Reproductive costs and litter size in the bank vole

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SUMMARY

The potential reproductive costs for free-ranging bank vole (Clethrionomys glareolus) offspring and mothers were assessed by manipulating litter size and by determining the effects of nursing varied numbers of offspring. Litter enlargement did not increase the number of weanlings per mother. The mass of juveniles was significantly lower in the enlarged litters and higher in the reduced litters, compared to the control group. However, the survival of juveniles from weaning aged three months did not depend on their mass at weaning. Data from a previous study (Mappes et al. 1995) indicated that a higher mass at weaning may increase juveniles' abilities to mature and breed during their summer of birth. Manipulation of litter size did not significantly affect the mass or survival of mothers or the success of subsequent breeding. The size of home ranges did correlate positively with the initial litter size. However, space use by females did not change with the degree of manipulation. Our results indicate that females nursing enlarged litters produce smaller offspring at weaning with no residual effects on future maternal survival or reproduction. Mothers did not seem to compensate the nursing costs with increased parental effort (which should be reflected in the condition of mothers or in the use of resources), for example, in an enlarged size of home range. Probably the possibility of obtaining a larger home range is constrained by the other breeding females, in a saturated breeding population. These results may support the optimal investment hypothesis that a female will produce a particular litter size which gives the best reproductive success in the particular environment where offspring are nursed.

1. INTRODUCTION

Life-history theory is based on the assumption that trade-offs exist between various life history traits of individuals (Williams 1966a, b; Stearns 1976). In field studies these trade-offs have been measured often by manipulating the clutch sizes of birds (see review by Roff 1992). Many studies have shown phenotypic effects of the manipulation on the current breeding success, for example, clutch enlargements decrease survival to fledging and survival of offspring until autumn or the next breeding season (Harris 1966; Lack 1966; Perrins et al. 1973; Tinbergen 1987; Smith et al. 1989; Tinbergen & Boerlijst 1990; Pettifor 1993). Some studies also indicate reproductive costs for parents, for example a decreased survival of parents (Askenmo 1977, 1979; Dijkstra et al. 1990) and decreased clutch size in future as a consequence of litter enlargement (Tinbergen 1987; Gustafsson & Sutherland 1988). However, the trade-off between the number of offspring and the performance of parents seems to be far less common than the trade-off between offspring number and survival (Linden & Møller 1989; Roff 1992).

In mammals, studies of optimal litter size and reproductive costs have been based only on unmanipulated phenotypic correlations in the field (Millar 1973; Clutton-Brock et al. 1982; Morris 1986, 1992; Boutin et al. 1988) or on a few litter manipulations in the laboratory (Machin & Page 1973;

Fleming & Rauscher 1978; Kaufman & Kaufman 1987). However, some possible biases exist that are difficult to control when analysing these studies (Roff 1992). For example, there are usually positive correlations between natural litter size and the quality of mother which may obscure possible reproductive costs (Högstedt 1980). On the other hand, some reproductive costs may be difficult to detect in laboratory studies in which nutritional level, physical environment or intraspecific interactions differ from the situation in the field (Stearns 1992).

This study is the first one to examine reproductive costs in free-ranging mammals by manipulating litter size. We studied the consequences of nursing different numbers of offspring for both the offspring and for the mothers in the bank vole (Clethrionomys glareolus). In this territorial species the breeding success of females is supposedly constrained by competition for space (see, for example, Bujalska 1973, 1985; Ylönen et al. 1988). Here we were able to investigate whether the size of home range correlates with the initial litter size of females and how home-range size will vary in response to litter size manipulation.

