COST OF REPRODUCTION IN THE WILD: MANIPULATION OF REPRODUCTIVE EFFORT IN THE BANK VOLE

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Abstract. For three years, we manipulated litter size by adding or subtracting pups in eight wild populations of the bank vole, *Clethrionomys glareolus*, to examine reproductive costs and allocation of reproductive effort between offspring number and size. In general, litter enlargements did not increase the number of weanlings per mother and significantly decreased the size of weanlings. Reproductive effort and the breeding success of individuals varied within breeding seasons, but time of breeding and litter manipulation did not interact to affect reproductive trade-offs. Our 3-yr field experiment revealed that litter enlargements also reduced survival and fecundity of mothers. Small mammals have been considered typical income breeders, in which potential reproductive costs may be masked due to their ability to compensate for increased energetic demands of reproduction. Our results provide evidence that, in the wild, females may be incapable of escaping the costs of reproduction.

Key words: bank vole; boreal forest; capital breeders; Clethrionomys glareolus; *income breeders; life-history trade-offs; litter size manipulation; mammals; offspring size; reproductive costs; seasonality.*

Introduction

A fundamental life-history trade-off, the cost of reproduction, is expected to occur between current and future reproduction and survival (Williams 1966, Stearns 1976). That is, an increased investment in present breeding decreases the energy available for other functions, such as maintenance or future breeding (Williams 1966, Bell 1980). Another trade-off can arise between the number and quality of offspring (Lack 1947, Smith and Fretwell 1974). The trade-off between the number and size of offspring has been demonstrated in many species, including birds (e.g., Robinson and Rotenberry 1991), lizards (Sinervo and Licht 1991), and small mammals (Kaufman and Kaufman 1987). All other trade-offs can be considered examples of these two major trade-offs (Lessells 1991).

Studies of life-history trade-offs have concentrated on birds (for reviews, see Linden and Møller [1989], Godfray et al. [1991], VanderWerf [1992]), and experiments examining trade-offs between life-history traits in mammals are still surprisingly scarce. Many studies on reproductive effort and the costs of reproduction in mammals are based on unmanipulated phenotypic correlations in the field (Millar 1973, Clutton-Brock et al. 1982, Murie and Dobson 1987, Boutin et al. 1988, Millar et al. 1992, Huber et al. 1999, Lambin and Yoccoz 2001) or on litter size manipulations in the laboratory (Fleming and Rauscher 1978, Kaufman and Kaufman 1987, Künkele 2000). Recently, experiments

also have been carried out in more natural settings in large outdoor enclosures (Mappes et al. 1995, Koskela 1998, Koskela et al. 1998, 1999, Oksanen et al. 2001, 2002) and in the wild (Hare and Murie 1992, Humphries and Boutin 2000, Neuhaus 2000). Because life-history trade-offs are often dependent on environmental factors (Stearns and Koella 1986, Sinervo 2000), some reproductive costs may only become apparent after long-term experiments under natural conditions. This is because, in seasonal environments, many ecological factors (e.g., predation pressure, intraspecific interactions, weather conditions) may affect the reproductive value (the number of offspring that an average individual in a particular age class can expect to have over the rest of its life; Stearns [1992]) of parents and offspring (e.g., Johansson and Rowe 1999). The scarcity of data on life-history trade-offs in the wild partially explains the difficulty in synthesizing a general theory for the role that reproductive costs play in shaping mammalian life histories (Tuomi et al. 1983, Tuomi 1990, Stearns 1992, Humphries and Boutin 2000).

We manipulated litter size to examine reproductive costs and allocation of reproductive effort between offspring number and size in free-ranging bank voles, *Clethrionomys glareolus* (see Plate 1). We assessed the effects of litter manipulation on (1) the number and body mass of weanlings, (2) the characteristics of mothers' subsequent breeding (litter size, litter mass), and (3) the survival of mothers. Moreover, we were interested in whether individuals cope with reproductive trade-offs differently in relation to different times of the breeding season.

