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Genetic and plastic responses of a northern mammal to climate change

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Climate change is predicted to be most severe in northern regions and there has been much interest in to what extent organisms can cope with these changes through phenotypic plasticity or microevolutionary processes. A red squirrel population in the southwest Yukon, Canada, faced with increasing spring temperatures and food supply has advanced the timing of breeding by 18 days over the last 10 years (6 days per generation). Longitudinal analysis of females breeding in multiple years suggests that much of this change in parturition date can be explained by a plastic response to increased food abundance (3.7 days per generation). Significant changes in breeding values (0.8 days per generation), were in concordance with predictions from the breeder's equation (0.6 days per generation), and indicated that an evolutionary response to strong selection favouring earlier breeders also contributed to the observed advancement of this heritable trait. The timing of breeding in this population of squirrels, therefore, has advanced as a result of both phenotypic changes within generations, and genetic changes among generations in response to a rapidly changing environment.

Keywords: phenotypic plasticity; evolution; selection; breeding values; *Tamiasciurus hudsonicus*; life-history traits

1. INTRODUCTION

Climate is predicted to change at an increasing rate in the future and several studies have demonstrated ecological changes in wild plant and animal populations in response to climate change (Walther *et al.* 2002). Most studies, however, have interpreted observed phenotypic changes as behavioural or physiological (i.e. plastic) responses to environmental change (Brown *et al.* 1994; Crick *et al.* 1997; Hofgaard *et al.* 1999; Inouye *et al.* 2000; Both & Visser 2001; but see Janzen 1994; Bradshaw & Holzapfel 2001; Etterson & Shaw 2001). While these mechanisms allow an organism to cope with short-term environmental change, microevolution (genetic response to consistent selection on heritable traits; Falconer & Mackay 1996; Roff 1997; Lynch & Walsh 1998) is thought to be essential for the persistence of populations faced with long-term directional changes in the environment (Lande & Shannon 1996; Lynch 1996).

Evolutionary responses to selection can be predicted using the breeder's equation $R = h^2S$, where R is the change in the trait mean from one generation to the next, h^2 is the heritability estimate of the trait z, and S is the selection differential on z (Falconer & Mackay 1996; Roff 1997). Despite the increasing number of studies showing consistent selection pressures on heritable traits, evidence for phenotypic responses to selection that are consistent with predictions from the breeder's equation are generally lacking for natural populations (Merilä *et al.* 2001*b*). This is due not only to the rarity of data available to predict evolutionary changes in natural populations, but also from studies reporting apparent evolutionary stasis or phenotypic responses in the opposite direction to the one predicted (Van Noordwijk *et al.* 1981*a*,*b*; Price *et al.* 1988; Price & Liou 1989; Alatalo *et al.* 1990; for a recent review see Merilä *et al.* 2001*b*).

Restricted maximum-likelihood 'animal models' developed in animal breeding science provide a powerful tool for estimating quantitative genetic parameters in natural populations (Merilä *et al.* 2001*b*). These animal models are particularly well suited to unbalanced datasets typical of natural populations, but have only recently been applied to wild populations in a limited though increasing number of studies (Réale *et al.* 1999; Kruuk *et al.* 2000, 2001; Milner *et al.* 2000; Réale & Festa-Bianchet 2000; Coltman *et al.* 2001; Merilä *et al.* 2001*a*; McAdam *et al.* 2002). A further advantage of the animal-model method is that it provides estimates of individual breeding values. A breeding value represents the combined additive effects of all an individual's genes for a given trait and changes in estimated breeding values (EBVs) across generations represent changes in additive genetic variance due to selection, drift or inbreeding (Lynch & Walsh 1998). As a result, this approach can be used to differentiate between temporal phenotypic changes due to genetic and environmental sources (e.g. Merilä *et al.* 2001*a*).

