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Effect of birth and weaning mass on growth, survival and reproduction in the bank vole

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ABSTRACT

Among mammals, physiological constraints and resource availability limit resources for reproduction. Limited resources can be allocated to either large litters with small offspring or to fewer but heavier pups. High birth weight is thought to be related to better survival and earlier onset of reproduction. We studied the effects of birth and weaning masses on future survival and reproduction of bank voles (*Clethrionomys glareolus*) in a combined laboratory and field experiment. We reared voles in the laboratory and cross-fostered pups after birth to randomize maternal effects before weaning. Using 256 laboratory-bred individuals, we conducted two separate field experiments over 3–4 weeks in large outdoor enclosures to study the effects of birth and weaning weights on individual survival and reproduction. Males that were heavy at birth were also heavy as adults. Females heavier at birth produced larger litters under favourable conditions of the earlier replicate, but not in the later one. Mass at birth or weaning did not affect survival. There was great variation in growth and reproduction over time presumably related to environmental conditions. The first run seemed to be more favourable, especially for body condition of adults. In the second run, the later season might have had a negative effect on the proportion of females breeding. However, most probably the voles suffered from food depletion due to heavy rains. In conclusion, we did not find any simple positive effect of birth mass on the success of individuals. It would appear that the effect of high birth mass is not an unambiguous issue in life-history evolution.

Keywords: bank vole, birth mass, compensatory growth, life histories, reproduction, survival, weaning mass.

INTRODUCTION

Life history can be described as an organism's lifetime pattern of growth, differentiation, storage and reproduction (Daan and Tinbergen, 1997). High mass at birth is considered an advantage because less needs to be invested in growth and reproduction can be started earlier in life. Conversely, life-history theory predicts that, as the number of offspring produced increases their quality decreases, as the resources allocated to each individual

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offspring decrease (Smith and Fretwell 1974). In mammals, physiological constraints set limits to the total litter mass produced, but at the same time there is great variation in litter size and the birth mass of an individual offspring (Sikes and Ylönen, 1998; Oksanen *et al.*, 2002). Hence, mammalian reproduction shows a clear trade-off between the size, quality and number of offspring (e.g. Smith and Fretwell, 1974).

Only a few studies of mammals have analysed the effect of birth weight on subsequent growth, survival and breeding success (Myers and Master, 1983; Calambodikis and Gentry, 1985; Fairbanks, 1993; Pélabon, 1997; Koskela, 1998). In fallow deer, a higher mass at birth correlated positively with mass at the onset of winter, the latter being an important factor for winter survival (Pélabon, 1997). Myers and Master (1983) found a sharp decrease in survival of very light deer mouse (*Peromyscus maniculatus*) pups. Northern seal pups that died prematurely were significantly lighter at birth than the average of the population (Calambodikis and Gentry, 1985). Size at birth significantly explained the probability of breeding and the size of first litter in bank voles (Koskela, 1998). Heavier pups also maturated earlier than small pups, but weaning weight did not affect the probability of breeding or the litter size. Experimental studies have revealed that enlargement of litter size often has a negative effect on body size at weaning (Koskela *et al.*, 1997; Humphries and Boutin, 2000). Long-term effects of birth or weaning mass on growth or survival are rare (Oksanen *et al.*, 2001).

Short-lived iteroparous species, such as the bank vole, *Clethrionomys glareolus*, may benefit from a high mass at birth. The amount and duration of maternal care is limited. Pups are weaned at the age of 20 days and the next litter is in late gestation at that time. It would be profitable to invest more energy in the litter during pregnancy than during lactation. Female bank voles compete for territories, a prerequisite for reproduction (Bujalska, 1973). Males have a hierarchical system that predicts the probability for mating (Horne and Ylönen, 1996). Thus having a large body mass as early as possible could increase both the probability of possession of territory by females and of being among successful males in the hierarchy.

The aim of this study was to examine experimentally the effects of mass at birth and weaning on growth, survival and reproduction of the bank vole, *Clethrionomys glareolus*. Raising animals in the laboratory provided us with knowledge of the origin of the study animals and their birth and weaning weights. The experiments were conducted in large field enclosures, which exposed the voles to normal environmental conditions during their normal breeding season. We tested the hypothesis that individuals heavy at birth and weaning are also heavy as adults, and that they survive better and produce larger litters than those born lighter. Thus the allocation of resources in favour of larger offspring at birth and/or weaning would increase fitness of the parent.