Methods

Study site and trapping procedure

Our study was conducted in eight 1-ha study plots in Konnevesi, central Finland (62°37′ N, 26°20′ E) dur-

PLATE 1. The bank vole, *Clethrionomys glareolus*, is a common rodent in the Palearctic region. It has become a model species in the study of life-history evolution. Our study demonstrates that female bank voles in the wild cannot compensate for the increased energetic demands of enlarged litters and suffer significant reproductive costs. Photograph by Matti Laine.

ing three years (1996–1998). Study areas were situated in boreal forests dominated by Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and various shrubs (e.g., *Calluna* sp., *Vaccinium* spp.). Plots were ≥0.5 km apart, and no dispersal was recorded between plots during the study.

Vole populations and individual voles were monitored using live trapping. We distributed 25 Ugglan special multiple-capture live traps (Grahnab, Hillerstorp, Sweden) in each area in a 5 × 5 grid with 20 m between trap stations. Trapping was conducted each year in early summer (May–June), midsummer (June–July), late summer (August–September), and autumn, when the breeding season was already over (late October). Trapping periods consisted of three discrete 36-h sets (traps were checked every 12 h), separated by 5 d when traps were kept open. Thus, each trapping period lasted 2 wk, during which traps were checked nine times. At each capture, vole identity, sex, body mass (to the nearest 0.5 g), reproductive status, and trap location were recorded. The trapping procedure was designed to maximize the number of individuals caught during the trapping period and to minimize the disturbance of animals. With this procedure, it also was possible to follow the development of pregnancy (body mass and abdominal swelling) and to take females to the laboratory near parturition.

As an indicator of population density, we used the minimum number of animals known alive, MNA

(Krebs 1966). The long trapping period and removal of pregnant females during the trapping prevented the use of more sophisticated density estimates. Because the trappability of bank voles is relatively high (Koskela et al. 1997), the minimum number of animals alive gives a reasonable population estimate.

Litter manipulations

All pregnant females were removed from the study areas during trappings and were housed in standard breeding cages in the laboratory until they gave birth. We checked mothers once per day for parturition. If pups were found, they were immediately measured, sex was determined (according to the length of the anogenital distance), and they were individually marked. A microscope was used to measure head width to the nearest 0.1 mm, and an electronic scale was used to measure body mass at birth to the nearest 0.1 g. Litters were manipulated within 2 d of birth. We assigned litters randomly to three treatment groups: R, reduced litters (initial litter size 3–10 pups, with two pups removed); C, control litters (2–10 pups, with the original litter size unchanged); and E, enlarged litters (original litter 2–7 pups, with two pups added). Pups needed for enlarged litters were obtained both from reduced litters and from wild-caught females (trapped outside the study plots) that gave birth in the laboratory. Bank vole females do not recognize their own pups from foreign ones, and the survival and growth of pups do not differ

TABLE 1. Breeding characteristics (mean ± 1 SE) of bank vole females in different years and seasons.

| | 1996 | | | 1997 | |
Variable	Early (8)	Mid (12)	Late (13)	Early (16)	Mid (12)
Litter size	5.13 ± 0.61	5.50 ± 0.34	5.38 ± 0.42	4.56 ± 0.44	6.42 ± 0.31
Offspring mass	1.84 ± 0.12	1.80 ± 0.04	1.88 ± 0.04	1.68 ± 0.05	1.73 ± 0.03
Postpartum body mass	23.69 ± 0.77	23.57 ± 0.78	24.21 ± 0.89	21.88 ± 0.57	24.54 ± 0.71
Mother head width	13.29 ± 0.10	12.91 ± 0.15	12.97 ± 0.13	13.04 ± 0.08	13.49 ± 0.16
Reproductive effort	0.742 ± 0.819	0.791 ± 0.438	0.786 ± 0.458	0.655 ± 0.523	0.881 ± 0.445

Notes: Seasons are defined as early (early summer, May–June), mid (midsummer, June–July), and late (late summer, August–September). For each season, the sample size of adult female voles is given in parentheses.

between the female's own pups and cross-fostered pups (Mappes et al. 1995).

After litter size manipulations, females and their pups were released in breeding cages to the study plots at their original site of capture, which we assumed to be in the vicinity of their nests (Mironov 1990). Cages were left open so that the mothers could carry pups back to their nests. This method has worked well in earlier studies by Mappes et al. (1995) and Koskela et al. (1999). During the next trapping period, the females were returned to the laboratory to give birth to the next litter (~20 d after possible mating, and when the first litter was at weaning age).