Here, we report a large advancement in the mean lifetime parturition date of female North American red squirrels (*Tamiasciurus hudsonicus*) that coincided with changes in spring weather and food abundance, in a population near Kluane Lake, Yukon, Canada. Parturition date in

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this population of red squirrels is both heritable ($h^2 = 0.16$) and has been under consistent directional selection ($i = -0.17$; D. Réale, D. Berteaux, A. G. McAdam and S. Boutin, unpublished data). In this paper, we estimated the degree of phenotypic plasticity in parturition date (*sensu* Przybylo *et al.* 2000) and used a restricted maximum-likelihood animal model to document changes in breeding values across four generations to determine the degree to which these documented changes in parturition date resulted from phenotypic plasticity and from microevolution.

2. MATERIAL AND METHODS

We studied North American red squirrels (*T. hudsonicus*) near Kluane Lake, Yukon, Canada. The habitat was open boreal forest with white spruce (*Picea glauca*) as the dominant canopy tree. The entire population of *ca.* 325 squirrels was ear-tagged and the reproductive activity of all females was monitored each year (1989–2001) from March to late August (Berteaux & Boutin 2000). Parturition dates were estimated from the trapping records of each female and the size of offspring when the nest was first inspected (Boutin & Larsen 1993; Berteaux & Boutin 2000; Humphries & Boutin 2000). Most identified young were monitored from birth through to adulthood. Weather data were collected at the Burwash weather station, located 50 km from the study site. Spring temperature (in °C) was calculated for each year from 1975 to 2001 as the average of mean monthly temperatures from April to June (the time of lactation). Spring precipitation was calculated as the total precipitation (in mm) from January to June. Temporal trends in climate were assessed using separate ordinary least-squares regressions based on annual values ($n = 27$).

(a) *Environmental changes and reproduction*

For each female born between 1989 and 1998 we calculated lifetime parturition date as the average of all her parturition dates during her reproductive lifetime (up to 2001) corrected for age effects (see D. Réale, D. Berteaux, A. G. McAdam and S. Boutin, unpublished data). Spruce cones stored in the autumn of a given year are an important source of food for reproductive females in the spring of the following year. The number of cones on the top 3 m of 296–315 trees were counted every August and averaged within years (Boutin & Larsen 1993). These values (log transformed) represented an annual index of the availability of food. Yearly spruce cone indices were averaged across each female's reproductive lifetime as a measure of the average food abundance she experienced during her reproductive lifetime.

We used weighted linear regressions to determine whether significant changes in food abundance and parturition date (mean lifetime values) had occurred in this area across the last 10 cohorts (1989–1998; $n = 10$). Regressions were weighted based on the number of females within each cohort.

(b) *Plastic changes in parturition date*

A linear mixed-effects model of multiple breeding events by individual females in more than 1 year was used to estimate the plastic response of females to variation in food abundance (Przybylo *et al.* 2000). All females born between 1989 and 1998 that bred in more than 1 year were included in the analysis ($n = 767$ observations, 277 females). Age and female identity were included as fixed and random effects, respectively, and the index of spruce cone abundance was fitted as a covariate.

(c) *Microevolutionary changes in parturition date*

Heritability, EBVs and environmental effects on parturition date were estimated through a mixed-effects 'animal model', using a derivative-free restricted maximum-likelihood program (DFREML v. 3.1 (Meyer 1989); for applications to natural populations see Réale *et al.* (1999), Kruuk *et al.* (2000, 2001), Milner *et al.* (2000) and Merilä *et al.* (2001*a*)). Unlike the plasticity analysis, this analysis did not require multiple breeding events per female, so the dataset increased to 1058 breeding events by 664 females (zero to six records per female) between 1988 and 2001 (372 base animals; 180 dams with progeny; 72 grand dams with progeny). Age was included as a fixed effect. The spruce cone index was included as a covariate to account for the documented response of females to food abundance and year of breeding was included as an additional random effect to account for common environmental effects experienced by breeding females other than cone abundance. The coefficient for the effects of cones on parturition date (-20.28 days cone index^{-1}) was similar to the estimate obtained in the plasticity analysis (-23.12 ± 0.85 days cone index^{-1}). The inclusion of permanent environmental effects did not significantly improve the fit of the model (likelihood ratio test; $p > 0.5$) so results are presented without the inclusion of these random effects. Breeding values were estimated for all females in the pedigree using the DFREML program, but only females from a known generation ($n = 374$) were used to examine changes in breeding values across generations. Paternity is not known in this population so we could not assess levels of inbreeding. Changes in the EBVs of females across generations were used to determine whether an evolutionary response to this environmental change had taken place. Females born between 1989 and 1991 were arbitrarily assigned to generation one. After 1991, daughters were assigned a generation one greater than their mother, regardless of the year in which they were born. Females born to mothers of unknown generation were not assigned a generation (see D. Réale, D. Berteaux, A. G. McAdam and S. Boutin, unpublished data).

