

Maternal effects and the response to selection in red squirrels

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Mothers often provide much of the early environment for their offspring. These maternal effects are predicted to result in unusual evolutionary dynamics in offspring traits if they are themselves heritable, but these important predictions have not previously, to our knowledge, been tested in the wild. Here, we quantified the responses of red squirrels (*Tamiasciurus hudsonicus*) to documented episodes of natural selection and found support for both of the fundamental predictions of models that describe maternal effect evolution. First, changes in juvenile growth rates across one generation of selection were five times greater than predicted by heritability (h^2) alone, but were consistent with the additional contribution of maternal genetic effects. Second, responses to selection were influenced not only by the strength of selection in the current generation, but also by selection in the previous generation, indicating the presence of evolutionary momentum. These results were in agreement with predictions of a simple model including litter size as the only maternal effect, and provide, to our knowledge, the first empirical evidence for the importance of maternal effects to evolutionary dynamics in a natural population.

Keywords: evolution; indirect genetic effects; maternal effects; natural population; selection; *Tamiasciurus hudsonicus*

1. INTRODUCTION

Maternal effects occur when the phenotype of a mother has phenotypic effects on her offspring (Mousseau & Fox 1998). These maternal contributions are experienced by offspring as environmental effects but can be genetically based and, therefore, can contribute to an evolutionary response to selection (Wolf *et al.* 1998). Models of maternal effect evolution (Kirkpatrick & Lande 1989, 1992; Lande & Kirkpatrick 1990) suggest that genetically based maternal effects (indirect genetic effects (Moore *et al.* 1997)) can greatly alter the rate of evolution and are predicted to introduce an evolutionary time-lag, in which the response to selection in the current generation also depends on the strength of selection in the previous generation (Kirkpatrick & Lande 1989). As a result, populations can continue to evolve after selection has ceased and evolution may also temporarily proceed in a direction that is opposite to the direction of selection (Kirkpatrick & Lande 1989).

These dramatic and sometimes counterintuitive predictions of maternal effect models, however, depend on the presence of a genetic basis to maternal variation (Kirkpatrick & Lande 1989; Wolf *et al.* 1998). The genetic basis to maternal effects has been frequently estimated in laboratory and agricultural species (Cheverud 1984; Roff 1997), but indirect genetic effects in non-domestic species (Agrawal *et al.* 2001; Hunt & Simmons 2002; Rauter & Moore 2002) and under natural field conditions have been investigated only recently (Byers *et al.* 1997; Thiede 1998; McAdam *et al.* 2002). As a result, the actual importance of maternal effects to evolutionary dynamics has not yet been tested. Given the prevalence of maternal effects (Roach & Wulff 1987; Rossiter 1996; Mousseau & Fox

1998; Milner *et al.* 2000; Kruuk *et al.* 2000) and their predicted implications for evolutionary dynamics (Kirkpatrick & Lande 1989, 1992; Lande & Kirkpatrick 1990; Wolf *et al.* 1998), this could represent a large gap in our understanding of the evolutionary process in natural populations.

In this study, we used 14 years of data (1989–2002) from a population of North American red squirrels (*Tamiasciurus hudsonicus*) to provide, to our knowledge, the first empirical evidence of the importance of genetically based maternal effects to the evolutionary dynamics of a natural population. Previous cross-fostering experiments with newborn red squirrels have indicated that juvenile growth in body mass is heritable ($h^2 = 0.10$), but it also experiences large heritable maternal effects and a large positive covariance between direct and maternal genetic effects (McAdam *et al.* 2002). Overall, these maternal genetic effects resulted in a much greater total heritability ($h_t^2 = 0.36$; McAdam *et al.* 2002) and hence a greater potential response to selection than would have been predicted from direct genetic effects alone. In addition, we have measured the strength of directional selection on juvenile growth rates based on the survival of offspring to potential breeding age (McAdam & Boutin 2003a). In this present reported work, we quantified the responses of juvenile growth rates to these selection episodes for each of 12 cohorts of squirrels born since 1989 to determine the importance of maternal effects in evolutionary responses to selection in this juvenile trait.

