

GENETIC BASIS OF THE TRADE-OFF BETWEEN OFFSPRING NUMBER AND QUALITY IN THE BANK VOLE

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Abstract.—One of the main tenets of modern life-history theory is the negative relationship (trade-off) between the number and quality of offspring produced. Theory predicts a negative genetic correlation between these traits since both are closely related to fitness of individuals. However, the genetic basis of the trade-off has only been tested to a limited extent in natural populations. We examined whether size and quality of offspring are negatively related to litter size in the bank vole *Clethrionomys glareolus*. First, we found a significant negative phenotypic correlation between the number and size of offspring at birth in both laboratory and field populations of the bank vole. Second, a larger size at birth decreased the maturation age of female offspring in the laboratory, and increased the probability of breeding and the size of the first litter in the field. Furthermore, manipulation of offspring size at weaning indicated that structural effects of birth size in mammals have a more profound effect on the expression of life-history traits than weaning size. Finally, in addition to the phenotypic negative correlation between the number and size of offspring, we found evidence for a negative genetic correlation between these two traits, which confirms the genetic basis of the trade-off. This negative genetic covariation may have considerable effects on the rate and direction of evolution of the two related life-historical traits.

Key words.—Antagonistic pleiotropy, litter size, mammal, maturation, phenotypic and genetic correlations, trade-off between offspring size and number.

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A commonly observed determinant of reproductive effort is the negative relationship between number and quality of offspring (first formulated by Smith and Fretwell 1974). According to this trade-off, a large size at birth should increase the quality of offspring through faster growth, faster maturation processes, or better survival rates. The trade-off generates covariation in offspring size when the number of offspring and hence the overall fecundity is energetically or mechanically constrained (e.g. Carriere and Roff 1995). This has also been experimentally verified in oviparous reptiles, in which egg size was increased by ablating follicles (Sinervo and Licht 1991a,b) or decreased by using exogenous gonadotropin hormones (Sinervo and Licht 1991a; in mammals see also Oksanen et al. 2002). These experiments indicate that fecundity selection favors females who lay large clutches of small offspring, and fecundity selection is balanced by survival selection that favors large female offspring (Sinervo 1999; Oksanen et al. 2002).

There is considerable evidence for a negative phenotypic correlation between litter size and size of neonates in mammals (see reviews in Roff 1992). However, the positive relationship between size at birth and quality of mammal neonates has not been verified. Furthermore, the negative phenotypic correlation does not guarantee the negative genetic correlation, which is the evolutionary basis of the trade-off (Roff 2002). The relationship between phenotypic and genetic correlations seems to be unreliable especially between life-history traits (Roff 1996). Still, the negative genetic correlation between the number and size/quality has only been reported in fish (Snyder 1991) and reptiles (Sinervo 2000). Despite a lack of genetic evidence, the trade-off between the size and number of offspring forms an essential component of most evolutionary models predicting optimal reproductive allocation in vertebrates (e.g. Morris 1987; Charnov and Downhower 1995; Charnov 1997).

In this study, we examined whether size and quality of offspring are negatively related to litter size in the laboratory and in free ranging populations of the bank vole *Clethrionomys glareolus*. Furthermore, we investigated the genetic basis of the trade-off between number and quality of offspring.

MATERIALS AND METHODS

Study Species

The bank vole *Clethrionomys glareolus* is a rodent common in the Palearctic region. In central Finland (62°37' N, 26°20' E) females reproduce from early May to September, during which they give birth to up to four litters (Koivula et al. 2003). Usually only females from the first cohort mature during the summer of their birth (Mappes et al. 1995a) and a great proportion of females reproduce during only one breeding season (Koivula et al. 2003). Breeding bank vole females are strictly territorial and possession of a territory is a prerequisite for breeding (Bujalska 1973; Jonsson et al. 2002). There is competition between individuals for the opportunity to start breeding, particularly when resources are scarce and population density is high. Thus, age at first reproduction is an important fitness component in female bank voles (Bujalska 1988; Prevot-Julliard et al. 1999; Lambin and Yoccoz 2001).

