

Sex-biased maternal investment in voles: importance of environmental conditions

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Adaptive bias in sex allocation is traditionally proposed to be related to the condition of mothers as well as to the unequal fitness values of produced sexes. A positive relationship between mother condition and investment into male offspring is often predicted. This relationship was also recently found to depend on environmental conditions. We studied these causalities experimentally using a design where winter food supply was manipulated in eight outdoor-enclosed populations of field voles *Microtus agrestis*. At the beginning of the breeding season in spring, food-supplemented mothers seemed to be in a similar condition, measured as body mass, head width, body condition index and parasite load (blood parasite *Trypanosoma*), to non-supplemented mothers. Food supplements affected neither the litter size, the reproductive effort of mothers, nor the litter sex ratios at birth. However, food supplementation significantly increased the birth size of male offspring and improved their condition, as indicated by reduced parasite loads (intestinal *Eimeria*). Interestingly, mothers in good body condition produced larger male offspring only when environmental conditions were improved by food supplements. Although the adaptiveness of variation in mammalian sex ratios is still questionable, our study indicates that mothers in good condition bias their investment towards male offspring, but only when environmental conditions are favourable.

Keywords: food supplementation; mammals; maternal condition; parasites; sex allocation; sex ratio

1. INTRODUCTION

The original question about the allocation of resources by parents between sons and daughters concerned the adjustment of sex ratios in response to the local operational sex ratio (Fisher 1930). Taking Fisher's idea from the population level to the family level, Trivers & Willard (1973) proposed that if one sex gains more from extra parental resources than the other, then parents with relatively more resources will bias their allocation towards the sex with the greater rate of reproductive investment. Originally, Trivers and Willard focused primarily on the predicted positive correlation between a mother's physical condition and the proportion of sons produced, but over the years the idea has been generalized to a broader statement (Charnov 1982; Trivers 1985).

In polygynous mammals, the sexes are often dimorphic with males being larger than females. This is considered to be due to male–male competition for mating partners, resulting in selection, among males, for greater body mass (Clutton-Brock *et al.* 1981). The hypothesis of Trivers & Willard (1973) predicts that in these circumstances females in good condition should allocate relatively more to male offspring than females in poor condition. Although the literature reporting sex-allocation patterns in mammals is abundant (reviewed in Williams 1979; Clutton-Brock & Iason 1986; Frank 1990), controversy still surrounds these predictions and no general conclusions have emerged (e.g. Brown 2001; Cameron & Linklater

2002; Krackow 2002; but see Sheldon & West 2004). Until now, the research on sex-allocation patterns has been biased towards ungulates. Another factor causing controversy may be the fact that no low-cost physiological mechanism for sex-ratio manipulation by the parent has, so far, been identified (Krackow 1995, 2002). However, even if mothers were unable to control the sex ratio of their offspring, the extended period of pre-natal and post-natal parental care in mammals may serve as an opportunity for mothers to invest differentially in male and female offspring (e.g. McClure 1981; Clark *et al.* 1990).

An important factor that may confound the relationship between maternal condition and sex allocation is the potential effect of environmental conditions. Recently it was reported that dominant red deer (*Cervus elaphus*) mothers, which have been found to bias their offspring sex ratios towards males, do not show this relationship at high population densities when food supplies are limited (Kruuk *et al.* 1999). According to the authors, this result illustrates the existence of more than one mechanism affecting sex-ratio variation. Although these mechanisms could not be easily recognized, it is necessary to accept their potential importance and to study sex-allocation decisions under varying environmental conditions.

To study the causalities between food resources, condition of mothers and sex-allocation patterns, we manipulated the winter food supply of field voles (*Microtus agrestis*) in eight 0.5 ha outdoor enclosures. At the start of the breeding season, females impregnated in enclosures were brought into the laboratory where the characteristics of females and their litters were measured.