2. METHODS

(a) Study site and experimental animals

The study was conducted at Konnevesi Research Station, central Finland (62°37′ N, 26°20′ E) during the summer of

Table 1. *Number of litters and initial litter sizes in each treatment group and division of litters into the enclosures*

	number of litters		
initial litter size	reduced	control	enlarged
4	2 (2,7[a])	1 (3)	1 (6)
5	6 (4,5,5,6,6,7)	5 (1,3,6,7,8)	5 (2,5,5,7,8)
6	3 (1,2,4)	3 (1,4,8)	4 (1,2,4,6)
7	3 (1,3,8)	2 (5,7)	2 (3,8)
8	1 (3)	0	1 (4)
9	0	1 (2)	0
total	15	12	13

[a] The eight enclosures where mothers and pups were released.

1994. Experimental populations of bank voles were established in eight 0.25 ha enclosures on a homogeneous abandoned field. The vegetation in the enclosures was typical of old fields. Many grasses were present (e.g. *Alopecurus pratensis*, *Phleum pratense*, *Elymus repens*, *Deschampsia* spp., *Poa* spp.), and herbs (e.g. *Ranunculus acris*, *Hypericum maculatum*, *Geum rivale*, *Alchemilla* spp., *Trifolium* spp.) dominated the field layer. All the experimental animals were caught in the Konnevesi area, where females produce three to four litters of two to nine young from May to September (T. Mappes *et al.*, unpublished data). Female bank voles are strictly territorial during the breeding season and juveniles maturate only if they can gain their own territory (Bujalska 1973, 1985; Ylönen *et al.* 1988).

(b) *Experimental design*

We used wild-caught, non-gravid, over-wintered females which had given birth once during the early summer before the experiment started. Forty females (five per enclosure) were randomly released into the eight enclosures at the beginning of July. At this density (20 individuals ha^{-1}), all females have an opportunity to gain their own territories and to breed (T. Mappes *et al.*, unpublished data). This density is also comparable the highest breeding densities observed in the earlier studies (see, for example, Bujalska 1970; Ylönen *et al.* 1988). If an experimental female disappeared during the experiment, a new female in the same reproductive condition was introduced to the population to ensure the same breeding density throughout the study. New females were not included in the analyses.

During the first ten days, females were allowed to gain their territories and to habituate to the environment. On day 11, three mature males were released into each enclosure. All females were captured just before parturition (17 days after males were released) and they all gave birth within 2–3 days in the laboratory. Litter size was manipulated when pups were 1–2 days old. We assigned litters from each original size category randomly to three treatment groups (see table 1): reduced litters, 'R', with two pups removed; enlarged litters, 'E', with two pups added; and control litters, 'C', where original litter size remained unchanged, but two pups were exchanged with another litter. This last exchange showed that the survival to weaning and the mass at weaning did not differ between a female's own pups and the two cross-fostered pups ($\chi^2 = 0.56, p = 0.453$; two-way ANOVA, $F = 0.051, p = 0.852$, respectively). In the analysis of variance, manipulation was also used as an explanatory variable in the model. The initial litter size did not differ among treatments (one-way ANOVA, $F_{(2,37)} = 0.067, p = 0.936$) (see table 1).

After the manipulation, individually marked females and their pups were simultaneously released to the activity centres of their territories, which should lie very close to their nests (Mironov 1990). The activity centre was calculated as the arithmetic mean point of each individual's capture coordinates. Females were captured again just before the births of their second litters to measure the size of the second litters. The females and second pups were released back into the enclosures.

For monitoring the populations, we used 25 multiple capture live traps in each enclosure with 10 m between the trap stations. Four trapping periods were conducted during the study: before parturition (20–22 July); during lactation about one week after parturition (6–8 August); after weaning of the manipulated litters (23–25 August); and after weaning of the second litters (12–14 October), when offspring from the manipulated litters were about three months old. During each trapping period (three days) traps were checked ten times at 6–9 h intervals. At each trapping period, the mass of individually marked voles was recorded to the nearest 0.5 g, and their home-range sizes were estimated by the inclusive boundary strip method (Stickel 1954). Trappability of individuals did not differ among the treatments (one-way ANOVA, $p > 0.5$, for all trapping periods).