Phenotypic Correlations

The phenotypic trade-off between number and size of offspring was determined separately for bank voles originating from laboratory and field populations. The field data consists of females ($N = 210$) trapped from the wild population in central Finland during the breeding seasons between 1995 and 1998. Females were trapped just before parturition and brought to the laboratory to give birth. The laboratory colony of females ($N = 184$) was maintained under an 18L:6D pho-

TABLE 1. Heritability estimates (h^2), additive (CV_A) and residual (CV_R) coefficients of variation, phenotypic variance (V_P), and mean (X) for number and size of offspring at birth (litter size, mean body mass, and head width of offspring within litter) and phenotypic (r_P) and genetic correlation (r_A) between these traits. N_1 , number of mother-daughter pairs; N_2 , number of mothers.

	$h^2 \pm SE (N_1)$	$CV_A (N_1)$	$CV_R (N_1)$	V_P	X	$r_P \pm SE (N_2)$	$r_A \pm SE (N_1)$
Litter size	$0.78 \pm 0.27 (62)^{**}$	20.60 (62)	10.55 (62)	1.44	5.15		
Head width	$0.83 \pm 0.24 (52)^{**}$	4.10 (52)	1.84 (52)	0.14	8.23		
Body mass	$0.86 \pm 0.23 (56)^{***}$	10.28 (56)	1.85 (56)	0.04	1.85		
Litter size vs. lab						$-0.40 \pm 0.07 (164)^{***}$	$-0.21 (52) \pm 0.07^*$
head width field						$-0.38 \pm 0.07 (203)^{***}$	
Litter size vs. lab						$-0.53 \pm 0.06 (184)^{***}$	$-0.40 (56) \pm 0.06^{**}$
body mass field						$-0.41 \pm 0.06 (210)^{***}$	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

toperiod in standard mouse cages with wood shavings and hay as bedding. Food (laboratory rodent chow) and water were available ad libitum. Laboratory females were first- to third-generation descendants of wild individuals. After parturition the number and size (body mass and head width) of pups were determined. Mothers were weighed and their head width measured, which served as a gauge for their structural size (T. Mappes and E. Koskela, unpubl. data).

Breeding Success Experiments

The effect of size at birth on the maturation age of females was studied in the laboratory. First, we chose 61 mothers from the laboratory colony of 184 females (see above). To study the size-number trade-off separately during pregnancy and nursing, the litter sizes of these 61 mothers were manipulated after parturition. Mothers were assigned to three treatment groups (reduced: -2 pups, $n = 21$; enlarged: $+2$ pups, $n = 20$, control: original litter size, $n = 20$). Pups were cross-fostered randomly between the mothers thereby randomizing maternal effects during nursing. In cross-fosterings all the pups in all the litters were randomly changed (no littermates in the same litter). Original litter size did not differ among litter manipulation groups (one-way ANOVA, $F_{2,58} = 1.53$, $P = 0.226$). Offspring size at birth did not differ among manipulation groups before (one-way ANOVA, body mass: $F_{2,58} = 0.211$, $P = 0.811$; head width: $F_{2,58} = 0.190$, $P = 0.827$) or after the litter size manipulation and cross-fosterings (one-way ANOVA, body mass: $F_{2,58} = 0.177$, $P = 0.838$; head width: $F_{2,58} = 0.139$, $P = 0.870$). The offspring were weighed and measured (width of head) at birth and at weaning. The offspring were weaned at the age of 20 days, the age at which independent juveniles can be caught in the field (Koivula et al. 2003). To determine the age of first breeding, 148 female offspring at the age of 40 days (29 from reduced, 47 from control and 72 from enlarged litters) were given the opportunity to mate with several males until their first parturition was observed. The females were put in a cage with a mature male for one week and the male was changed for a new one every week until the female was pregnant.

Breeding success of females was also estimated in the field. For this study, 56 female offspring were randomly chosen from 18 mothers. These mothers and their female offspring were not included in the above maturation estimates in the laboratory. The mothers gave birth and nursed their offspring in the laboratory. Female offspring were measured at birth, at weaning (20 days), and at the age of 50 days. In June, at

the age of 50 days, those 56 female offspring were released simultaneously and evenly to eight outdoor enclosures (each 0.25 ha, density 28 females/ha). For a description of habitat and the enclosures see Koskela et al. (1998). After a habituation period of one week, three mature males were introduced to each enclosure. Twenty days after the release of males, all remaining females ($n = 29$) were removed from the enclosures into standard breeding cages in the laboratory, where they gave birth.