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Table 1. The jack-knife estimator for population density (mean \pm s.e.m.; Otis *et al.* 1978) and sex ratio (males/all trapped individuals) in different enclosures (A–D) during April.

enclosure/treatment	density	sex ratio
A/food supplement	92 \pm 13	0.42
B/food supplement	132 \pm 26	0.40
C/food supplement	94 \pm 15	0.51
D/food supplement	73 \pm 12	0.76
A/non-supplemented	100 \pm 15	0.59
B/non-supplemented	93 \pm 16	0.56
C/non-supplemented	0	—
D/non-supplemented	0	—

2. MATERIAL AND METHODS

(a) Study site and experimental design

The study was carried out in Alajoki farmland in Lapua (63° N, 23° E), western Finland, in eight 0.5 ha predator-proof enclosures, which were constructed in pairs on four distinct agricultural field sites (see Klemola *et al.* 2000*a,b*). Enclosures were built using a wire-netting fence (1.27 cm mesh), which extended 0.5 m below ground and 1.3 m above ground. To prevent intrusion by mammalian predators, a 40 cm wide metal sheet was fastened on the outer upper edge of the fence, and to prevent access by avian predators, the enclosures were covered with nylon netting (mesh 10 cm).

Six mature field voles (three males and three females) were introduced as founder populations into each enclosure between late May and early June 1999. Vole abundances in the enclosures were monitored by using a standard capture–mark–recapture method. Live traps were set for 3 days and checked three times per day. Each vole was marked individually when first captured. Trapping grids consisted of 50 trap stations at 10 m intervals. Each trapping station comprised one multiple-capture Ugglan live trap covered by a plastic box (40 cm \times 30 cm \times 25 cm), which reduced exposure to rain, wind and temperature extremes.

Winter food supplementation was initiated in four enclosures in October 1999. The other four enclosures were used as controls with no extra food. Food supplementation occurred at 50 feeding sites, which were established at 10 m intervals (at every trapping station). Feeders were made of 20 l plastic (PVC) buckets anchored to the ground. Three entrance holes were made at the base of the buckets to allow voles access to food. The contents of the feeders alternated between hay (mainly timothy (*Phleum pratense*) and red clover (*Trifolium pratense*)) and oats (*Avena sativa*). Approximately 30 kg of hay and 200 kg of oats were distributed among the treatment enclosures during the course of the winter (feeders were checked regularly and filled when necessary). Winter food supplementation was terminated in late April, after the snow had melted and grass had started to grow.

In late April, before the first litters were born, vole live-trapping was performed to monitor the condition and abundance of voles. During the winter, enclosed vole populations had gone extinct in two non-supplemented enclosures (table 1). Simultaneously, free-living field and bank vole populations in the surrounding study area had crashed to very low levels, indicating that overwintering environmental conditions had probably been harsh for the voles (E. Korpimäki, K. Norrdahl, O.

Huitu and T. Klemola, unpublished data). A representative sample (50% or more of individuals trapped from each enclosure) of overwintered females ($n = 38$ and $n = 67$, from non-supplemented and food supplement areas, respectively) were taken into the laboratory, where their body size was measured (head width to the nearest 0.1 mm using a calliper rule and body mass to the nearest 0.1 g using an electronic scale) and a retro-orbital blood sample was taken for the analysis of blood parasites (flagellated trypanosomes, *Trypanosoma* spp.; Hoarc 1972). Blood samples were collected from each individual using 75 μ l haematocrite tubes, which were centrifuged at 5000 r.p.m. for 5 min to separate the serum from the blood cells. Thereafter, trypanosomes were screened by inspecting each tube under a light microscope at magnification $\times 40$.

After measurements, non-pregnant females were released back into the enclosures at the point of capture, while pregnant females were kept in the laboratory until they gave birth (no difference in time to parturition between the treatments, two-sample *t*-test, $p > 0.5$). Females were housed in standard breeding cages and checked once a day for parturition. Newborn pups were measured and sexed (according to visual inspection and anogenital distance) and marked individually. A microscope was used to measure head width to the nearest 0.1 mm, and an electronic scale to weigh body mass at birth to the nearest 0.1 g. Females and their pups were returned in breeding cages to the place of capture, in the vicinity of the females' nests. Cages were left open so that mothers could carry the pups back to their nests. This method has worked well in earlier studies with bank voles (*Clethrionomys glareolus*), for example (Mappes *et al.* 1995; Oksanen *et al.* 2001).