2. MATERIAL AND METHODS

North American red squirrels (*T. hudsonicus*) within a population of approximately 325 adults located in the southwest Yukon, Canada have been monitored consistently and without interruption since 1987. Details of the population are given elsewhere (Humphries & Boutin 2000; McAdam & Boutin 2003a).

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Growth rates were defined as the linear increase in mass from soon after birth until just prior to first emergence from the natal nest (at *ca.* 30 days of age; see McAdam & Boutin (2003a) for details). In this population, females rarely raised more than one successful litter within a single breeding season (Réale *et al.* 2003). Here, we examined only the growth rates of offspring from first litters of the season, to remain consistent with previous selection analyses (McAdam & Boutin 2003a). In addition, cross-fostered offspring and those subjected to food or litter size manipulations were excluded from this analysis. There is no paternal care in this species.

(a) Environmental effects on growth

Observed responses to selection can be concealed by changes in environmental conditions across generations (Grant & Grant 1995, 2002; Merilä *et al.* 2001), so we corrected juvenile growth rates for the influence of annual environmental effects prior to estimating the response to selection. In southwest Yukon, red squirrels feed primarily on the seeds of white spruce (*Picea glauca*) cones. The abundance of spruce cones varies annually over three orders of magnitude and is positively correlated with offspring growth rates (McAdam & Boutin 2003a). We corrected for environmental effects on growth by examining the growth rates of offspring raised by mothers that bred in multiple years. The raw residual (r_{ij}) of the average growth rate of offspring raised by mother i in year j from the average of all litters raised by mother i in her lifetime was used as a measure of the environmental effect of that year on offspring growth for mother i . These residuals, therefore, represented the combined effects of all environmental sources of variation. Females breeding in a greater number of years experienced a wider range of environmental conditions (e.g. cone abundances), so a weighted average of residuals across females within each year was used to calculate the environmental effect for each year (e_j) according to the equation

$$e_j = \frac{\sum_{i=1}^n r_{ij} \times y_i}{\sum_{i=1}^n y_i},$$

where residuals were weighted by the number of years in which each female bred (y_i). All juvenile growth rates were corrected for the environmental effects experienced in the year of their birth (e_j) prior to estimating the response to selection. Annual environmental effects on growth were positively correlated with the abundance of spruce cones produced in the previous autumn (linear regression coefficient $b = 0.193 \pm 0.055$, $n = 12$, $r^2 = 0.55$, $p = 0.006$; see also McAdam & Boutin (2003a)).

(b) Response to selection

Because the strength and direction of selection on growth varied among cohorts (McAdam & Boutin 2003a), the observed response to selection was measured separately for each cohort as the change in the average growth rate of offspring from prior to selection to one generation after selection (Falconer & Mackay 1996; Grant & Grant 2002). The mean phenotype prior to selection was calculated for each cohort as the average growth rate (corrected for environmental effects) of all offspring born that year. The mean phenotype one generation after selection was calculated for each cohort as the average growth rate (corrected for environmental effects) of all offspring born to mothers from that cohort, regardless of the year in which the offspring were born. For example, the mean phenotype after

selection for the 1990 cohort was the mean growth rate of all offspring raised by mothers born in 1990.

Realized heritabilities (h_r^2) have previously been calculated as the slope of the regression of the response to selection (Δz_t) on directional selection differentials (S_t) (Falconer & Mackay 1996). Models of maternal effect evolution, however, predict that the response to selection in the current generation (Δz_t) will also depend on the strength of selection in the previous generation (S_{t-1}) (Kirkpatrick & Lande 1989; Lande & Kirkpatrick 1990). As a result, we included both the strength of selection in the current generation (S_t ; viability selection experienced by each juvenile cohort) and the strength of selection in the previous generation (S_{t-1} ; viability selection experienced by each maternal cohort as juveniles) in a multiple regression of the observed response to selection (Δz_t).