(c) *Effects of weanling masses*

The effect of weanling mass on the probability of maturation was analysed from the data of a previous study (Mappes *et al.* 1995), carried out in the same study area (although four 0.5 ha enclosures were used at that time). In that study we investigated the effects of kin interactions on breeding success of bank vole females. The kin manipulation did not affect the maturation rate of juveniles and thus we were able to analyse maturation data from the study. We had 61 weanlings (27 females and 34 males) in the first cohort, from which seven females and 14 males matured during the experiment. We weighed all juveniles aged one month as the juveniles in the litter manipulation, and further estimated whether this mass would predict the maturation of juveniles during the summer of their birth.

3. RESULTS

As the experiment was conducted in eight separate enclosures, we first analysed whether the enclosure in which the experimental animals lived affected the dependent variables of the study or had joint effects with the treatments. We did not find any significant effect on the characteristics of offspring or mothers throughout the experiment (two-way ANOVA, $p > 0.05$, for all dependent variables; see figures 1 and 2, and tables 2–4). For this reason, we did not use enclosure as a separate factor in the following statistical analyses.
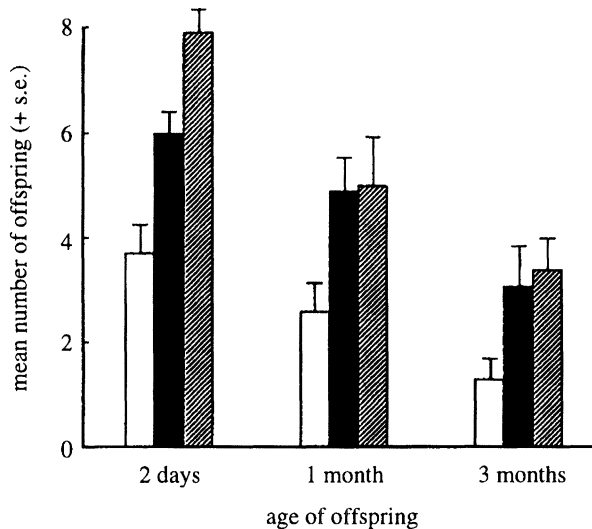
Figure 1. Mean number of offspring among the litters in the beginning of the experiment, at weaning, and just before the winter. Treatment groups: reduced litters ($n = 15$), open squares; control ($n = 11$), filled squares; and enlarged litters ($n = 12$), cross-hatched squares, For statistics see the text.
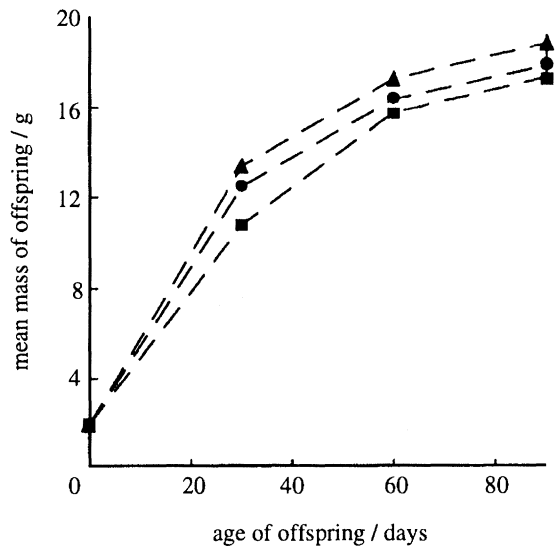

Figure 2. Mass of offspring among the three treatment groups from birth to three months old (prewinter mass): filled triangles, reduced litters; filled circles, control; and filled squares, enlarged litters.