(d) *Maternal effects*

We tested whether our EBVs were confounded by maternal effects. Ordinary least-squares regression ($n = 663$) was used to correlate EBVs from the animal model with five characteristics of the neonatal environment experienced by females that may have affected their future parturition date as adults: maternal age, litter size, postpartum body mass (within 10 days of parturition), a measure of maternal reproductive investment (increase in maternal mass from parturition to emergence (Humphries & Boutin 1996), and the spruce cone index in the autumn prior to birth (i.e. food availability for the mother during gestation and lactation). When data on a given maternal characteristic were missing in a cell, we filled the missing cell by the average value for this characteristic.

(e) *Predicted changes*

Changes in EBVs across generations were compared with the predicted response of parturition date to selection from the breeder's equation $R = h^2 i\sigma_z = h^2 S$, where R is the change in the trait mean from one generation to the next, h^2 is the heritability estimate of the trait z, i is the standardized selection differential ($i = S/\sigma_z$), and σ_z is the standard deviation of z (Falconer & Mackay 1996; Roff 1997). We ran a bootstrap procedure with

5000 replicates (Manly 1997) using females with a known generation that died prior to 2000 to estimate, i and the mean predicted response to selection (R_{pred}) and their associated standard error. The selection differential on parturition date ($i = -0.17 \pm 0.05$) was estimated in a previous study (D. Réale, D. Berteaux, A. G. McAdam and S. Boutin, unpublished data), based on the covariance between relative lifetime fitness and average standardized parturition date (Lande & Arnold 1983) for all females for which lifetime data were available ($n = 303$; see D. Réale, D. Berteaux, A. G. McAdam and S. Boutin, unpublished data). To account for temporal heterogeneity in environmental conditions, which may affect the covariance between traits and fitness and may bias estimates of selection differential, we calculated relative lifetime fitness $W_i' = [\Sigma_{l=1}^{n}(w_{i,a,l}/\overline{w}_{a,l})]/\overline{W}$, where $w_{i,a,l}$ is the fitness value (total number of offspring weaned) for the ith female at the ath age at a particular year l, $\overline{w}_{a,l}$ is the mean fitness of females of the same age for the same year, n is the number of reproductive events of the female i during her lifetime, and $\overline{W}$ is the average lifetime fitness value in the population. For each female, we calculated the standardized lifetime value of the trait: $z_i = 1/n\Sigma_{l=1}^{n}[(x_{i,a,l} - \overline{x}_{a,l})/s_{x_{a,l}})]$, where the $x_{i,a,l}$ is the trait value of the ith female at the ath age at a particular year l, and $\overline{x}_{a,l}$ and $s_{x_{a,l}}$ are respectively the mean value and the standard deviation of the trait for females of the ath age at the lth year, in the population.

3. RESULTS

(a) *Environmental changes and reproduction*

In the southwest Yukon, spring temperature has increased by nearly 2 °C (regression: $F_{1,25} = 3.6$, $p = 0.07$; $b = 0.074 \pm 0.039$ °C yr^{-1}) and there has been no particular trend for precipitation over the last 27 years (regression: $F_{1,25} = 0.5$, $p = 0.49$; $b = -0.6 \pm 0.9$ mm yr^{-1}). Over the past 10 years the average number of cones available over a female's lifetime has increased by over 35% (figure 1*a*; $F_{1,8} = 2.2$; $p = 0.056$; $b = 0.053 \pm 0.024$ cone index cohort^{-1}; $n = 10$ cohorts). During this same 10-year period, mean lifetime parturition date of female squirrels advanced from *ca.* 128 days from 1 January (8 May) for females born in 1989 to *ca.* 110 days from 1 January (20 April) for females born in 1998 (figure 1*b*; $F_{1,8} = 5.9$; $p = 0.0003$; $b = -2.02 \pm 0.34$ days cohort^{-1}; $n = 10$ cohorts). This represents a change of over two weeks in just 10 years or *ca.* 6 days generation^{-1} (figure 2).