Directional selection gradients for each cohort were previously estimated based on the survival of offspring from birth to potential breeding age, while controlling for variation in litter size and parturition date and differences in survival between males and females (McAdam & Boutin 2003a). The strength of selection on growth rates varied among cohorts (McAdam & Boutin 2003a) and there was no evidence of temporal autocorrelation in the strength of selection on growth rates (McAdam & Boutin 2003a), so we treated each cohort as an independent replicate. In the multiple regression analysis, these selection gradients (β_t) were converted to selection differentials (S_t) based on the phenotypic variance of growth rates for each cohort. The use of S_t rather than β_t allowed us to estimate the realized heritability from the regression rather than the realized direct genetic variance.

(c) Maternal effects model

In addition to providing qualitative support for the predictions of a maternal effects model, the observed responses to selection also allowed us to estimate realized maternal effect parameters using likelihood techniques. We used a simple model in which litter size was the only maternal effect (Kirkpatrick & Lande 1989, 1992) to calculate maximum-likelihood estimates of the maternal effect coefficient (m) and the genetic correlation between growth rate and litter size (r_{mo}) based on observed responses to selection ($n = 12$ cohorts). Changes in growth rates were predicted for each cohort following Kirkpatrick & Lande (1989, 1992; see also Lande & Kirkpatrick (1990)) using the equation

$$\begin{aligned} \Delta z_o(t) = & (G_{mo}/2 + mG_{mm})\beta_m(t) + (G_{oo} + mG_{mo}/2)\beta_o(t) \\ & + m(G_{mo} + mG_{mm}/2)\beta_o(t-1) + mP_{mo}(t)\beta_o(t) \\ & - mP_{mo}(t-1)\beta_o(t-1), \end{aligned}$$

where $\Delta z_o(t)$ is the change in the mean growth rate of offspring at time t . In this equation the subscript o refers to the offspring trait (juvenile growth rates), while the subscript m refers to the maternal trait (litter size). Litter size in this population has experienced stabilizing selection but there is no evidence for directional selection on this maternal trait (Réale *et al.* 2003). Because we were only concerned with directional changes in the mean growth rate, we set the directional selection gradient (Lande & Arnold 1983) for litter size ($\beta_m(t)$) to 0. The strength of selection on growth rates in the current generation ($\beta_o(t)$) was previously estimated for each cohort as described above (McAdam & Boutin 2003a; see also table 1). The strength of selection in the previous generation ($\beta_o(t-1)$) was estimated as the average strength of juvenile viability selection experienced by mothers of that cohort. Additive genetic variance in litter size (G_{mm}) has been previously calculated for this population as 0.102 (Réale *et al.* 2003). Direct additive genetic variance (G_{oo})

Table 1. Observed responses of daily juvenile growth rates (g d^{-1}) to one generation of selection for cohorts born between 1989 and 2000.

(Growth rates prior to selection are the average of all offspring born in each cohort, whereas the growth rate after selection is the average of offspring born to mothers from each cohort. The standardized directional selection gradient (β' ; Lande & Arnold 1983) on juvenile growth rates for each cohort (McAdam & Boutin 2003a) is also indicated. Significant selection gradients are indicated by asterisks.)

cohort	prior to selection		after selection		response (g d^{-1})	t	p	β'
	n	mean \pm s.e. (g d^{-1})	n	mean \pm s.e. (g d^{-1})				
1989	32	1.49 \pm 0.09	69	1.68 \pm 0.05	0.195	1.90	0.06	0.78
1990	33	1.76 \pm 0.09	53	1.93 \pm 0.06	0.166	1.52	0.13	0.16
1991	98	1.76 \pm 0.04	165	1.71 \pm 0.04	-0.048	-0.92	0.36	0.36*
1992	117	1.56 \pm 0.04	103	1.91 \pm 0.06	0.351	4.79	< 0.0001	1.06*
1993	131	1.97 \pm 0.04	251	1.90 \pm 0.03	-0.064	-1.23	0.22	0.01
1994	160	1.88 \pm 0.04	66	2.00 \pm 0.07	0.126	1.64	0.10	0.36
1995	151	1.89 \pm 0.04	180	1.87 \pm 0.03	-0.019	-0.34	0.74	-0.18*
1996	70	1.80 \pm 0.05	54	1.77 \pm 0.05	-0.031	-0.44	0.66	0.09
1997	155	1.92 \pm 0.03	190	1.75 \pm 0.04	-0.163	-3.34	0.001	-0.10
1998	88	1.88 \pm 0.07	237	1.72 \pm 0.03	-0.165	-2.31	0.02	0.17
1999	211	1.81 \pm 0.03	30	1.86 \pm 0.09	0.054	0.56	0.58	0.87*
2000	57	1.65 \pm 0.06	11	1.62 \pm 0.14	-0.026	-0.17	0.87	0.65