Data analysis

We first analyzed whether the litter size and reproductive effort of females differed between seasons and years. By season, we mean the time of breeding: early summer (May–June), midsummer (June–July), and later summer (August–September). We used female body mass as a covariate in the ANOVA test of litter size by season. Reproductive effort (RE) of mothers was estimated using relative litter mass: $RE = L \times M_o^{0.75}/M_m^{0.75}$, where L is the litter size at birth; M_o is mean offspring body mass at birth; and M_m is the postpartum body mass of the mother (Millar 1977, Ebenhard 1990). Secondly, we analyzed whether the dependent variables (initial litter size and body mass at birth and at weaning) differed among study plots. We did not find a significant effect of plot on any of these traits (all P > 0.1), and therefore ''plot'' was not used as a separate factor in subsequent statistical analyses. Similarly, we did not find a significant effect of population density on initial litter size or on body mass at birth and at weaning (all P > 0.1). Thus, in all further analyses, only litter manipulation, season, and year were used as independent variables. Logistic regression was used to estimate the factors affecting weaning success, probability of producing a second litter, and subsequent survival of mothers and offspring. In these analyses, the dependent variable was treated as a binary variable and different explanatory factors were treated as categorical variables. The main effects and their interactions were entered into our analyses, and the best-fit model was chosen by stepwise model selection. The significance of the models was estimated using likelihood ratio tests (LRT).

RESULTS

Breeding characteristics

Litter size for bank voles in the study area ranged from 2 to 10 (5.27 ± 1.32 pups, mean ± 1 SE) with newborn pups weighing from 1.0 to 2.5 g (1.76 ± 0.01 g). First litters were born in mid-May, and breeding continued until mid-September, when the last litters were born. During the last trapping period, in late October, none of the captured females was pregnant. Population density of voles on the study plots increased over the summer, peaked in late summer, and then de-
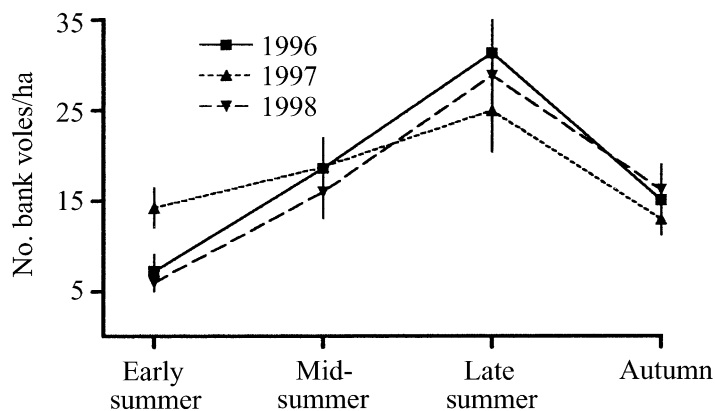

FIG. 1. Population densities (mean ± 1 SE) of bank voles (*Clethrionomys glareolus*) expressed as minimum number known alive (MNA) in each trapping period on eight 1-ha study plots.

TABLE 1. Extended.

1997	1998		
Late (9)	Early (9)	Mid (12)	Late (12)
4.78 ± 0.28	5.00 ± 0.29	5.33 ± 0.31	5.33 ± 0.40
1.87 ± 0.41	1.82 ± 0.09	1.84 ± 0.04	1.83 ± 0.08
23.87 ± 1.36	22.51 ± 0.68	23.99 ± 0.70	24.24 ± 1.17
12.86 ± 0.30	13.18 ± 0.14	13.04 ± 0.10	13.16 ± 0.18
0.716 ± 0.501	0.750 ± 0.312	0.776 ± 0.388	0.760 ± 0.454

creased toward autumn (Fig. 1). Breeding character-istics of females in different years and seasons are listed in Table 1. Litter size differed among seasons and was largest in midsummer; year or female's body mass did not affect litter size (ANCOVA: for season, $F_{2,97}$ = 3.414, P = 0.037; for year, $F_{2,97}$ = 0.050, P = 0.95; interaction NS; for female body mass, $F_{1,97}$ = 1.151, P = 0.28). However, mean offspring mass at birth was not affected by season, year, or body mass of females (ANCOVA: for season, $F_{2,97}$ = 1.428, P = 0.24; for year, $F_{2,98}$ = 0.734, P = 0.48; interaction NS; for female body mass, $F_{1,97}$ = 0.575, P = 0.45). Reproductive effort of mothers differed among seasons (highest in midsummer) but not among years (ANOVA: for season, $F_{2,98}$ = 3.723, P = 0.028; for year, $F_{2,98}$ = 0.135, P = 0.87; interaction NS).