MATERIALS AND METHODS

Study species

The bank vole, *Clethrionomys glareolus*, is a common rodent inhabiting forests, forest edges and brush woods throughout Europe (Stenseth, 1985). It lives approximately one year and most females reproduce only during one summer (Tkadlec and Zejda, 1998; Prevot-Julliard *et al.*, 1999). Individuals born in spring can reproduce during the summer of their birth. Those born in the later cohorts overwinter as immature animals. In Central Finland, bank

voles inhabit various environments from bushy fields to forests and breed from late April to September (Ylönen *et al.*, 1988). Females give birth to up to four litters during one breeding season, ranging from 1 to 11 (usually 4–8) individuals (Eccard and Ylönen, 2001; Oksanen *et al.*, 2002). Pregnancy lasts for 19–20 days (in lactating females 21–24 days). Pups are weaned before the age of 3 weeks. Reproducing female bank voles are territorial, while male ranges are large and overlap (Bujalska, 1973). Bank voles do not recognize their neonate pups from foreign ones. This enables litter size manipulations and cross-fostering (e.g. Koskela *et al.*, 1997).

Raising the animals

The animals used in our experiment were third- and fourth-generation laboratory stock, established from animals caught in the wild and raised in the facilities of the Experimental Animal Unit, University of Jyväskylä. Fertile female and male bank voles (P-generation, no sibs) were paired and then checked daily. Pairs were housed in standard mouse cages ($43 \times 26 \times 15$ cm) with wood shavings and dry hay as bedding. Food and water were available *ad libitum*. Photoperiod in the laboratory was 18 h : 6 h light : dark and air in the animal room was changed 15 times each hour. Pregnant females were separated from their mates and thereafter checked daily for parturitions. All pups were weighed, sexed and individually marked within 24 h of their birth, and then weighed every second day until weaning.

To randomize the effects of litter size and maternal care during lactation, all litters were cross-fostered. The pups from two or three litters born on the same day or one day apart were distributed among the mothers of other litters, such that dams had litters with some of their own pups and some pups from other females. The original litter sizes were not manipulated. A total of 90 litters from 66 mothers and 51 fathers were produced.

The pups (F1-generation) were weaned at the age of 20 days, but were still housed together as litters. Large litters (more than 5 pups) were divided in two to avoid over-crowding in the cage. They were kept under constant laboratory conditions. Before the field experiment at Konnevesi Research Station, the voles were acclimatized for 5 days in the field laboratory under normal outdoor light regime and temperature.

Field study area and trapping procedure

The field study was carried out using eight outdoor enclosures, each 0.25 ha in size. There were two replicates, the first from 10 June until 7 July (27 days) and the second from 12 July until 6 August (22 days). Both replicates were within the breeding season of the species (Kaikusalo, 1972; Ylönen *et al.*, 1988). The habitat within the enclosures was old field, with tall grasses and herbs and some bushes (Ylönen *et al.*, 1990). In each enclosure, we established a grid of 25 Ugglan Special live traps, 5×5 traps at 10-m intervals. Traps were covered with trap chimneys made of galvanized metal sheet ($50 \times 50 \times 40$ cm) to protect the trapped voles against sun and rain.

At the start of the study, F1-generation voles were 39–70 days old and well beyond the age of maturity. There were 8 females and 8 males in each enclosure (64 voles $\cdot$ ha^{-1}). This density of 32 females per hectare reflects a high density in terms of number of breeding females (Ylönen *et al.*, 1988) and creates competition for breeding possibilities among females.

Voles were assigned to the enclosures following two criteria: (1) to randomize the environmental and social conditions, no siblings were put in the same enclosures; and (2) age differences in each enclosure were kept to a maximum of 14 days to control for possible age-dependent competitive ability. All animals were weighed before the experiment and released in the centre of each enclosure.

Live trapping was used to monitor individual movements, body mass, reproduction and survival. Traps, baited with sunflower seeds and potatoes, were checked twice a day, at 08.00–09.00 h and 23.00–24.00 h, for 5 days a week. Traps were kept open during the day to avoid overheating and to allow the voles to move freely from the morning trapping until 16.00–17.00 h. The identity of the vole and the trap station were recorded at each capture and all animals were weighed once a week. Pregnant females were captured a few days before their expected time of delivery and placed in standard mouse cages, sheltered from sun and rain, in the centre of their home range estimated from the trapping data. Females were checked three times a day for parturition, the litter size was determined and the mother was released back into the enclosure. This was done to keep the female density and population structure as constant as possible. The pups (F2-generation) were kept in the laboratory, were individually weighed and placed in the care of foster mothers.