Quantitative Genetic Analyses

The genetic basis of trade-off between the size and number of offspring was studied by using quantitative genetics analyses. The individuals used in the analyses were a random sample of first- to third-generation descendants of wild individuals originating from the population in central Finland (see number of individuals in Table 1). This group does not include the individuals of breeding success experiments described above. Mothers and daughters were paired with a random sample of males of the same population. Each male was used only once. All daughters were randomly cross-fostered between the mothers to decrease phenotypic covariance between the mothers and their daughters (maternal effects).

Heritabilities (h^2), coefficients of additive genetic variance (CV_A), residual variance (CV_R), and genetic correlations (r_A) were calculated for litter size and mean offspring size at birth (body mass and head width) using mother-daughter regressions (Becker 1985; Lynch and Walsh 1997; Roff 1997). All reproductive traits were measured for the mother and then for one of her daughters. Because the single parent-offspring covariances estimate half of the additive genetic variance, they were multiplied by two to obtain heritability estimates (Falconer and Mackay 1996). CV_A and CV_R were obtained as in Houle (1992): $CV_A = 100 \sqrt{V_A}/X$ and $CV_R = 100 \sqrt{(V_P - V_A)}/X$, where additive variance (V_A) is twice the mother-daughter covariance, V_P is the phenotypic variance and X is the mean of mothers. Further, $V_A = h^2 V_P$ and residual variance, $V_R = (1 - h^2)V_P$. Genetic correlation is given by $r_A = (\text{Covariance}_{x_m y_d} + \text{Covariance}_{y_m x_d}) / 2 \sqrt{\text{Covariance}_{x_m x_d} \text{Covariance}_{y_m y_d}}$ where, for example, $\text{Covariance}_{x_m y_d}$ refers to the covariance across traits (trait x for mother and trait y for daughter) and $\text{Covariance}_{x_m x_d}$ refers to the covariance within traits. Standard errors of genetic correlations were estimated using the formula of Hammond and Nicholas (1972).

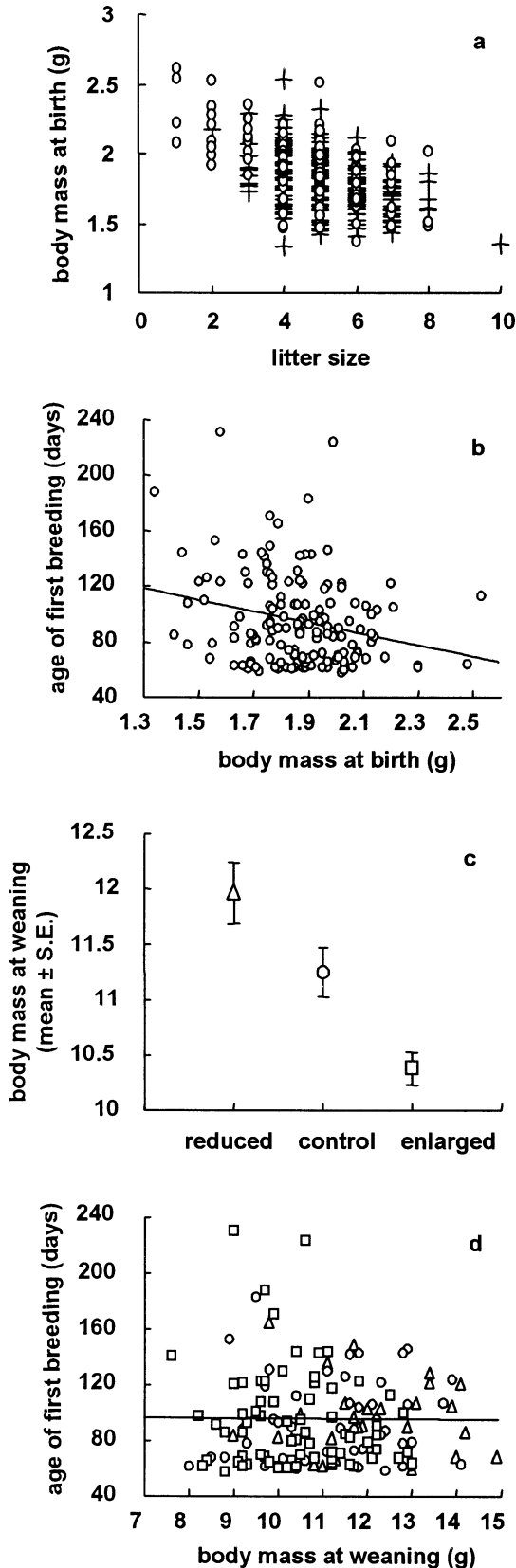


FIG. 1. (a) Litter size correlates negatively with mean body mass of offspring at birth both in the laboratory (circles) and in field populations (crosses) of the bank vole (see statistics in Table 1). (b) Larger size at birth decreases maturation age in female bank

