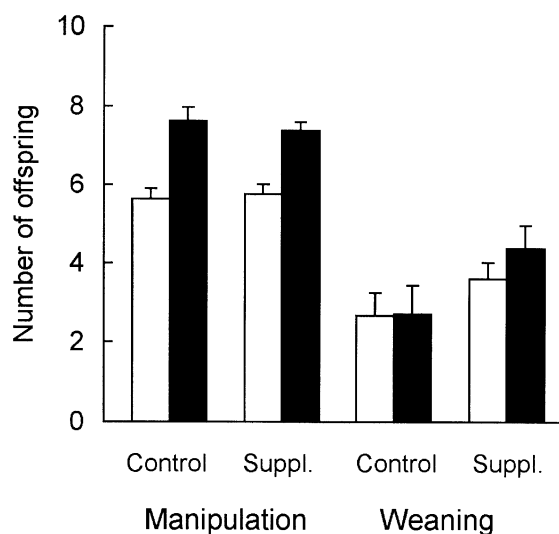


Figure 2. Number of offspring per female after manipulation and at weaning in different treatments. Control = unsupplemented females, supplemented = food-supplemented females, control litters = white bars, enlarged litters = black bars. Bars show the mean ± s.e.

$p<0.001$; food, $F_{1,46}=5.11$, $p=0.029$; litter, $F_{1,46}=0.25$, $p=0.622$; food × litter, $F_{1,46}=0.05$, $p=0.821$; figure 4).

The proportion of females producing subsequent litters in the four treatment groups was as follows: CC, 58% ($n=12$); CE, 86% (14); FC, 80% (15); and FE, 92% (13). The probability of subsequent breeding was analysed using a logit model with breeding as a dependent variable, and food and litter manipulations as explaining factors. In the analyses, food did not affect subsequent breeding, but there was a tendency, although not significant, for females nursing enlarged litters to be more likely to breed (logit model: food, $\chi^2=1.76$, d.f. =1, $p=0.185$; litter, $\chi^2=3.36$, d.f. =1, $p=0.067$; food × litter, $\chi^2=0.05$, d.f. =1, $p=0.820$). Subsequent litter size tended to be larger in response to supplementary feeding, whereas litter enlargements did not affect subsequent litter sizes (mean ± s.e.: CC, $5.3\pm0.6$; CE, $6.1\pm0.4$; FC, $6.6\pm0.3$; FE, $6.2\pm0.2$; ANOVA: food, $F_{1,36}=3.50$, $p=0.069$; litter, $F_{1,36}=0.25$, $p=0.622$; food × litter, $F_{1,36}=2.62$, $p=0.114$).

**Table 1.** *Body mass and size (head width) of weanlings in different treatments*

(Food = food manipulation, litter = litter manipulation. ANOVA models used where individual offspring of the foster female (random effect) were nested within treatments (fixed effects). See also figure 3*a,b*.)

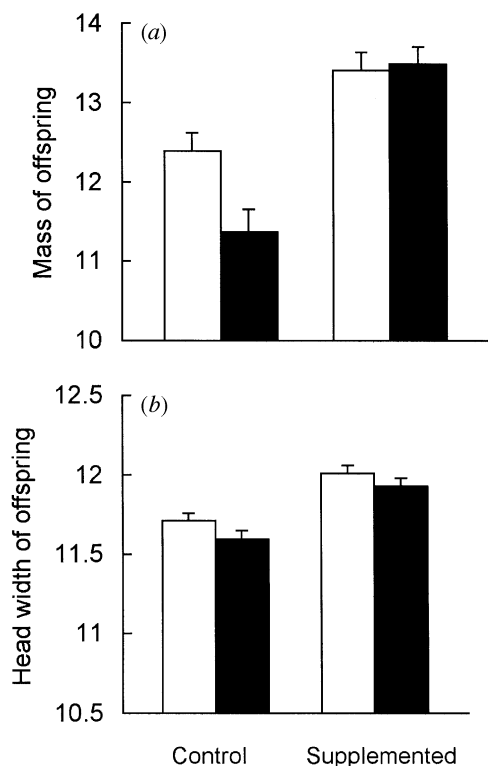|  | d.f. | MS | *F* | *p* |
|---|---|---|---|---|
| body mass |  |  |  |  |
| food | 1 | 92.96 | 44.47 | < 0.001 |
| litter | 1 | 14.77 | 7.07 | 0.015 |
| food × litter | 1 | 10.94 | 5.23 | 0.033 |
| foster female | 20 | 2.09 | 0.79 | 0.719 |
| error | 56 | 2.64 | — | — |
| total | 179 | — | — | — |
| head width |  |  |  |  |
| food | 1 | 3.49 | 33.41 | < 0.001 |
| litter | 1 | 0.62 | 5.91 | 0.025 |
| food × litter | 1 | 0.09 | 0.9 | 0.353 |
| foster female | 20 | 0.10 | 0.83 | 0.671 |
| error | 151 | 0.13 | — | — |
| total | 174 | — | — | — |



Figure 3. Characteristics of offspring at 30 days in food-supplemented (supplemented) and control (control) treatment. (*a*) Body mass (in g). (*b*) Body size (head width, in mm). Control litters = white bars, enlarged litters = black bars. Bars show the mean ± s.e.