After each replicate, all survivors were removed to the laboratory and weighed. Pregnant females were housed singly in mouse cages until they gave birth to determine the litter sizes and the weights of the pups conceived during the experiment. Males were killed and their testes and preputial glands weighed.

Analysis of fitness effects

To determine whether mass at birth or at weaning was related to reproductive success, it was correlated with adult body mass and survival, and possibilities for reproduction during the replicate. We used litter size and mean birth mass of pups (F2-generation) as measures of female reproductive success. We were not able to determine male reproductive success. Instead, we controlled for male effects by randomizing mating in the laboratory and estimating male quality using the mass of their testes and of their preputial glands. Preputial gland mass is related to dominance rank among bank voles (Gustafsson *et al.*, 1980) and females are attracted to dominant males (Hoffmeyer, 1982; Horne and Ylönen, 1996).

Adult body mass is an indicator of body condition, especially that of males (Singleton *et al.*, 2001). Heavy males may have an advantage over lighter males when competing for the chance to mate. For females, larger body size can mean increased fecundity (Roff, 1992). Males and females were weighed weekly, but the body masses of reproducing females were not used in the statistical analysis because pregnancy would have confounded the results.

Survival in the field was recorded as the percentage of the total study length an individual survived. If the animal was captured alive after the experiment, its survival was 100%.

RESULTS

Comparison of the two replicates

Preliminary analysis of the data revealed that physiological variables differed significantly between the two replicates. The experimental procedure was the same and both replicates were well within the natural breeding season. However, there were heavy rains during the

week between the two replicates and we suspect that this might have decreased seed availability of the habitat. This might have resulted in differences in mean body mass between the replicates (Table 1). The voles gained weight in the first replicate but it declined in the second. Reproductive success also differed between the two replicates. In the first replicate 50% of the 64 females reproduced, but in the second only 22% reproduced. There was no difference in mean litter size between the replicates. Male testes and preputial gland sizes also differed significantly. Because of these differences between replicates, statistical tests were applied separately to the early (favourable conditions) and the late (unfavourable conditions) replicate.

Fitness-related variables and body mass at birth

In the first replicate, body mass at birth predicted the body mass of males in the field each week. In the second replicate, male body mass at birth also correlated positively with field body mass in the first 2 weeks of the experiment. Among non-reproducing females, there was no clear pattern between birth weight and adult body weight in either of the replicates (Table 2).

Females that were heavy at birth had larger litters in the first replicate, but the pups were the same size. In the second replicate, there was no correlation between birth mass and the

Table 1. Comparison of body masses, survival and reproduction of bank voles between the two replicates of the experiment

Variable	Replicate 1	Replicate 2	d.f.	*t*	*P*
Mass before experiment (g)	16.82 ± 0.22	17.86 ± 0.25	125 (replicate 1) 127 (replicate 2)	−3.07	0.002
Body mass change (g)	5.17 ± 0.83	−1.25 ± 0.64	57 (replicate 1) 56 (replicate 2)	6.13	<0.001
Survival percentage	86.54 ± 2.23	86.45 ± 2.00	126 (replicate 1) 127 (replicate 2)	0.03	0.976
No. of reproducing females	32	14	1	10.99*	0.009
Mean no. of pups	4.63 ± 0.21	4.36 ± 0.34	29 (replicate 1) 10 (replicate 2)	0.67	0.509
Mean preputial mass (mg)	5.87 ± 0.51	2.61 ± 0.53	46 (both replicates)	4.47	<0.001
Mean testes mass (mg)	333.46 ± 12.19	148.67 ± 20.30	46 (both replicates)	7.81	<0.001
Mean body mass at birth (g)	1.77 ± 0.23 (F) 1.81 ± 0.30 (M)	1.81 ± 0.20(F) 1.86 ± 0.27(M)	126 (F) 125 (M)	−1.19 −0.33	0.235 0.739
Mean body mass at weaning (g)	10.30 ± 1.73 (F) 9.95 ± 2.14 (M)	10.43 ± 2.05(F) 10.30 ± 1.58(M)	96 (F) 99 (M)	−1.01 −0.87	0.315 0.387

Note: Values represent the overall mean ± standard error in each replicate. The asterisk denotes chi-square test value. F = female, M = male.