(a) Number and mass of offspring

Enlargement of litter size decreased the mean number of offspring surviving to weaning (see figure 1) compared to other treatments. Thus when the size of litters differed significantly among treatments at the beginning due to the manipulation (one-way ANOVA, $F_{(2,35)} = 46.15$, $p = 0.000$, Student-Newman-Keuls $p < 0.05$ for all), the number of offspring at weaning did not differ significantly between the E and C litters (S-N-K $p < 0.05$), but was significantly lower for R litters compared to E and C litters ($F_{(2,35)} = 3.93$, $p = 0.029$, S-N-K $p > 0.05$). Number of disappeared offspring until the weaning did not correlate with the initial litter sizes (for R litters: $r_s = 0.08$, $n = 15$, $p = 0.782$; for C litters: $r_s = -0.03$, $n = 11$, $p = 0.935$; for E litters: $r_s = 0.05$, $n = 12$, $p = 0.875$). R litters were still significantly smaller in number than the others in the autumn when the juveniles were three months old ($F_{(2,35)} = 4.65$, $p = 0.016$, S-N-K $p < 0.05$) indicating no effects of manipulation on the survival of juveniles after the weaning (see figure 1).

When the litter sizes were manipulated, the initial masses of offspring did not differ among the treatments (see figure 2, table 2). However, the mass of weanlings was significantly lower in the E litters and higher in the R litters compared to the C group. The differences in masses among treatments still differed significantly from each other at the age of two months (see figure 2, table 2).

(b) Mass of weanlings and probability of maturation

Analysis of the earlier data (Mappes *et al.* 1995) showed that the mass of weanlings predicts their probability of maturing. Juveniles that matured during their summer of birth were significantly heavier at the age of 30 days ($X \pm$ s.e. $= 13.8 \pm 0.2$, $n = 21$) than were juveniles which stayed immature (13.4 ± 0.1, $n = 40$) (two-way ANOVA, the effect of maturation: $F_{(1,44)} =$

Table 2. *Analyses of two-way ANOVA for the effects of manipulation and litter on the mass of offspring*

(Repeated contrast methods were used in pair-wise comparisons where each manipulation group was compared to the group that precedes it. E = enlarged, C = control, and R = reduced litters.)

	d.f.	MS	F	t	p
mass at birth					
litter	36	1.04	19.52		0.000
manipulation	2	0.00	0.05		0.951
mass at weaning					
litter	28	11.12	8.33		0.000
manipulation	2	81.26	60.86		0.000
E versus C				4.83	0.000
R versus C				2.32	0.021
mass at 60 days					
litter	26	5.10	3.15		0.000
manipulation	2	22.76	14.03		0.000
E versus C				1.95	0.050
R versus C				2.55	0.012
prewinter mass					
litter	24	5.59	6.01		0.000
manipulation	2	17.53	18.82		0.000
E versus C				1.64	0.104
R versus C				2.55	0.012

5.59, $p = 0.026$). In the analyses the effect of litter was also controlled for ($F_{(1,15)} = 1.80$, $p = 0.066$). All females that matured also gained their own territories and bred during the summer of birth; the mating success of mature males could not be estimated.

(c) Litter size and space use of females

The home-range sizes of females before parturition correlated positively with their initial litter size ($r_s = 0.48$, $n = 30$, $p = 0.008$) (see figure 3a). Home-range size before parturition was also correlated with home-range size at lactation ($r_s = 0.61$, $n = 30$, $p = 0.000$).