(b) *Phenotypic plasticity*

Food abundance had a significant effect on breeding date within individual females ($F_{1,482} = 733.2$, $p < 0.0001$), indicating a large amount of phenotypic plasticity for this trait, and a strong phenotypic effect of food abundance on the timing of breeding ($b \pm$ s.e. $= -23.12 \pm 0.85$ days cone index^{-1}). As a consequence, this effect of food availability on timing of breeding, together with an increase in cone abundance over time, accounted for most, but not all of the observed advancement in breeding among generations (3.7 days generation^{-1}; figure 2).

(c) *Microevolutionary changes*

The mean estimated breeding value of female red squirrels differed consistently between generations ($F_{3,369} = 5.3$, $p = 0.001$). EBVs advanced by an average of 0.8 days per generation (range: 0.62 to 0.95 days) such that EBVs of females in generation 4 were 2.5 days earlier than those of females in generation 1 (figure 3).

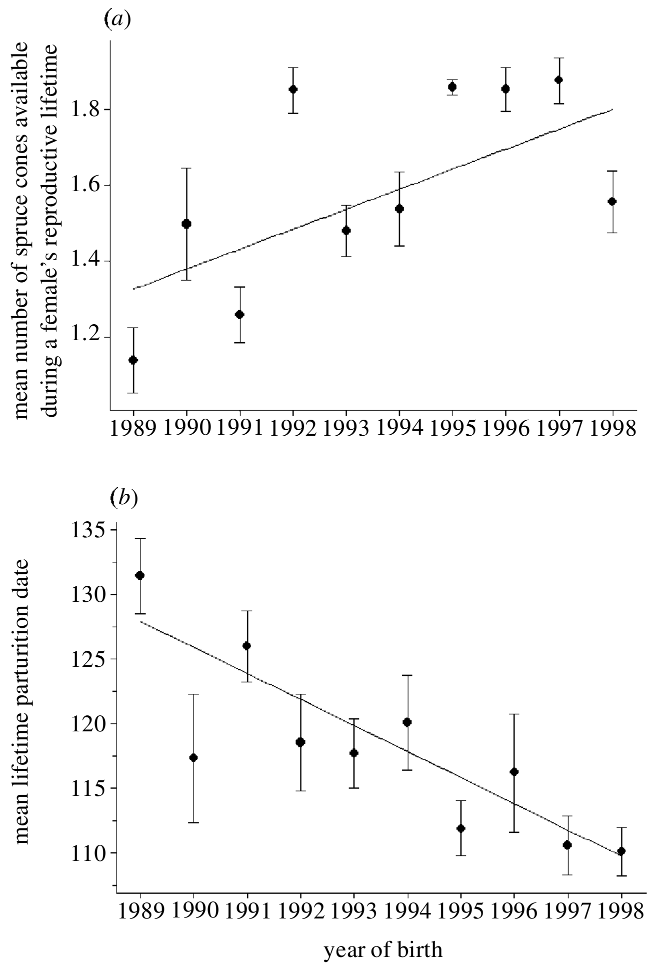

Figure 1. Variation in parturition date and food abundance in a North American red squirrel population at Kluane Lake, Yukon, Canada. (*a*) Average spruce cone index (log transformed) experienced by females during their reproductive lifetime as a function of cohort. (*b*) Average parturition date (Julian date ± s.e.) for each cohort of females born between 1989 and 1998. Each data point represents the mean for average lifetime parturition date of individuals from a given cohort corrected for age effects.