Table 2. Correlations between birth weight and subsequent weight development, reproduction and survival in male and female bank voles

		Replicate 1			Replicate 2		
		r_s	N	P	r_s	N	P
Weight in enclosures							
Males	Week 1	0.407	57	0.002	0.328	62	0.009
	Week 2	0.393	51	0.004	0.308	58	0.019
	Week 3	0.453	46	0.002	0.166	38	0.320
Non-reproducing females	Week 1	0.264	21	0.247	0.171	49	0.239
	Week 2	–0.075	18	0.767	0.346	41	0.027
	Week 3	0.090	15	0.750	0.394	22	0.069
Reproduction							
Males	Mean preputial mass	0.157	46	0.296	0.016	47	0.917
	Mean testes mass	0.093	46	0.541	–0.088	47	0.558
Females	Litter size	0.487	30	0.006	0.165	11	0.628
	Pup weight	–0.250	29	0.731	0.464	7	0.294
Survival							
Males		0.145	63	0.255	–0.070	64	0.581
Females		0.046	63	0.719	–0.074	64	0.561

number of pups produced. The number of reproducing females was much lower in the second replicate ($n = 11$) than in the first ($n = 30$).

The mass of males at birth did not affect the mean size of testes or preputial glands in either of the replicates. However, organ masses correlated positively with body masses in the first week. In both replicates, heavy males also had heavy testes (replicate 1: $r_s = 0.599$, $n = 46$, $P < 0.001$; replicate 2: $r_s = 0.594$, $n = 35$, $P < 0.001$) and heavy preputial glands (replicate 1: $r_s = 0.578$, $n = 46$, $P < 0.001$; replicate 2: $r_s = 0.616$, $n = 36$, $P < 0.001$).

The effect of neonate mass on survival was not significant in either sex or replicate (Table 2).

Fitness-related variables and weaning mass

There was a highly significant positive correlation between mass at weaning and weekly body masses of both sexes in the first replicate. In the second replicate, a positive correlation was evident only during the first 2 weeks in both sexes (Table 3).

Heavy females at weaning tended to have larger litters than lighter females, but pup weights did not differ between heavy and light females at weaning. The second replicate could not be analysed because of the small sample size.

In males, the masses of both testes and preputial glands were positively correlated with body mass at weaning in the first replicate, but not in the second. Survival was not related to weaning mass of males in either replicate or sex (Table 3).

Table 3. Correlations between weaning weight and subsequent weight development, reproduction and survival in male and female bank voles

		Replicate 1			Replicate 2		
		r_s	N	P	r_s	N	P
Weight in enclosures							
Males	Week 1	0.771	58	0.000	0.498	35	0.002
	Week 2	0.735	52	0.000	0.308	34	0.004
	Week 3	0.685	47	0.000	0.060	22	0.792
Non-reproducing females	Week 1	0.652	21	0.001	0.619	28	0.000
	Week 2	0.545	18	0.019	0.511	21	0.018
	Week 3	0.663	15	0.007	0.528	13	0.063
Reproduction							
Males	Mean preputial mass	0.294	47	0.045	0.037	27	0.856
	Mean testes mass	0.298	47	0.042	−0.145	27	0.470
Females	Litter size	0.346	30	0.061	0.633	4	0.368
	Pup weight	0.119	29	0.540	N.S.	1	N.S.
Survival							
Males		0.013	64	0.916	−0.279	37	0.094
Females		−0.081	63	0.524	0.216	34	0.219

DISCUSSION

Our results provide evidence that mass at birth can influence subsequent mass and reproduction. Survival of bank voles was not related to either birth or weaning weights, although such differences in survival had been noted earlier also in short-term experiments (Eccard and Ylönen, 2002). However, our results also indicate that birth mass is not such an unambiguous trait in the life-history evolution of mammals, at least of small mammals, as regarded until now. Also, Sikes (1998) and Oksanen *et al.* (2001) have shown the importance of compensatory growth in early age for survival and reproductive success of lighter individuals at birth.

Body size is generally regarded as an indicator of body condition and fitness. Large individuals often have better competitive ability, reproductive success and survival than small individuals. In this study, the neonate mass of female voles was not related to adult body size in the field. There was, however, a significant positive relation between weaning mass and adult body mass. Thus, it would appear that the birth mass of female pups is not as important a factor in growth as we expected (Millar, 1983). Instead, weaning weight as a result of maternal care and gestation seems to have a stronger effect on adult body mass than neonate mass.