As an index of body condition we used standardized residuals of a linear regression of body mass on body size (head width, a measure of structural size; e.g. Dobson & Michener 1995). The linear regression was used as it was significant ($R^2 = 0.51$, $F_{1,36} = 35.74$, $p < 0.001$), whereas quadratic or cubic parameters were not significantly different from zero (*t*-tests, $p > 0.5$). The 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 the mean offspring body mass at birth and M_m is the post-partum body mass of the mother and the exponent 0.75 is derived from the assumption that individuals can use 25% of their energy intake for maintenance and 75% for other activities (Millar 1977).

In early June, vole populations were monitored again. To measure the rate of infection by intestinal protozoa (coccidian parasites of the genus *Eimeria*), faecal samples were collected from all trapped juvenile voles (*ca.* 45 days old). *Eimeria* parasites cause coccidiosis, which is a major stress factor leading to malnutrition and lowered performance of individuals, and it can also sometimes cause death (Fuller & Blaustein 1996; Yun *et al.* 2000). Young animals (especially males) are usually more vulnerable to coccidiosis, whereas older animals are relatively resistant to infection (Ball & Lewis 1984). Animals were placed individually in a small plastic container for 15–30 min to gather faeces. The faeces were stored in a volume of 2.5% aqueous potassium dichromate ($K_2Cr_2O_7$) to make a total of 1 ml. The suspension was centrifuged for 3 min at 1750 r.p.m. and the pellet was resuspended in a saturated magnesium sulphate ($MgSO_4$) flotation solution. The intensity of parasite infection was estimated by counting the number of oocysts in a McMaster counting chamber, and the count was transformed into the number of *Eimeria* spp. oocysts per gramme of the original sample (Laakkonen *et al.* 1998; Oksanen *et al.* 2003).

(b) Data analysis

As two of the non-supplemented populations had gone extinct during the winter, the data consist of a total of 39 breeding females and 181 pups from four food-supplemented and two non-supplemented populations (table 1). There were no differences in the densities and sex ratios (arcsine transformed) of the six populations between the treatments (t -test, $t_4 = -0.07$, $p = 0.950$; $t_4 = 0.38$, $p = 0.720$; respectively). Furthermore, as the densities or sex ratios of populations did not affect the condition and reproductive traits of mothers and offspring (ANCOVA, $p > 0.1$ in all cases), these population-level variables were omitted from treatment and litter-level analyses.

Characteristics of mothers (body condition) and their litter size and reproductive effort in food supplemented and non-supplemented enclosures were studied using two-way ANOVA models where treatment (fixed) and enclosure (random, nested within treatment) were added as independent variables. In the analyses of litter size and reproductive effort mother condition was used as a covariate. Litter sex-ratio variation between the treatments were tested in SAS v. 8.02 software using the GLIMMIX macro (Krackow & Tkadlec 2001) with treatment (fixed), enclosure (random, nested within treatment), mother condition and interaction between treatment and mother condition as factors. The possible differential allocation into male and female offspring (size at birth) was analysed using ANOVA models including the factors treatment (fixed), sex (fixed), enclosure (random, nested within treatment) and mother identifier (random, nested within enclosure). The relationship between mother condition and allocation to the two sexes (offspring size at birth) was first analysed using a full ANCOVA model including the factors treatment (fixed), sex (fixed), mother condition, enclosure (random, nested within treatment) and mother identifier (random, nested within enclosure). As the three-way interaction among treatment, sex and mother condition was significant ($F_{1,147} = 4.09$, $p = 0.045$), the sexes were treated separately in subsequent statistical analyses. Throughout the paper, sex ratios refer to the proportion of male pups in a litter. All F -tests were based on Type III mean squares. Unless otherwise mentioned, the statistical analyses were performed by using SPSS 11.0 for Windows.