Number of offspring and weaning success

The initial litter sizes for bank vole females (before manipulation) did not differ among the treatment groups (three-way ANOVA: for manipulation, $F_{2,88}$ = 1.29, P = 0.28; for season, $F_{2,88}$ = 4.02, P = 0.021; for year, $F_{2,88}$ = 0.08, P = 0.93; all interaction terms NS), but differed significantly after manipulation (for manipulation, $F_{2,88}$ = 67.09, P < 0.001; for season, $F_{2,88}$ = 4.58, P = 0.013; for year, $F_{2,88}$ = 0.193, P = 0.83; all interactions NS; see Fig. 2A). Litter enlarge-ment did not increase the number of weaned young compared to controls, but litter reduction produced the smallest litters at weaning (for manipulation, $F_{2,87}$ = 3.37, P = 0.039; for season, $F_{2,87}$ = 3.10, P = 0.050; for year, $F_{2,87}$ = 3.74, P = 0.028; interactions NS; for initial litter size, $F_{1,87}$ = 8.14, P = 0.005; see Fig. 2B). Mothers appeared to nurse enlarged litters more suc-cessfully in midsummer than in the other seasons, al-though differences were not statistically significant (separate ANOVA for midsummer: manipulation, $F_{2,33}$ = 1.623, P = 0.21).

Weaning success of females was rather low in all manipulation groups, and 55.3% of all females failed to wean any young (manipulation categories: R, 54.5%; C, 53.3%, E, 57.9%). The factors affecting weaning success were estimated by logistic regression with litter manipulation, season, year, survival of mother, and ini-tial litter size as explanatory variables. Only survival of the mother and initial litter size were retained in the selected model (survival LRχ^2 [likelihood-ratio chi-

square] = 14.467, df = 1, P < 0.001; initial litter size LRχ^2 = 9.164, df = 1, P = 0.002). Mothers with orig-inally larger litters had a higher probability of suc-cessfully weaning at least one offspring, independent of the manipulation. In most cases in which the mother had died during the nursing period, the pups also died (only six out of 37 mothers not surviving to the next trapping still successfully weaned offspring).

Survival and fecundity costs for mothers

The factors affecting subsequent breeding of females were estimated by logistic regression with litter ma-nipulation, season, and year as explanatory variables. A total of 30% of females (31 out of 103) gave birth to a second litter (manipulation categories: R, 50.0%; C, 31.0%; E, 48.0%). The probability that females would produce a second litter did not differ between
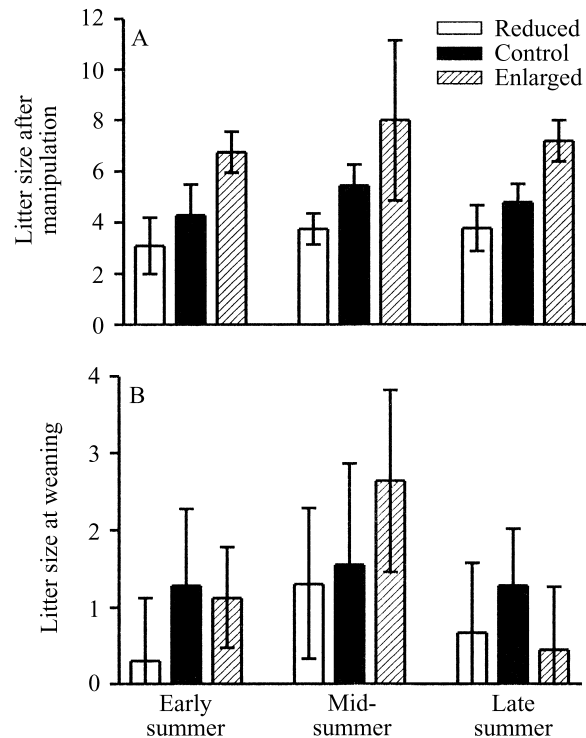