RESULTS

Phenotypic Relationship between Number and Quality of Offspring

Litter size correlated negatively with size of offspring (mean body mass and head width) at birth both in the laboratory and in the field populations of the bank vole (Fig. 1a; Table 1). The relationship between size and quality was first studied in the laboratory by determining the maturation age of female offspring. We found that a larger size at birth (body mass and head width) predicted an earlier age at maturation ($B = -46.11 \pm 14.34$ (SE), $n = 148$, $P = 0.002$; $B = 27.79 \pm 8.36$ (SE), $n = 148$, $P = 0.001$, respectively; Fig. 1b; Table 2).

Litter size enlargements decreased—whereas reductions increased—the size of offspring at weaning in relation to the control litters (one-way ANOVA: $F_{2,58} = 15.06$, $P < 0.000$; Fig. 1c). Nevertheless, size at weaning (20 days) did not explain age at maturation in females (Fig. 1d; Table 2).

Furthermore we tested whether the older age at maturation is still beneficial for females. There was no correlation between maturation age of females and their litter size ($r = -0.12$, $n = 145$, $P = 0.150$) indicating that females maturing later did not have higher fecundity.

The relationship between size and quality was studied further in the field experiment. Size at birth had a significant effect on the probability of breeding and on the size of the first litter (Fig. 2a,b). Probability of breeding is predicted by a logistic regression model, in which the effect of body mass was significant ($G = 8.85$, $P = 0.003$; Fig 2a). Furthermore, a female's body mass at birth correlated positively with the number of offspring produced (Spearman rank correlation, $r_s = 0.57$, $n = 26$, $P = 0.003$; Fig 2b). To control for the possible effects of mother and enclosure on the dependent variables, separate analyses were carried out. For the analyses in which only one female per mother ($n = 18$) was used, body mass had a significant effect on probability of breeding (logistic regression, $G = 5.36$, $P = 0.021$) and litter size ($r_s = 0.58$, $P = 0.011$). Enclosure as a factor did not affect the probability of breeding ($G = 11.2$, $df = 7$, $P = 0.130$) or litter size ($F = 1.96$, $df = 7$, $P = 0.122$). Body mass at weaning (20 days) or just before the experiment (50 days) did not affect probability of breeding ($G = 0.08$, $n = 29$, $P = 0.772$; $G = 1.99$, $n = 29$, $P = 0.159$, respectively), nor did body mass correlate with litter size ($r_s = 0.15$, $n = 26$, $P = 0.46$; $r_s = 0.23$, $n = 26$, $P = 0.26$, respectively). Of 56 breeding females, 27 died during the experiment. Loss of females was not related to their head width and body mass at birth ($G = 2.38$, $P = 0.112$; $G = 1.28$, $P = 0.258$, respectively) or head width and body mass at weaning ($G = 0.92$, $P = 0.338$; $G = 0.34$, $P = 0.560$, respectively).

The breeding data of the whole laboratory colony were used to analyze the relationship between mother's size during

voles (see the linear regression equations in Results). (c) Litter size manipulation affects the body mass at weaning (see statistics in Results), but (d) greater size at weaning does not enable earlier maturation in female bank voles (see statistics in Table 2).

TABLE 2. ANCOVA table for the effects of head width or body mass at birth and at weaning on the age at first breeding. In the models, mother, foster treatment (litter size manipulation) and initial litter size of mother and foster were used as independent factors. All interactions between the treatment and head width or body mass at birth and at weaning were not significant ($P > 0.223$).