was calculated separately for each cohort based on the total phenotypic variance in growth rates for that cohort and a direct genetic heritability of 0.10, which was derived from previous cross-fostering experiments (McAdam *et al.* 2002). The phenotypic covariance between growth rate and litter size ($P_{\text{mo}}(t)$) was also calculated separately for each cohort (McAdam & Boutin 2003a) and we used the average P_{mo} experienced by mothers as an estimate of $P_{\text{mo}}(t-1)$. β_0 and P_{mo} were not measured prior to 1989, but values of β_0 and P_{mo} calculated for all cohorts combined (1989–2001; 0.725 and -0.105, respectively) were used for mothers born prior to 1989.

Likelihoods were calculated for values of r_{mo} [$r_{\text{mo}} = G_{\text{mo}}/\sqrt{(G_{\text{oo}}G_{\text{mm}})}$] between -1 and 1 and m between 0 and -0.9 using a systematic grid scan, whereas maximum-likelihood estimates were not restricted to this parameter space. Observational uncertainty in the response to selection was assumed to be normally distributed with an unknown standard deviation. Likelihoods were scaled relative to the null model, which excluded maternal effects ($m = 0$), for ease of comparison. Models based on parameter combinations of m and r_{mo} were tested against the null model using the likelihood ratio test (Hilborn & Mangel 1997). Values are presented as means \pm 1 s.e. unless otherwise stated.

3. RESULTS

(a) Observed responses to selection

The observed responses of juvenile growth rates differed in direction and magnitude among cohorts (table 1). Some cohorts exhibited a significant increase in growth rates in response to selection (e.g. 1992), whereas others exhibited a significant decrease in growth (e.g. 1997, 1998) ranging in magnitude from 0.04 to 0.72 standard deviations per generation.

These observed changes in growth rates across one generation of selection were correlated with both the strength of selection in the current generation (overall model: $n = 12$, $r^2 = 0.65$, $p = 0.009$; current generation:

$b = 0.556 \pm 0.169$; $t_9 = 3.3$, $p = 0.009$; figure 1a) and the strength of selection in the previous generation, although the latter was marginally significant ($b = 0.684 \pm 0.306$, $t_9 = 2.2$, $p = 0.052$; figure 1b). Cohorts from early in the study (1989–1991) contained many mothers born prior to 1989. The exclusion of these cohorts (for which we did not have complete data on the strength of selection in the previous generation) improved the fit of the overall relationship ($n = 9$, $r^2 = 0.78$, $p = 0.01$; current generation: $b = 0.594 \pm 0.160$, $t_6 = 3.7$, $p = 0.01$), particularly the effect of selection in the previous generation ($b = 0.893 \pm 0.324$, $t_6 = 2.8$, $p = 0.03$).

(b) Maximum-likelihood estimates of maternal effects

Observed responses to selection for these 12 cohorts also indicated that combinations of a genetic correlation (r_{mo}) of less than zero and a maternal effect coefficient (m) of between -0.25 and -0.55 resulted in a significant improvement in the fit of the model predictions to the observed changes in growth over a model with no maternal effects (i.e. $m = 0$; $\chi^2 > 3.94$, $p < 0.05$; figure 2). Predictions from this simple maternal effect model, using maximum-likelihood estimates of m (-0.30) and r_{mo} (-3.1), explained 57% of the variation in observed responses to selection across these 12 cohorts ($n = 12$, $r^2 = 0.57$, $p = 0.004$). In addition, the relationship between predicted and observed responses to selection had a slope and intercept that did not differ significantly from one (1.37 ± 0.37 , $t_{10} = 0.98$, $p = 0.35$) and zero (-0.06 ± 0.04 , $t_{10} = -1.56$, $p = 0.15$), respectively.