FIG. 2. Number of offspring (mean ± 95% CI) per female bank vole in different treatments and seasons (A) after litter manipulation and (B) at weaning (including zero litters).
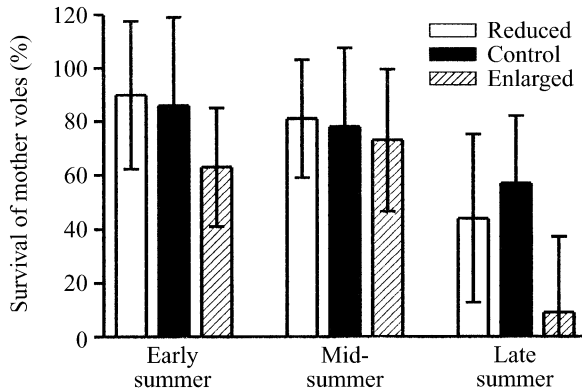
FIG. 3. Survival of mother bank voles (mean ± 95% CI) in different treatments and seasons.

manipulation groups and the only difference found was among years (LRχ^2 = 8.148, df = 2, P = 0.017). However, litter manipulation appeared to affect the fecundity of mothers because litter size and litter mass in subsequent breeding attempts differed slightly between manipulation groups, indicating that litter enlargement may be costly for mothers (litter size, mean ± 1 SE: R, 6.15 ± 0.22 pups, C, 6.2 ± 0.49, E, 5.54 ± 0.29; manipulation, $F_{2,17}$ = 3.541, P = 0.052; season, $F_{1,17}$ = 3.265, P = 0.089; year, $F_{2,17}$ = 4.880, P = 0.021; all interaction terms NS). Litter mass (mean ± 1 SE) of the manipulation categories is as follows: R, 11.2 ± 0.71 g; C, 10.26 ± 0.38 g; E, 9.79 ± 0.77 g (manipulation, $F_{2,17}$ = 3.107, P = 0.072; season, $F_{1,17}$ = 0.588, P = 0.454; year, $F_{2,17}$ = 6.227, P = 0.009; all interactions NS). After the third trapping period, breeding had ceased. Therefore, only the first and the second trapping periods were included in the analyses of subsequent breeding performance.

The probability of mothers surviving to the next trapping period was affected by litter manipulation (LRχ^2 = 7.691, df = 2, P = 0.021), and mothers with enlarged litters had the lowest survival. In addition, survival of mothers was dependent on breeding season, being lowest in late summer (LRχ^2 = 16.414, df = 2, P < 0.001; Fig. 3). Dispersal of adult bank vole females is suggested to be rather low (Lambin 1997, Prévot-Julliard et al. 1999), but dispersal still could have biased our survival estimates (Doligez et al. 2002), so we studied whether the mobility of females differed between litter manipulation groups. The distances (mean ± 1 SE) that females moved between trapping stations before litter manipulations were not different from those moved after manipulations, and litter manipulation did not affect the mobility of mothers (R, 21.09 ± 4.43 m, C, 23.71 ± 4.26 m, E, 20.74 ± 4.84 m; ANOVA: manipulation, $F_{2,44}$ = 0.167, P = 0.85; season, $F_{2,44}$ = 1.099, P = 0.34; year, $F_{2,44}$ = 0.339, P = 0.72, all interaction terms, NS).