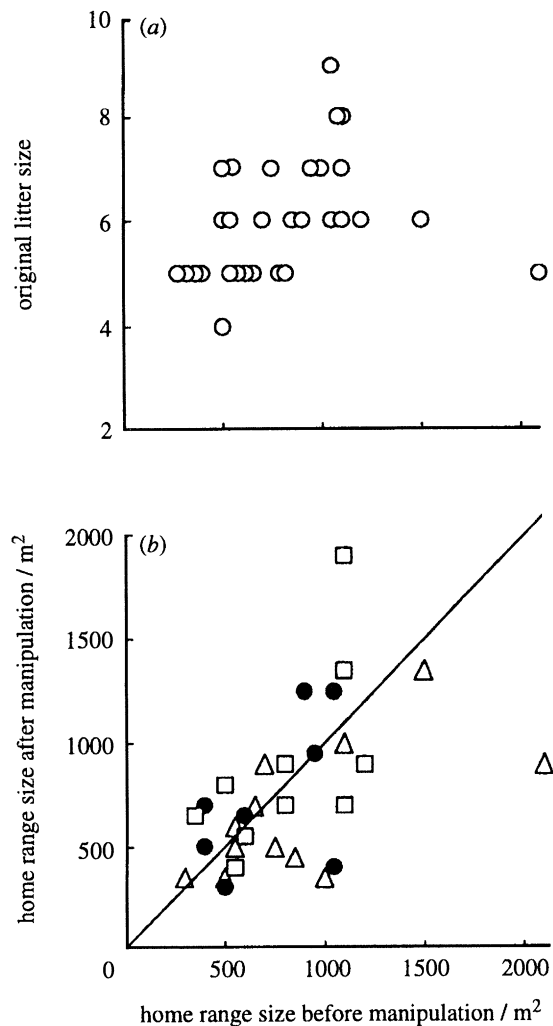Figure 3. (*a*) Positive correlation between the size of home range (m^2) and the number of offspring before the manipulation: $r_s = 0.48$, $p = 0.008$. (*b*) The effect of manipulation on home range size among the treatments: open triangles, reduced litters; filled circles, control; open squares, enlarged litters. The line indicates an equal size of home range before and after the manipulation.

However, the sizes of home ranges did not change from pregnancy to lactation as a function of the degree of manipulation (ANCOVA, $F_{(2,26)} = 1.90$, $p = 0.170$, home-range size before manipulation were used as a covariate) (see figure 3*b*). Furthermore, the initial masses of females tended to correlate positively with their home-range size before parturition ($r_s = 0.39$,

$n = 25$, $p = 0.052$). Masses of females were not significantly correlated with their initial litter size ($r_s = 0.31$, $n = 25$, $p = 0.129$).

(*d*) *Condition of mothers and success of subsequent breeding*

Litter manipulation did not affect the mass or survival of breeding females from the beginning of the experiment to the autumn (see table 3). Probability of breeding, pregnancy delay, size of litters and many other characteristics of subsequent breeding did not differ as a result of the degree of manipulation (see table 4).

4. DISCUSSION

Our results indicate that the nursing costs of enlarged litters affect only the success of current reproduction, especially the survival and quality of the offspring. No costs in terms of survival or future fecundity of mothers were evident as a consequence of litter manipulation. Furthermore, the original number of offspring to which bank vole females gave birth seemed to produce the highest number of high quality offspring supporting the optimal investment hypothesis (Morris 1985, 1987; Pettifor *et al.* 1988). These results agree with most of the studies in birds where trade-offs between the number and quality of offspring were more common than between the number of offspring and performance of parents (Linden & Møller 1989; Roff 1992).

The phenomenon, that females do not trade-off their condition against the quality of offspring, can be explained at least in two ways.

1. A female does not invest more in enlarged litters because the higher investment can decrease her own survival during the current breeding event. Juvenile survival is tightly linked to parental survival during the present breeding event. Mothers should maximize their current breeding success by decreasing survival costs of reproduction, thereby avoiding the risk of complete reproductive failure (Tuomi 1990). Moreover, the control of reproductive investment can be advantageous for a mother if allocation to survival and to the next breeding attempt maximizes her life-time reproductive success (Williams 1966*a*).

2. It is also possible that a female cannot increase her effort to breeding because other individuals limit the utilization of resources necessary for reproduction (Cooke *et al.* 1990).

Table 3. *Survival and mass of breeding females*

	reduced	control	enlarged	d.f.	χ^2	F	p
survived to autumn, % (*n*)	46.7 (15)	63.6 (11)	66.7 (12)	2	1.30		0.521
initial mass (g), $X \pm$ s.e. (*n*)	25.1 ± 1.1 (15)	24.8 ± 0.7 (11)	23.7 ± 1.2 (12)	2		0.47	0.630
non-pregnant mass after the manipulation (g), $X \pm$ s.e. (*n*)[a]	30.2 ± 1.2 (15)	31.8 ± 1.7 (11)	30.3 ± 1.1 (11)	2		0.44	0.645
prewinter mass (g), $X \pm$ s.e. (*n*)	27.3 ± 0.9 (6)	25.5 ± 1.0 (7)	27.6 ± 0.7 (8)	2		1.67	0.216

[a] Weighed after production of second litter.