4. DISCUSSION

Observed changes in juvenile growth rates across one generation of selection varied in direction and magnitude among the 12 cohorts of red squirrels born since 1989. In the absence of maternal effects, we would have expected

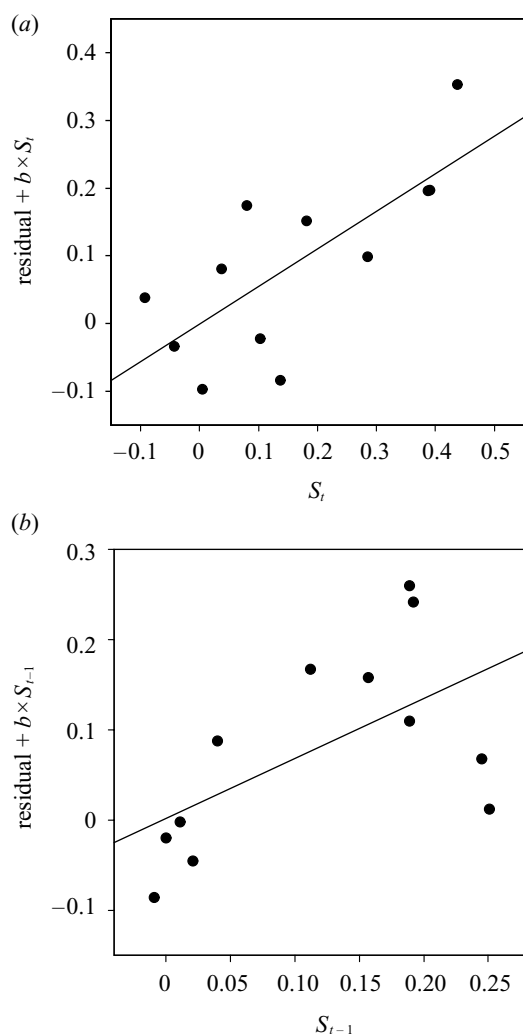


Figure 1. Partial regression plots of the effects of the strength of directional selection (a) in the current generation and (b) the strength of selection in the previous generation on the evolutionary response of juvenile growth rates in red squirrels ($n = 12$ cohorts). In both plots the vertical axis represents the observed response to selection corrected for effects of the other variables in the regression model (intercept and S_{t-1} in (a) or intercept and S_t in (b)).

significant responses in growth rates to coincide with significant selection episodes. However, 1992 was the only cohort that exhibited a significant response to significant directional selection. Three other cohorts that experienced significant directional selection on growth (1991, 1995 and 1999) did not exhibit significant responses to selection, and more surprisingly, two cohorts exhibited significant responses to very weak selection (1997 and 1998).

These observed responses to selection, however, supported both of the general predictions of models of maternal effect evolution (Lande & Kirkpatrick 1990). First, there was a strong positive correlation between the change in juvenile growth rates and the strength of selection in the current generation, corresponding to a realized heritability ($h_r^2 = 0.56 \pm 0.17$) that was five times greater than our previous estimate of heritability for this trait considering direct genetic effects alone ($h^2 = 0.10$; McAdam *et al.* 2002). This realized heritability, however, was not significantly different from our previous estimate of the potential for evolution including indirect maternal genetic