Body size and survival of individual offspring

Offspring mass at birth did not differ between manipulation groups ($F_{2,523}$ = 1.831, P = 0.16), but the body mass and head width of weanlings was lowest in enlarged litters (Fig. 4). Results of an ANCOVA, in which offspring of the mother (random effect) were nested within manipulation (fixed effect), and offspring age was used as a covariate, are as follows for body mass: manipulation, $F_{2,90}$ = 3.500, P = 0.036; season, $F_{2,90}$ = 18.686, P < 0.001; year, $F_{2,90}$ = 0.391, P = 0.678; mother, $F_{11,90}$ = 0.743, P = 0.695; age, $F_{1,90}$ = 16.091, P < 0.001; all interaction terms NS. For head width, ANCOVA results are as follows: manipulation, $F_{2,86}$ = 4.025, P = 0.025; season, $F_{2,86}$ = 5.850, P = 0.004; year, $F_{2,86}$ = 8.582, P < 0.001; mother $F_{11,86}$ = 1.559, P = 0.126; age, $F_{1,86}$ = 15.966, P < 0.001; all interactions NS). The size of weanlings also differed within the breeding season and among years. Even so, it appeared that litter manipulation did not affect the probability of offspring survival after they had achieved independence (offspring surviving to the age of >30 d). However, survival prospects differed among seasons, being lowest in late summer (LRχ^2 = 13.261, df = 2, P = 0.001), and among years (LRχ^2 = 6.289, df = 2, P = 0.043; Table 2). The origin of pups did not affect the survival of offspring because there was no difference in survival prospects of cross-fostered pups (19.8% survived to weaning) and a female's own pups (20.3% survived to weaning; χ^2 = 0.010, df = 1, P = 0.92).
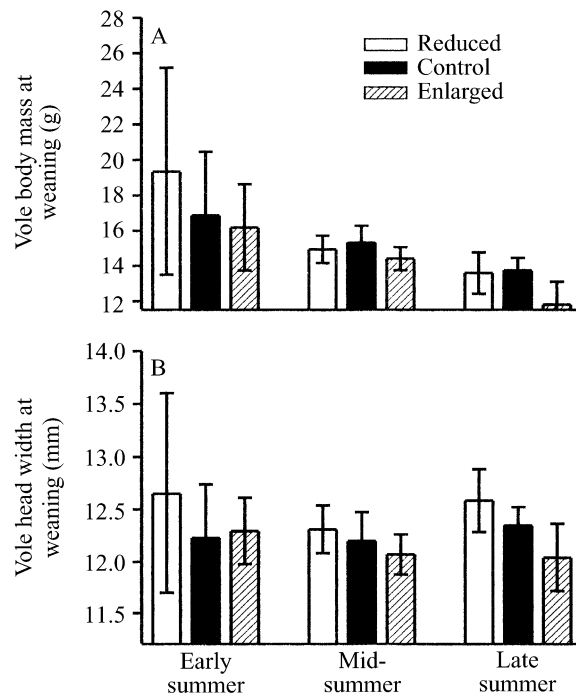

FIG. 4. Offspring size at weaning age (mean ± 95% CI): (A) body mass and (B) head width.

TABLE 2. Percentages of bank vole offspring surviving from weaning to the age of >30 days in relation to year, season, and litter manipulation.

Litter size manipulation	1996			1997			1998		
	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Reduced	0 (1)	0 (4)	0 (4)	100 (2)	0 (7)			40.0 (10)	0 (3)
Control	33.3 (3)	25.0 (4)	0 (10)	0 (2)	50.0 (2)		25.0 (4)	50.0 (8)	12.5 (8)
Enlarged	60.0 (5)	22.2 (9)		50.0 (4)	28.6 (14)		77.8 (9)	50.0 (6)	20.0 (5)

Notes: Seasons are defined as early (early summer), mid (midsummer), and late (late summer). Cells are blank where no pups survived to weaning; sample sizes are given in parentheses.

DISCUSSION

Most studies on optimal litter size and reproductive costs in small mammals have been conducted in the laboratory (e.g., Fleming and Rauscher 1978, Kaufman and Kaufman 1987) or in seminatural outdoor enclosures (e.g., Mappes et al. 1995, Koskela et al. 1999), where conditions remained relatively constant throughout the study. However, life-history traits are often phenotypically plastic, and individuals have been found to cope with reproductive trade-offs differently in different environments (Stearns and Koella 1986, Koskela et al. 1999, Lambin and Yoccoz 2001). Moreover, reproductive costs may only become apparent in natural environments (Huber et al. 1999, Humphries and Boutin 2000, Neuhaus 2000, Lambin and Yoccoz 2001). Consequently, to advance our understanding of reproductive trade-offs in mammals, it is necessary to study trade-offs in the wild, where individuals face both the ecological and physiological costs of reproduction.