3. RESULTS

The proportion of pregnant females did not differ between the treatments (37.5% (15 out of 40) and 35.8% (24 out of 67) in non-supplemented and food supplement areas, respectively, Fisher's exact, $p = 1.00$), and was not affected by population density or sex ratio (logistic regression, density: $G_1 = 0.47$, $p = 0.495$; sex ratio: $G_1 = 0.84$, $p = 0.359$; interaction: $G_1 = 1.16$, $p = 0.282$). The timing of parturition was similar in both treatments (mean parturition dates \pm s.d. in days: non-supplemented, 7 May \pm 1.27; supplemented, 8 May \pm 4.0).

Food supplementation did not seem to affect the condition of females at the beginning of the breeding season. No character indicating condition of supplemented mothers differed significantly from those of the non-supplemented mothers (table 2). Nor did the prevalence of *Trypanosome* parasites differ between the treatments (non-supplemented: 0%, $n = 15$, supplemented: 12.5%, $n = 24$, Fisher's exact, $p = 0.221$). Food supplementation did not increase the litter size or reproductive effort of females and

these characteristics were not related to the condition of mothers (table 2).

Litter sex ratios in food-supplemented and non-supplemented enclosures did not differ significantly from a 1 : 1 sex ratio (supplemented: 0.57, $\chi^2_1 = 1.96$, $p = 0.162$; non-supplemented: 0.49, $\chi^2_1 = 0.04$, $p = 0.841$) or between the treatments (treatment: $F_{1,25.1} = 1.03$, $p = 0.319$; enclosure: $Z = 0.11$, $p = 0.456$). As mother condition and its interaction with treatment were not significant (interaction: $F_{1,33} = 1.13$, $p = 0.294$; condition: $F_{1,34} = 0.69$, $p = 0.411$) they were omitted (one at a time) from the final model.

Newborn male offspring from food-supplemented areas were larger than female offspring, both in terms of body mass and structural size (head width; table 3; figure 1). Food-supplemented male offspring also had lower vulnerability to intestinal *Eimeria* parasites. The intensity of *Eimeria* infection was higher in non-supplemented than in food-supplemented areas, particularly in males (table 3; figure 1). Mothers in better condition produced larger male offspring under high food resources in terms of body mass and head width (mother condition by treatment interaction: body mass: $F_{1,65} = 25.65$, $p < 0.001$, figure 2; head width: $F_{1,65} = 20.02$, $p < 0.001$). These interactions were not evident for female offspring (body mass: $F_{1,57} = 0.38$, $p = 0.539$, figure 2; head width: $F_{1,57} = 0.60$, $p = 0.441$).

4. DISCUSSION

According to our results, reproducing female field voles did not seem to adjust their own condition according to the prevailing environment; overwintered mothers in food-supplemented areas were in no better condition in spring, as measured by head width, body mass, body condition index and parasite load, than mothers in non-supplemented areas (but see also discussion below). Furthermore, no differences were found between treatments in the timing of reproduction, pregnancy rates, litter sizes or the reproductive efforts of females. In fact, sex allocation was the only characteristic found to differ between food-supplemented and non-supplemented mothers. This was not, however, seen as biased sex ratios of litters, but as increased allocation to the size of male offspring. The higher quality of larger males was further demonstrated by their lower vulnerability to intestinal *Eimeria* parasites. Interestingly, the positive relationship between maternal body condition and greater allocation to male offspring was found only when the environment indicated larger food resources.

According to sex-allocation theory (Trivers & Willard 1973; Charnov 1982), females in good condition should invest more heavily in the sex with the highest reproductive success. Data on polygynous mammals, such as most voles, often show that males with the highest reproductive success are relatively larger than the other males in the population (e.g. Sheridan & Tamarin 1988; Nelson 1994). Consequently, in the present case with field voles, selection could favour a relatively larger investment into male offspring either by producing male-biased litters or by transferring a greater proportion of a mother's body reserves to male offspring. Furthermore, as males are the more expensive sex to produce, it would be expected that

Table 2. Characteristics of mothers and their breeding parameters in food-supplemented (supplemented) and non-supplemented enclosures (mean \pm s.e.m.).