Table 4. *Characteristics of females and offspring from the second reproductive episode*

	reduced	control	enlarged	d.f.	χ^2	F	p
proportion of produced second litters (n)	83.3 (12)	70.0 (10)	58.3 (12)	2	1.81		0.405
pregnancy delay (days), $x\pm$s.e. (n)[a]	23.0±1.9 (10)	21.0±1.3 (7)	21.6±1.7 (7)	2		0.37	0.698
Size of second litters, $X\pm$s.e. (n)	6.6±0.4 (10)	5.9±0.6 (7)	6.7±0.5 (7)	2		0.90	0.421
mass of second offspring at birth (g), $X\pm$s.e. (n)	1.83±0.02 (10)	1.82±0.02 (7)	1.80±0.07 (7)	2		0.13	0.875
number of second weanlings, $X\pm$s.e. (n)	2.4±0.6 (10)	2.9±1.2 (7)	4.0±0.8 (7)	2		0.92	0.416
mass of second weanlings (g), $X\pm$s.e. (n)[b]	16.8±0.4 (6)	16.6±0.5 (4)	16.2±0.6 (6)	2		0.26	0.779

[a] Days from the first possibility to copulate to the second parturition.
[b] Weighed at age of six weeks.

(a) Does intraspecific competition limit reproductive effort?

We suspected that the home-range sizes of females should correlate quite accurately with the amount of available food resources in the relatively homogenous environment of the enclosures. The home-range size before manipulation of litter sizes correlated significantly with the number of pups produced. Furthermore, the range sizes of females seemed to be related to their ability to defend their own exclusive area or territory (E. Koskela *et al.*, unpublished data). Thus the amount of resources available for reproduction is likely to depend on females' dominance rank in the breeding population. Under these circumstances manipulation did not change the size of home ranges. This may indicate that females with enlarged litters were not able to compensate the higher nursing costs with increased resources in the saturated breeding populations (Cooke *et al.* 1990). This seems quite obvious because bank vole females defend their home ranges, particularly when nursing their young, and their ranges overlap relatively little during that period (E. Koskela *et al.*, unpublished data). Thus as proposed by Cooke *et al.* (1990), selection may act upon both litter size and some behavioural components that correlate with territory quality of bank vole females.

(b) Phenotypic selection to higher juvenile masses

Decreased mass of weanlings of enlarged litters is consistent with the few experiments already conducted in the laboratory (Machin & Page 1973; Fleming & Rauscher 1978; Kaufman & Kaufman 1987). In these studies, however, the effects of mass at weaning on later survival or breeding success of juveniles were not investigated under more natural conditions. In our study, mass of weanlings did not affect juvenile survival during the experiment. However, phenotypic selection may act in relation to the mass of juveniles at least in two ways. First, the probability of maturation and breeding may depend on the mass at weaning. Here, juveniles were not able to breed in the summer of birth, but data from an earlier study (Mappes *et al.* 1995) indicate that the probability of maturation before winter increases with the mass at weaning. Second, large juveniles could have higher survival to the next breeding season. Unfortunately, we were not able to estimate this possible advantage.

In conclusion, the study demonstrates how free-ranging bank vole females respond phenotypically to manipulated litter size. Our results indicate that a trade-off exists between the number of offspring produced and the success of current reproduction: no evidence for reproductive costs in mothers was found. However, the accurate verification of this trade-off or the lack of reproductive costs requires estimation of genetic correlations between the measured traits, as argued by Reznick (1985, 1992). Still, our study supports the existence of trade-offs that can be important in the evolution of litter size in mammals.

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