The general conclusion from experiments manipulating brood size has been that trade-offs between parental reproduction and survival are far less common than trade-offs between current reproduction and fecundity, or between current reproduction and offspring size or survival (Lindén and Møller 1989, Hare and Murie 1992, Mappes et al. 1995). Lindén and Møller (1989) suggested that lifetime reproductive success depends more on parental survival than fecundity (Clutton-Brock 1988). However, reproductive costs may differ, for example, between short- and long-lived species, capital or income breeders (Jönsson 1997), or organisms with different types of parental care. Because survival costs have been found only rarely, it has been hypothesized that in species with extensive parental care, females do not trade off their condition against the quality of offspring by investing more in enlarged litters at the expense of their own survival (Tuomi 1990). This hypothesis has gained support from studies of bank voles (Mappes et al. 1995, Koskela et al. 1999), as well as from other experiments in small mammals (Hare and Murie 1992, Humphries and Boutin 2000, Neuhaus 2000). Potential costs of reproduction may also be masked by compensatory adjustments in resource allocation: if reproducing individuals have access to abundant resources, they could compensate for the energetic demands of reproduction by increasing energy intake rather than draining somatic energy reserves (Tuomi et al. 1983). This strategy is possible for income breeders, which can adjust their energy intake concurrently with breeding, and not for capital breeders, which mostly use stored energy for reproduction (Stearns 1992, Jönsson 1997). Accordingly, reproductive costs should be more evident in capital breeders than in income breeders such as bank voles and other small mammals. Our data, however, suggest that litter enlargement resulted in both survival and fecundity costs for bank vole females. Moreover, in a recent experiment in which reproductive effort of bank vole females was hormonally manipulated during pregnancy, experimental females suffered significant reproductive costs (Oksanen et al. 2002). Thus, bank vole females in the wild appear incapable of compensating for the increased energetic demands of enlarged litters. Nursing a larger number of pups may require a greater foraging effort, and offspring defense may be costly (Koskela et al. 2000).

Enlarging litter size did not increase the number of weanlings entering the breeding population, which indicates that the survival of pups during nursing decreased with increased litter size. Many studies indicate that the survival of juveniles in the wild is low and that the losses of whole litters are common (Innes and Millar 1990, McAdam and Millar 1999, Getz et al. 2000), emphasizing that manipulation per se did not increase offspring mortality. At weaning, individual offspring from enlarged litters were smaller than those from reduced litters. These results are consistent with those of our earlier enclosure studies, which report a trade-off between litter size and offspring size in bank voles (Mappes et al. 1995, Koskela et al. 1998, 1999; but see Oksanen et al. 2001). After they reached independence, juveniles had similar survival in all manipulation groups. Oksanen et al. (2001) also showed that initially smaller offspring from enlarged litters ultimately grew to the same size as control individuals, and did not suffer lowered survival. In general, our results are in agreement with those of other experimental studies on small mammals in the wild. Litter size enlargements did not increase the number of surviving offspring per female, but reduced the growth rate of offspring in both Columbian ground squirrels, *Spermophilus columbianus*, and red squirrels, *Tamiasciurus hudsonicus* (Hare and Murie 1992, Humphries and Boutin 2000, Neuhaus 2000). In contrast to earlier

experiments (e.g., Hare and Murie 1992, Mappes et al. 1995, Koskela et al. 1999, Humphries and Boutin 2000, Neuhaus 2000), however, increased litter size resulted in survival costs for mothers.

The timing of reproduction during the breeding season affected reproductive effort, survival, and breeding success of female bank voles. Survival of females and the number of weanlings were highest during midsummer and lowest in autumn. Breeding success of female small mammals can be negatively affected by limited food resources (Boutin 1990, Duquette and Millar 1995, Wauters and Lens 1995, Koskela et al. 1998) and increasing density (Ostfeld and Canham 1995, Koskela et al. 1999). In our study, conditions for breeding were probably best during midsummer, when food resources and competition for space probably did not limit breeding. However, in spite of large variation in the breeding success of bank vole females, the effect of litter manipulation was independent of season and year. Litter enlargement was always costly for both mothers and offspring, indicating that females were not able to compensate for higher nursing costs when facing both the ecological and physiological costs of reproduction. Many studies indicate that small-mammal metabolism may approach maximum sustainable metabolism (Koteja 1991); the basal metabolic rate (BMR) of bank voles is highest during summer (Aalto et al. 1993). The BMR may be functionally linked with energy budgets in natural conditions. Thus, litter enlargement may exceed the physiological capacity of bank vole females.

Previous studies of mammals have detected reproductive costs in the form of offspring trade-offs, whereas trade-offs experienced by parents were rarely found. In our study, both reduced survival and fecundity of dams were detected. Consequently, to further advance our understanding of reproductive trade-offs, reproductive costs should be studied in the wild where life-history tactics are shaped by environmental constraints.

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