The reproductive success of males is often related to dominance and body size (Horne and Ylönen, 1996, 1998). In this study, the birth mass of males was significantly correlated to adult masses in the field. But why is there such a difference between males and females? It might be related to their different systems of dominance. Dominance in males is based on body size, aggression and olfactory cues (Hoffmeyer, 1982; Gipps, 1985; Horne and Ylönen,

1996). Female hierarchy is based on territoriality, and the ability to protect a territory is not as strongly size-dependent (Koskela *et al.*, 1997; K. Köhler *et al.*, unpublished data). Males may start competing with each other earlier than females, during weaning and the dispersal process. This could explain why some male pups born heavier are heavier at weaning and might be more successful during dispersal and competition for mates. Later in life, female mass is confounded by reproduction and cannot be used for direct comparisons between neonate and adult masses.

Testes and preputial mass was not correlated with body mass of males at birth and only weakly related to weaning mass. However, both testes mass and preputial gland mass were significantly related to adult body mass in both replicates. Thus heavier males at weaning were able to grow larger organs related to dominance and reproductive success than lighter males (Horne and Ylönen, 1998).

Body mass at birth had some consequences for subsequent female reproductive success. In the first replicate, heavy females at birth had larger litters. In terms of pup weight, there was no decline observed compared with pups from smaller litters of lighter females. This might be important in determining age at first reproduction and litter size in the daughter generation (Millar, 1983). However, in females weaning mass was a much clearer predictor of future body size, which stresses the importance of gestation and maternal care for early growth of pups (Millar and Millar, 1989; Sikes, 1998).

In previous studies (Myers and Master, 1983; Calambodikis and Gentry, 1985; Pélabon, 1997), higher mass at birth or weaning has been related to enhanced survival. We did not observe such a positive effect in the present study. Also, in a more long-term study by Oksanen *et al.* (2001), lighter weaning mass of pups from experimentally enlarged litters did not have a negative effect on their overwinter survival. Survival differences due to interspecific competition have been shown in short-term experiments over 3 weeks (Eccard and Ylönen, 2002). However, individual differences based on birth and weaning weights might be too small to be evident within this short time.

A quite peculiar result in our study was the large difference in individual performance between the two replicates. It was normal summer weather during both replicates, but there were heavy rains during the week between the two replicates. This might have had an adverse effect on the seed supply for granivorous bank voles. Seeds and buds are considered the main food source for bank voles (Hansson, 1985). There were significant negative effects on physiological measures of adults in the second run; body mass decreased and male preputial and testes mass decreased. This indicated a decrease in food supply. However, there were no effects observed in survival rates, litter size or pup weight. The proportion of reproducing females decreased from 50 to 22% in females introduced to the enclosures. Besides food depletion, the effects could possibly be explained by differences in seasonal strategy between females. That is, daughters of females breeding early in summer can still breed and multiply genetic output of the line into the population. The probability of breeding decreases for females born later, as was the case in our second experiment. Thus the early replicate females might have adopted the 'breed as fast you can strategy', and the females of the later replicate might have selected a strategy maximizing survival to the next breeding season. This kind of dichotomy in breeding strategies was suggested in a model by Oksanen and Lundberg (1995), and any kind of stochastic resource depletion – like that which occurred between our two replicates – should favour adoption of the survival strategy over the breeding one. However, we think that the strong negative effects of the environmental conditions on male breeding physiology, in the form of preputial and testes weight,

point more strongly to physiological constraints than individual breeding strategy. However, both may well function at the same time.

Our study provides some evidence that fitness-related variables are positively affected by higher mass at birth. However, adult mass was more strongly related to weaning mass than that of neonates. In males, the effect of birth weight is clearer than in females. It may be that maternal care and compensatory growth during early life might be more pronounced in females than in males. As suggested previously (Leamy, 1981; Millar, 1983), a kind of polymorphic mixture of strategies between large clutches and lighter pups and vice versa could be regarded as the most optimal strategy in a variable environment, as between our treatments. Only exceptionally bad conditions require 'better' than average individuals, as was the case in the second replicate of our study. Under favourable conditions, a large litter size rather than heavy pups at birth could be the best reproductive strategy for a female iteroparous small rodent.

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