Source	df	MS	F	P
Head width at birth	1	13749.22	11.81	0.001
Head width at weaning	1	214.39	0.18	0.670
Treatment	2	678.11	0.58	0.563
Mother	35	1712.94	1.47	0.110
Foster	35	1022.34	0.88	0.652
Litter size of mother	1	752.01	0.65	0.426
Litter size of foster	1	436.32	0.38	0.543
Error	45	1165.94		
Body mass at birth	1	6139.79	4.61	0.037
Body mass at weaning	1	1967.05	1.48	0.231
Treatment	2	1152.75	0.87	0.428
Mother	35	1627.22	1.22	0.262
Foster	35	901.43	0.68	0.884
Litter size of mother	1	517.75	0.39	0.536
Litter size of foster	1	21.70	0.02	0.899
Error	45	1333.01		

breeding and her reproductive effort. There was no significant relationship between the size of the mother and the size or total mass of her litter (postpartum head width of mother vs. litter size: $r = 0.02$, $n = 153$, $P = 0.794$; vs. litter mass: $r = 0.07$, $n = 150$, $P = 0.367$).

Genetic Basis of the Trade-Off

Heritabilities (h^2) and coefficients of additive genetic (CV_A) and residual variance (CV_R) for the number and the size of offspring (head width and body mass) at birth in the bank vole are presented in Table 1. Estimates of genetic variance (h^2 and CV_A) are high for all the traits, whereas coefficients of residual variance (CV_R) are rather low, indicating low environmental and/or nonadditive genetic variance in the traits. Still, it is possible that cross-fostering not having entirely removed a common environmental effect. Furthermore, negative phenotypic and genetic correlations exist between the number and size of offspring (Table 1).

DISCUSSION

Phenotypic Trade-Off between Number and Quality of Offspring

Evidence for the first assumption of the trade-off between number and quality of offspring, a negative phenotypic correlation between the traits, has been observed in many vertebrates (see review Roff 1992). This also applies to our findings in the bank vole, because the litter size correlated negatively with mean body mass and head width of offspring at birth both in the laboratory and in the field. Further more, according to the number-size trade-off, a large size at birth should increase the quality of offspring (Smith and Fretwell 1974). In this study, the relationship between quality and size was investigated first by determining the maturation age of female offspring in the laboratory. To study the size-number trade-off separately during pregnancy and nursing, the litter sizes of mothers were manipulated after parturition. The re-

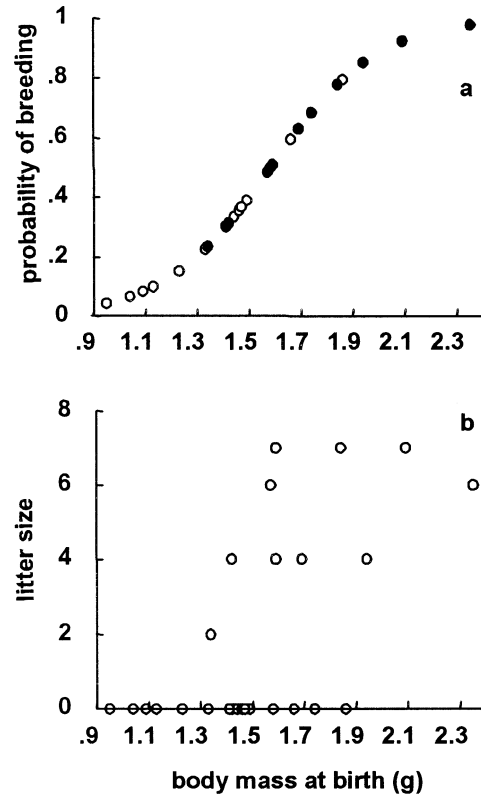


FIG. 2. Breeding success of bank vole females in relation to their body mass at birth in the field experiment. (a) Probability of breeding is predicted by a logistic regression model (see statistics in Results): filled circles represent females that bred ($N = 13$) and unfilled circles those that did not breed ($N = 16$) during the experiment. (b) Females' body mass at birth correlates positively with number of offspring they produce (see statistics in Results).

sults showed that natural size variation of female bank voles at birth explains their subsequent breeding success: the larger the size at birth, the earlier the age at maturation. Experimental variation in weaning size did not explain the age at maturation in females. We further studied whether size at birth predicts the breeding success of bank vole females in natural conditions. The results of the field experiment suggest that size at birth significantly explains the probability of breeding and the size of the first litter, but body mass at weaning did not affect either breeding probability or litter size. This further emphasizes the relative importance of size at birth for the breeding success of females.