## 4. DISCUSSION

According to our results, weaning success of bank vole females is limited by food availability. When females were provided with extra food, they weaned larger (body mass and size) offspring than control females. Enlarging the
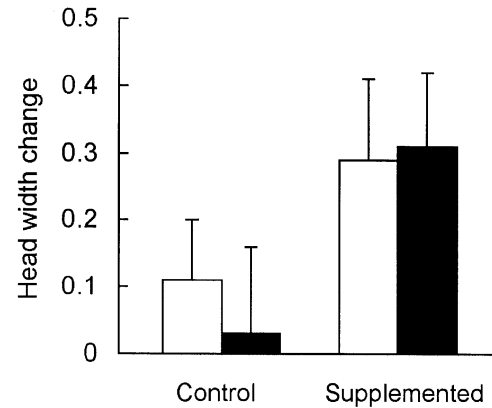
Figure 4. The growth of females during the experiment measured as head width change (in mm) in food-supplemented (supplemented) and control (control) treatment. Control litters = white bars, enlarged litters = black bars. Bars show the mean ± s.e.

litter size decreased the body mass and size of weaned offspring (as in Mappes *et al.* 1995). However, when food was supplemented, offspring body mass was unaffected by litter enlargement. This indicates that the nursing effort of mothers (i.e. the amount of milk for pups) was limited by food availability. Female body size was also affected by extra food: with supplemental food, females grew bigger during nursing. The results also indicate that food availability may increase the subsequent litter size of females but not the probability of subsequent breeding. However, these latter non-significant results may be caused by inadequate sample sizes and should be taken as questions for further studies.

Food-supplemented females had better weaning success and tended to wean more offspring than unsupplemented females. This can be considered as obvious evidence for food limiting reproductive success of bank vole females. The size at fledging has been found to explain future survival or probability of breeding in birds (e.g. Perrins 1965; Gustafsson & Sutherland 1988), but similar evidence for size at weaning is scarce in mammals. Most of the studies demonstrating benefits of large size are correlative and have not controlled for maternal effects arising from mother quality or number of offspring (e.g. Myers & Master 1983; Dobson & Michener 1995). However, higher mass at weaning of autumn-born bank vole females has been found to correlate with over-winter survival probability (Koskela 1988). Further, the probability that bank vole females will start reproducing during the summer of birth increases with higher body mass at weaning (Mappes *et al.* 1995). Consequently, larger size of weanlings may indicate better quality, and suggests higher reproductive success for food-supplemented mothers.

Positive effect of food on size and/or growth of adults has been found in most studies on birds and mammals (for reviews, see Boutin (1990), Garcia *et al.* (1993) and Wiehn & Korpimäki (1997)). In the current study, females with extra food grew larger by the end of the experiment. Large size may reflect better condition and better reproductive potential in future, e.g. head width of bank vole females correlated positively, although not significantly, with litter size ($r_s = 0.22$, $n = 64$, $p = 0.081$).

Furthermore, in the present study, food-supplemented females tended to have larger subsequent litters than control females. This would suggest that the litter size in bank voles is affected by physiological condition and/or future breeding environment of females and their offspring.

The proportion of weaned offspring per litter was higher in the supplemental food treatment than in the control treatment, suggesting that survival of pups is limited by food availability. Because extra food was removed before pups were at a trappable age, we suggest that the effect of food on offspring was mediated through better nursing ability of mothers. We propose three possible mechanisms for different mortality of pups between food treatments: (i) dying from undernourishment or starvation, (ii) dying from detrimental effects of adults during partial independence from mother (Boonstra 1978), or (iii) killing of pups in their nest by neighbouring females (infanticide) (Ylönen *et al*. 1997). We cannot differentiate between these factors, because we were unable to monitor the survival of pups before trappable age. However, in the present study the home range overlaps of females were smaller when food was supplemented (P. Jonsson, T. Hartikainen, E. Koskela and T. Mappes, unpublished data). This might indicate decreased disturbance caused by adult females towards juveniles and/or result in smaller risk of infanticide. We conclude that the weaning success of mothers increases with supplemental food when density-dependent effects are controlled for. However, the complete mechanism is unclear.

To conclude, our study suggests that the energy requirements of lactating females are an important constraint on the number of offspring that can successfully be raised, in agreement with Lack's (1948) argument. Availability of food resources during nursing may also affect individuals' future reproductive success, because females can use more energy for somatic growth. Whether reproduction is food-limited also in bank voles' more common habitats (in old deciduous or spruce forests, according to Myllymäki (1977)) remains open to question. In addition, in enclosed populations the normal dispersal of voles is not possible, which may confound the results. More experimental studies are needed before these results can be generalized for mammals.

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