(Only treatment effects are reported from ANOVA models where treatment (fixed) and enclosure (random, nested within treatment) were added as independent variables. In the analyses of litter size and reproductive effort, mother condition was used as a covariate. The effects of mother condition and condition by treatment interaction were not significant ($p > 0.4$ in all cases). To account for unequal sample sizes among cells, the error term for treatment was calculated using Satterthwaite's approximation.)

	supplemented (<i>n</i>)	non-supplemented (<i>n</i>)	$F_{d.f.}$	<i>p</i>
post partum body mass (g)	40.9 \pm 1.0 (24)	38.7 \pm 1.3 (13)	2.97 _{1,5,1}	0.144
head width (mm)	15.7 \pm 0.1(24)	15.5 \pm 0.1 (15)	2.32 _{1,5,7}	0.181
condition index	0.14 \pm 0.21 (24)	-0.26 \pm 0.23 (13)	2.89 _{1,6,9}	0.134
litter size	5.0 \pm 0.2 (24)	5.1 \pm 0.3 (15)	0.02 _{1,8,0}	0.884
reproductive effort	0.64 \pm 0.02 (24)	0.65 \pm 0.04 (13)	0.02 _{1,27,2}	0.895

Table 3. ANOVA tables for the effects of treatment (fixed) and sex (fixed) on body mass and head width of offspring at birth and number of their intestinal *Eimeria* parasites.

(In the analyses, enclosure (random, nested within treatments) and mother (random, nested within enclosures) were used as additional independent variables. Number of *Eimeria*: variable was square-root transformed before the analyses. To account for unequal sample sizes among cells, the error terms were calculated using Satterthwaite's approximation. MS, mean square.)

source of variation	MS	$F_{d.f.}$	<i>p</i>
body mass			
treatment	0.052	0.144 _{1,0,995}	0.769
sex	0.266	4.878 _{1,151}	0.029
treatment by sex	0.414	7.590 _{1,151}	0.007
head width			
treatment	0.169	0.222 _{1,0,995}	0.720
sex	0.268	2.496 _{1,151}	0.116
treatment by sex	0.506	4.709 _{1,151}	0.032
number of <i>Eimeria</i>			
treatment	4404.71	5.539 _{1,8,115}	0.046
sex	3253.20	4.705 _{1,72}	0.033
treatment by sex	6536.67	9.453 _{1,72}	0.003

increased allocation to males is only possible for females that are not limited by food and/or are in good condition. However, although food supplementation was performed during the time of year when northern field vole populations are often limited by food supply (Klemola *et al.* 2000a, 2002; Hansson 2002; Huitu *et al.* 2003), none of the measures of mother condition differed significantly between non-supplemented and food-supplemented females. Moreover, we found no biased sex ratios in the offspring of control or food-supplemented females or a significant difference between the treatments. In agreement with the predictions of Trivers & Willard (1973), we did find evidence that mothers in good body condition allocated more resources to male offspring, even though their overall reproductive effort was not greater following food supplementation. This relationship was found only when our manipulations of the environment indicated larger food resources, which in turn indicates that the differences in the allocation of resources between sexes may require favourable environmental conditions, as previously suggested for red deer (Kruuk *et al.* 1999).

The most compelling evidence of adaptive manipulation of sex ratio in mammal populations arises from studies on red deer (Clutton-Brock & Iason 1986; Clutton-Brock *et al.* 1986; Kruuk *et al.* 1999). Increased vulnerability of

male fetuses to mortality has been suggested as a mechanism for sex-biased maternal investment, but it is currently unclear whether this happens under parental control. According to empirical data and recent models, in a situation where sons and daughters differ in their energy requirements and primary sex ratios cannot be controlled, allocation will become skewed in favour of the more profitable sex (Lessels 2002). The present study gives new empirical support for this prediction, and proposes that mothers may use alternative allocation patterns to optimize their life histories. Moreover, it seems that in voles these energy allocation patterns could be adjusted according to prevailing conditions.