In general, breeding earlier should be beneficial in an increasing population (Caswell 1982). These conditions are typical in small rodent populations, in which densities usually increase during the breeding season. In fact, empirical results indicate that early rather than delayed maturation is beneficial for lifetime breeding success in female bank voles (Prevot-Julliard et al. 1999). Furthermore, a recent study in *Microtus townsendii* showed that even when precocious reproduction carries a higher survival cost compared to nonprecocious females, early pregnancy will ultimately lead to higher fitness (Lambin and Yoccoz 2001). Still, a negative relationship between age at maturation and growth could also exist that would favor a later maturation age and larger adult size

(Lande 1982). However, this trade-off is not supported by our data, because females maturing later did not have higher fecundity (i.e. larger litters).

Mother's size (e.g. size of reproductive tract) is supposed to be an important mechanical factor determining the trade-off between number and size of neonates in mammals (Roff 1992). However, we did not find any clear relationships between the size of mother and litter size or total mass of the litter. This may indicate that in the bank vole some other factors (e.g. energetic) are more important determinants of the trade-off than pure mechanical factors.

These results indicate that the trade-off between size and number of offspring is a more important determinant of optimal reproductive effort during pregnancy than size-induced lactation effects. This is further supported by our earlier litter size manipulations in the field (Mappes et al. 1995b; Koskela 1998; Oksanen et al. 2001), in which the number of offspring during nursing did not clearly affect the quality of offspring. Obviously trade-offs can differ physiologically and behaviorally between mammals and birds. It seems that the time spent feeding offspring and size at fledging are more critical for optimal reproductive allocation in birds (e.g. Gustafsson and Sutherland 1988). Thus the structured effects of birth size in mammals seem to have a more profound effect on the expression of life-history traits than weaning size. However, further studies should focus on the most important physiological or ecological factors affecting the possible differences in number-size trade-offs between birds and mammals.

Genetic Trade-Off

We estimated the heritabilities (h^2), coefficients of genetic variances (CV_A), and residual variances (CV_R) for the number and the size of offspring at birth in the bank vole. These estimates of genetic variance, h^2 , are rather high compared to those reported for life-history traits in other species (Mousseau and Roff 1987). However, as suggested by Houle (1992) and Merilä and Sheldon (2000), narrow-sense h^2 estimates can be biased by environmental and nonadditive genetic variance. This should not be the case in our study, where the estimate of environmental and nonadditive genetic variance, CV_R , was rather low for all life-history traits. Furthermore, high variance was confirmed by CV_A , which can be a more reliable estimate of genetic variance in some cases (Houle 1992; however see Roff 1997). Still, in the present analyses it was not possible to control for all the prenatal maternal effects purely by cross-fostering, and thus this environmental variance may bias our estimation of quantitative genetics.

Trade-offs between traits mold the evolution of life-history strategies (Stearns 1976). However, it has been argued that this reasoning requires information about the genetic basis and covariance of the traits in question (Reznick 1985; Pease and Bull 1988; Roff 1996). This negative relationship has theoretically been predicted to occur when both traits are closely related to fitness (Rose 1985). However, empirical support for the genetic trade-off between number and size of offspring has been reported earlier only twice, in three-spined sticklebacks (Snyder 1991) and in side-blotched lizards (Sinervo 2000). Whether our results, or the earlier results, were caused by antagonistic pleiotropy or by linkage disequilibrium,

they may, at least in part, explain the observed higher genetic variation in the life-history traits (Slatkin and Frank 1990; Curtsinger et al. 1994). However, antagonistic pleiotropy can be confirmed only if the genetic correlation is maintained by several generations or different populations (Roff 1997) or if the experimental basis of antagonistic pleiotropy is elucidated with manipulations of the endocrine system (Sinervo 2000).

Future studies should focus not only on the genetic basis of the trade-off, but also on ecological and environmental mechanisms, which may determine the optimal energetic investment in each offspring (Charnov and Downhower 1995; Sikes 1998). For example, litter size manipulations should be performed during pregnancy to be able to experimentally manipulate offspring size at birth and litter size during pregnancy. This is because manipulations of litter size after parturition are clearly not early enough to capture all the cascading effects of life-history traits in mammals.

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