None of the five maternal variables (maternal age, litter size, postpartum weight, reproductive investment and food abundance) were significantly correlated with EBVs ($F_{1,657} < 1.0$, $p > 0.3$) and together they explained a negligible proportion of the variation in EBVs ($r^2 = 0.002$, $n = 663$). Analysis of only females with a complete set of maternal characteristics gave similar results ($F_{1,173} < 1.35$, $p > 0.17$).

Parturition date in this population was found to have significant levels of genetic variation ($h^2 = 0.16 \pm 0.03$) and has been subject to strong directional selection ($i = -0.17 \pm 0.05$; D. Réale, D. Berteaux, A. G. McAdam and S. Boutin, unpublished data). Predicted changes in parturition date using the breeder's equation ($R_{\mathrm{pred}} \pm$ s.e $= -0.60 \pm 0.17$ days generation^{-1}) were not significantly different from the average observed changes in EBVs across the four observed generations ($t_{\infty} = -1.177$, $p > 0.1$).

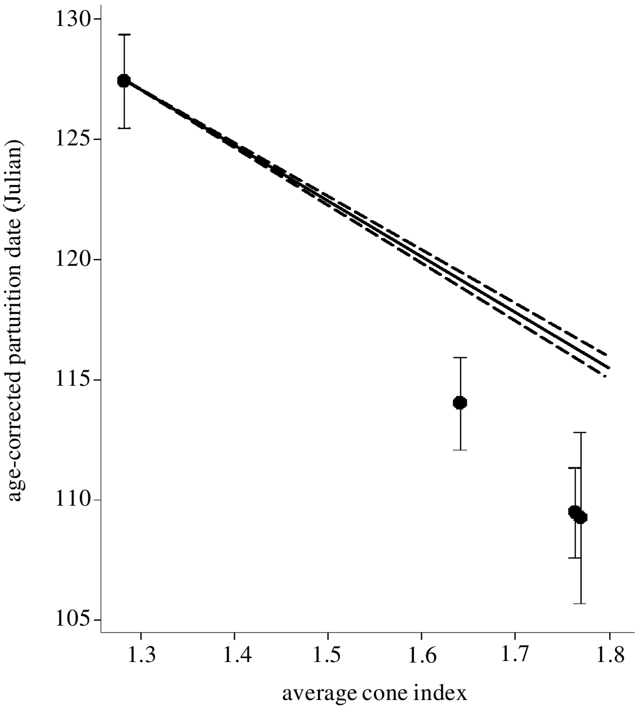

Figure 2. Changes in mean parturition date across generations. Closed circles represent mean observed parturition date (±s.e.) and average cone abundance for each generation (1–4 from left to right). The solid line represents the predicted within-generation change in parturition date (phenotypic plasticity ± s.e. (dashed lines)) in response to observed changes in cone abundance.

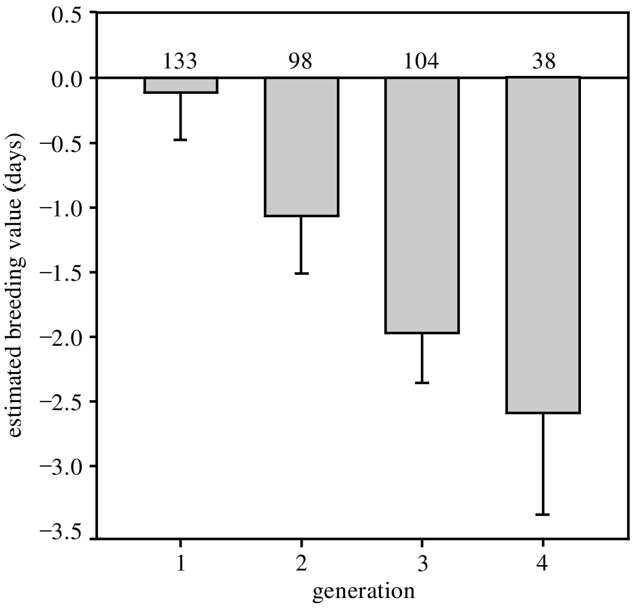

Figure 3. Changes in EBVs (−s.e.) across generations. Sample sizes within each generation (number of females) are indicated above each bar.