Reproductive and morphological traits in voles have been found to show large phenotypic variation in relation to various ecological factors such as season, population density and food (e.g. Prévot-Julliard *et al.* 1999; Yoccoz *et al.* 2000; Ergon *et al.* 2001b; Norrdahl & Korpimäki 2002a,b; Koivula *et al.* 2003). In general, the effects of food supply on life-history traits of vertebrates are poorly understood. Although there are many studies where the effects of food supplementation on vole populations have been examined (reviewed in Boutin 1990), experimental data on the plasticity of life-history traits at the individual level are almost completely lacking. The two experiments

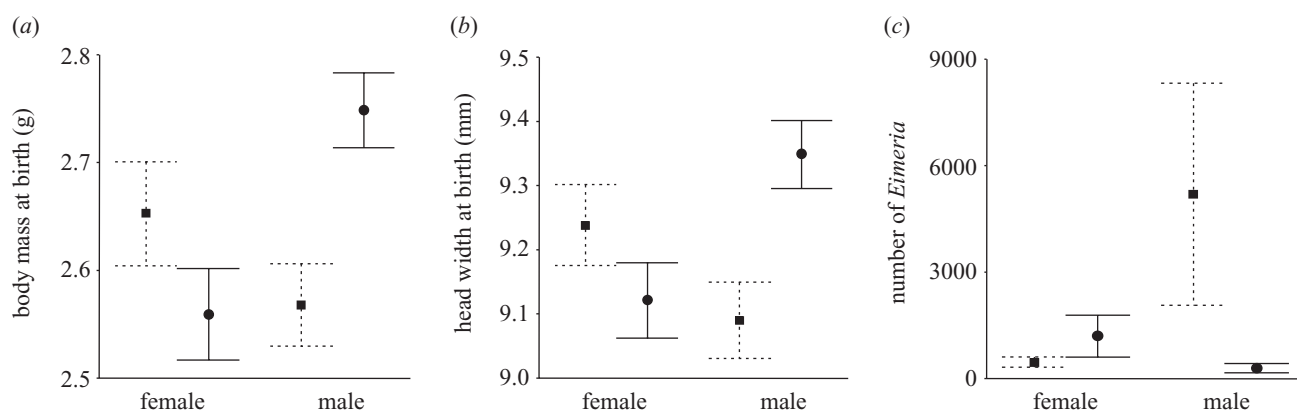


Figure 1. Quality of female and male offspring in different treatments (food-supplemented (circles) and non-supplemented (squares)) measured as (a) body mass and (b) head width at birth and (c) number of *Eimeria* parasites (mean \pm s.e.m.). For statistics see table 3.

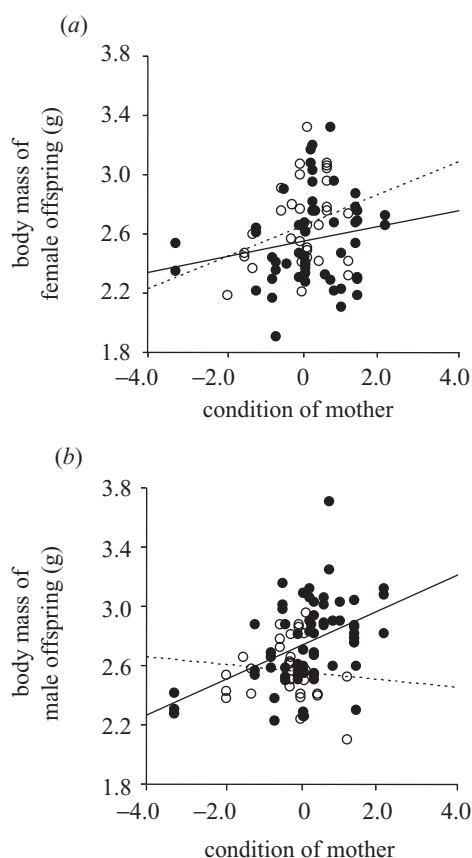


Figure 2. The relationship between mother condition and birth size of (a) female and (b) male offspring in different treatments (food-supplemented (filled circles) and non-supplemented (open circles)). Mothers in better condition produced larger male offspring but only under high food resources (significant mother condition by treatment interaction). This interaction was not evident for female offspring (for statistics see table 3).