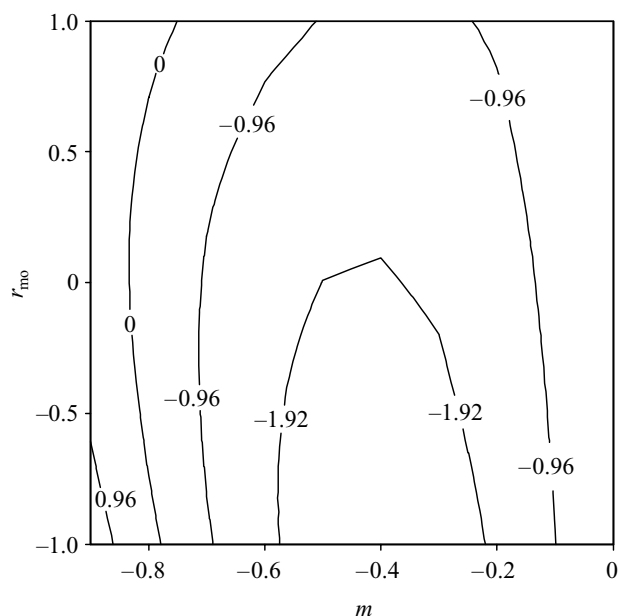


Figure 2. Likelihood surface of the strength of the maternal effect coefficient (m) and the genetic correlation between growth rate and litter size (r_{mo}). Contours represent changes in negative log-likelihoods relative to the model in which maternal effects are absent ($m = 0$), where increasingly negative contours represent more likely combinations of parameters. Values of m and r_{mo} resulting in a significant improvement in the fit of predicted responses to selection over predicted responses in the absence of maternal effects fall within the -1.92 region (i.e. $\chi^2 > 3.84$, $p < 0.05$).

contributions ($h_r^2 = 0.36$; McAdam *et al.* 2002). Second, there was a positive correlation between the response of juvenile growth rates in the current generation and the strength of selection in the previous generation. These results indicated that changes in growth between parental and offspring generations (response to selection) depended not only on selection experienced in the parental (current) generation, but also on the strength of selection in the grandparental (previous) generation. This intergenerational effect of previous selection episodes is consistent with predictions of models of maternal evolution, and has been referred to as evolutionary momentum (Kirkpatrick & Lande 1989; Lande & Kirkpatrick 1990).

These results were supported by the maximum-likelihood analysis, which indicated that inclusion of a single maternal character (litter size) resulted in a significant improvement in the fit of a simple maternal effect model to observed changes in growth rates when compared with the predictions of a model with no maternal effects. Clearly, litter size is not the only maternal effect on offspring growth, but this simple model captured the overall direction and magnitude of the observed response to selection of this juvenile trait. In addition, the maximum-likelihood estimate of the maternal effect coefficient ($m = -0.30$) was very similar to previous estimates from cross-fostering experiments ($m = -0.29$ (McAdam & Boutin 2003b)) and from experimental litter size manipulations in this population ($m = -0.21$ to -0.27 (Humphries & Boutin 2000)). However, the maximum-likelihood estimate of the realized genetic correlation between growth rate and litter size was far less than one

($r_{mo} = -3.1$), suggesting that other maternal effects are also genetically correlated with growth rates and contribute similarly to the response to selection in this juvenile trait. Taken together, the negative effect of litter size on growth rates ($m < 0$) and the negative genetic correlation between litter size and growth rates indicate an overall positive correlation between direct and maternal genetic contributions to juvenile growth rates. Previous estimates of the direct maternal genetic correlation from cross-fostering experiments (McAdam *et al.* 2002; McAdam & Boutin 2003b) and these observed responses to selection both indicate a large positive association between direct and maternal contributions to offspring growth rates and, therefore, an acceleratory influence of maternal genetic effects on the response of this juvenile trait to selection.

Maternal effects have generated a great deal of interest in recent years as a result of both their widespread phenotypic influences and their potential implications for evolutionary dynamics (Mousseau & Fox 1998). In red squirrels, mothers have large heritable effects on the growth of their offspring (McAdam *et al.* 2002). Here, we have shown that these maternal genetic effects have important influences on the evolutionary dynamics of this juvenile trait in a natural population as predicted by models of maternal effect evolution. Identification of the importance of maternal effects to evolutionary dynamics inspires a broader view of phenotypes and selection, which encompasses not only heritable variation and selection in the current generation, but also genetic contributions from previous generations. While it is clear that the evolution of some traits can be explained by direct genetic effects alone (e.g. Grant & Grant 1995; Reznick *et al.* 1997; Merilä *et al.* 2001), the ubiquity of maternal effects suggests that for many other traits in natural populations our understanding of the evolutionary process will be incomplete without consideration of maternal genetic effects.

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