4. DISCUSSION

The results of our study clearly demonstrate the ability of a life-history trait in a natural population to respond to large changes in environmental conditions. During the last 27 years the southwest Yukon has experienced increased spring temperatures and more recently there has been a large increase in the abundance of food experienced by female squirrels. This population of squirrels responded to these large environmental changes by advancing breeding by 18 days over the last 10 years (6 days generation^{-1}).

This dramatic advancement in breeding comprised a plastic response to increased food abundance as well as a microevolutionary response to selection. EBVs were advanced by *ca.* 2.5 days over this 10-year period, representing a genetic advancement in breeding comparable in magnitude to most previously reported phenotypic responses to climate change (see Walther *et al.* 2002). The paucity of previous evidence of a genetic response to climate change is not entirely surprising (but see Bradshaw & Holzapfel 2001). It is extremely difficult to thoroughly document microevolutionary responses to selection in natural populations (but see Grant & Grant 1995, 2002; Reznick *et al.* 1997; Merilä *et al.* 2001*a*).

Significant maternal effects have been documented in natural populations of mammals (Kruuk *et al.* 2000; Milner *et al.* 2000) including red squirrels (McAdam *et al.* 2002) and heritability and EBVs from animal models, such as the one used in this study, are potentially confounded by maternal effects (Milner *et al.* 2000). For example, mothers in good condition may both breed earlier and raise offspring that subsequently breed earlier. As a result the influence of maternal condition (maternal effect) on both maternal and offspring breeding date would bias EBVs negatively (condition and EBVs would be negatively correlated). Previous studies have accounted for maternal effects generally (m^2; proportion of total phenotypic variation due to maternal variation (Kruuk *et al.* 2000; Milner *et al.* 2000)) using paternity information. In the absence of paternity data, we took the alternative approach of estimating the influence of a suite of potentially important maternal characteristics on EBVs directly. None of the five maternal variables we examined were significantly correlated with EBVs. This analysis, however, was fully capable of identifying confounding maternal effects on EBVs. A separate analysis of juvenile growth rates, which are known to be influenced by maternal effects ($h^2 = 0.10$, $m^2 = 0.81$; McAdam *et al.* 2002), using the same pedigree as above (sample size was reduced due to missing data; 428 females; fixed effect: birth year; covariate: cone index) resulted in an inflated estimate of h^2 (0.51) for juvenile growth rates as expected. In addition, EBVs from this growth rate animal model were significantly correlated with litter size (regression: $F_{1,388} = 4.4$, $p = 0.04$; $b = -0.026 \pm 0.012$), indicating that litter size either confounded these EBVs or was genetically correlated with growth rates. Both of these results are consistent with previous work in this population (McAdam *et al.* 2002). The absence of a correlation between parturition date EBVs and the five maternal characteristics examined here, suggests that these characters did not significantly confound our EBVs and were not genetically correlated with parturition date. It remains possible, however, that some other unmeasured maternal effect may have confounded our EBVs.

Parturition date in this population was found to have significant levels of genetic variation ($h^2 = 0.16$), has been subject to strong directional selection ($i = -0.17$; D. Réale, D. Berteaux, A. G. McAdam and S. Boutin, unpublished data) and predicted changes in parturition date using the breeder's equation matched observed changes in breeding values across the four observed generations. Together with the significant advancement in breeding values, these results provide strong evidence that in addition to the very large plastic response within generations, there has also been a significant advancement in breeding among generations due to directional selection in this heritable trait. In this case, the response to directional selection was accentuated by large environmental effects, resulting in a greater than predicted phenotypic response to consistent directional selection (cogradient variation *sensu* Conover & Schultz 1995). The combination of phenotypic changes within generations and microevolutionary changes among generations resulted in large phenotypic responses to rapid changes in environmental conditions experienced by this population of squirrels over the past 10 years.

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