we are aware of (Duquette & Millar 1995; Koskela *et al.* 1998) both reported that supplemental food increases the reproductive success of females and demonstrated significant effects on the growth of mothers and/or their offspring. In a recent paper, Ergon *et al.* (2001a) concluded that life-history traits of voles are mostly determined by their immediate environment. In their field transplant

experiment, field voles adjusted their body mass and timing of reproduction according to the new environment and not to the previous one. In our study, individuals did not seem to adjust their breeding characteristics (e.g. timing of breeding, litter size) or body condition (body mass, head width, condition index) according to the prevailing environment, as significant differences between the food-supplemented and non-supplemented females were not observed. Moreover, suggestions based on field data (Norrdahl & Korpimäki 2002b) propose that if the availability of winter food might cause variation in the characteristics of voles, these should be apparent with no or minimal time delay and thus should have been detectable during our study. However, as body condition could also be measured using other factors and our sample size was only moderate ($n = 39$), the lack of a statistically significant effect of food resources on mother condition should be treated with caution. To examine this issue more closely we calculated effect sizes for body condition indices (Pearson product moment correlation r) based on estimated marginal means following Cohen (1988) and using G*POWER (Faul & Erdfelder 1992). The effect sizes for body mass, condition index and head width were determined to be medium (0.36, 0.26, 0.27, respectively), illustrating that treatment explains (r^2), on average, 7.9% of the observed variation in body condition. These effect sizes are relatively large (Møller & Jennions 2002) and of the same magnitude as a previously reported statistically significant effect of supplemental food on the growth (head width) of bank vole *Clethrionomys glareolus* mothers ($r = 0.30$; calculated from Koskela *et al.* (1998)). In addition, the four values are not statistically heterogeneous from each other ($\chi^2_3 = 0.25$, $p > 0.9$; Rosenthal 1991). Therefore, the present non-significant results could even be cautiously interpreted as biologically significant effects of supplemental food on the body condition of field vole mothers.

We used the intensity of infection by intestinal *Eimeria* spp. parasites as a measure of offspring quality. *Eimeria* parasites cause coccidiosis that has been considered as an important stress factor leading to malnutrition and lowered performance of individuals, with young males being especially vulnerable to coccidiosis (Ball & Lewis 1984; Fuller & Blaustein 1996). In the present study, the

significant interaction between sex and treatment indicated that male offspring born to food-supplemented females had the lowest parasite loads. Both abiotic (e.g. temperature, humidity) and biotic (e.g. population density) factors may regulate the frequency of coccidiosis (Fuller 1996). The current results indicate that size at birth may also be associated with the infection rate by *Eimeria*, as larger male offspring seem to have better resistance to coccidiosis. However, verifying the link between size at birth and parasite resistance would require experiments where the parasite load of different sized offspring is directly manipulated.

It is not known how successfully the study design (food supplemented versus non-supplemented) mimicked naturally occurring food limitation in the wild. Thus, it is even possible that field voles from surviving non-supplemented populations were coincidentally in comparably as good environments as food-supplemented individuals, which may partly be the reason why significant differences in body condition indices between the treatments were not observed. Moreover, although data are scarce, even absent, on the size of newborn pups for any vole species, males are usually considered to be heavier than females, contrary to what was observed in the 'control group' from this study. If we accept that males are normally the heavier sex at birth, then it would not be clear whether the supplemented mothers in the present study increased their investment in male offspring or the non-supplemented ones decreased it. Nevertheless, regardless of the direction of maternal investment, the current results indicate that the size of male offspring (potential measure of sex-biased maternal allocation) was significantly positively related to mother condition (figure 2), supporting the arguments by Trivers & Willard (1973).

In summary, our experiment indicates that field vole mothers experiencing good food conditions bias their reproductive investment towards sons by producing larger male offspring. The positive relationship between mother quality and allocation to male offspring, as predicted by current theories, is dependent upon environmental conditions, as biased investment was evident only in food-supplemented populations. This indicates that the possible adaptive decisions of sex-biased maternal investment depend not only on the condition of the mothers but also on the set of circumstances under which the individuals are living.

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