

Cohort effects in red squirrels: the influence of density, food abundance and temperature on future survival and reproductive success

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Summary

1. Environmental conditions experienced early in life may have long-lasting effects on individual performance, thereby creating 'silver-spoon effects'.
2. We used 15 years of data from a North American red squirrel (*Tamiasciurus hudsonicus* Erxleben) population to investigate influences of food availability, density and spring temperature experienced early in life on reproduction and survival of female squirrels during adulthood.
3. We found that spring temperature and food availability did not affect female survival after 1 year of age, whereas higher squirrel densities led to lower survival, thereby affecting longevity and lifetime fitness.
4. In addition, both food availability experienced between birth and weaning, and spring temperature in the year of birth, had long-lasting positive effects on female reproductive success. These results emphasize the critical effect environmental conditions during the early life stages can have on the lifetime performance of small mammals.
5. These long-term effects of early food and temperature were apparent only once we controlled for conditions experienced during adulthood. This suggests that silver-spoon effects can be masked when conditions experienced early in life are correlated to some environmental conditions experienced later in life.
6. The general importance of silver-spoon effects for adult demographic performance might therefore be underestimated, and taking adult environment into account appears to be necessary when studying long-term cohort effects.

Key-words: cone production, delayed quality effects, North American red squirrel, silver-spoon effects, *Tamiasciurus hudsonicus*

Introduction

Environmental conditions experienced early in life may have important influences on individual fitness and population dynamics (Saether 1997; Lindström 1999; Gaillard *et al.* 2000). Immediate or short-term environmental effects on offspring survival, and thereby recruitment, have often been reported (for case studies see Gaillard *et al.* 1997 on roe deer; McAdam & Boutin 2003b on American red squirrel; Reed *et al.* 2003 on

snow goose; Wauters *et al.* 2004 on European red squirrel). However, it is now clear that environmental conditions experienced during early life can also have long-lasting influences on individual fitness and shape individual life history through phenotypic plasticity (Albon, Clutton-Brock & Guinness 1987; Saether 1997; Lindström 1999; Gaillard *et al.* 2000; Metcalfe & Monaghan 2001; Beckerman *et al.* 2002; Gaillard *et al.* 2003). Such 'delayed quality effects' can greatly affect population dynamics (through stabilizing or destabilizing effects) by increasing heterogeneities in performance among individuals within a population (Lindström & Kokko 2002).

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Permanent signatures of the early environment on life-history traits correspond to what Grafen (1988) called 'silver-spoon effects' and can operate through cohort variation (delayed quality effects: Albon *et al.* 1987; Gaillard *et al.* 1997). Long-lasting cohort effects have been reported in birds (Reid *et al.* 2003; van de Pol *et al.* 2006), mammals (Albon *et al.* 1987; Forchhammer *et al.* 2001; Gaillard *et al.* 2003) and reptiles (Madsen & Shine 2000), and often involve variation in body growth among individuals. Studies of the occurrence and implications of cohort variation require an identifiable and relevant environmental gradient that exhibits large amounts of variation among cohorts. Weather conditions (Gaillard *et al.* 1997; Forchhammer *et al.* 2001), population density (Forchhammer *et al.* 2001; Mysterud *et al.* 2002; Pettorelli *et al.* 2002) and food availability (Madsen & Shine 2000) during the early stages of life seem to be the most important environmental gradients shaping such cohort variation. Resource-pulse systems, which are characterized by high variability in resource levels over time (Ostfeld & Keesing 2000), seem particularly likely to exhibit important cohort effects. The responses of consumers to large pulses of resources such as mast seeding provide excellent models to test for long-lasting influences of variations of resources on lifetime performance. While the immediate effects of resource pulses on life history and population dynamics have been documented (Schmidt 2003; Bieber & Ruf 2005; Boutin *et al.* 2006), few studies have assessed the persistent effects of such large variation in resource availability on reproductive performance during adulthood (but for examples see Meikle & Westberg 2001 on captive house mice; King 2002 on stoats; Lummaa & Clutton-Brock 2002 on humans).

We examined a northern population of North American red squirrels (*Tamiasciurus hudsonicus* Erxleben) for evidence of long-lasting effects of conditions experienced early in life on female demographic performance. Red squirrels in the south-west Yukon are part of a typical resource-pulse system (Boutin *et al.* 2006) in which the production of white spruce (*Picea glauca*) seeds, the main food resource for red squirrels in this area, exhibits large annual variation from mast years to complete cone crop failures (McAdam & Boutin 2003a; Boutin *et al.* 2006; LaMontagne & Boutin 2007). Consequently, food available during pre- and postweaning stages of juvenile growth and development in this population varies substantially among cohorts. The cone availability around birth has been shown to influence red squirrel survival between birth and weaning (Humphries & Boutin 2000) and between weaning and 1 year old (McAdam & Boutin 2003b), generating marked cohort differences in recruitment. In addition to these direct numerical effects, variation in cone availability early in life is expected to have delayed effects on adult performance through potential cohort differences in growth of body mass (Humphries & Boutin 2000; McAdam & Boutin 2003a). Moreover, a previous experiment in this red squirrel population showed that differences in maternal food resources during lactation (within a breeding season) had persistent effects on offspring survival well beyond weaning (Kerr *et al.* 2007).

Thermoregulatory costs during spring are also likely to influence the energy budgets of reproducing female squirrels (Humphries & Boutin 2000), so that cold temperatures in spring should lead to increased energetic costs. Females experiencing low spring temperatures are thus expected to be able to allocate less to their offspring than females experiencing warmer spring temperatures, potentially leading to reduced offspring performance. Spring temperature may also directly affect offspring quality by changing energy allocation to early development in homeothermic species (Ardia 2005; Dawson, Lawrie & O'Brien 2005). When offspring thermoregulate on their own, they have to trade the energy received from their mother between their growth and the maintenance of their body temperature. As a consequence, low temperature during offspring growth should negatively affect their development, with potential cascading effects on their survival and reproductive potential.

Given the importance of cone production (food availability) and spring temperature to female red squirrel life history, we predicted that high cone availability and high spring temperatures during the year of birth would have positive long-term effects on cohort-specific demographic performance. As juvenile growth, and thus development, does not stop at weaning, we predicted that food availability both between birth and weaning, and between weaning and 1 year of age, would have long-lasting effects on female survival and reproduction (Metcalf & Monaghan 2001).

Density varied widely in our red squirrel population (from 2.3 to 6.4 squirrels ha⁻¹ between 1989 and 2000), and affected territory sizes (an increase in density led to a decrease in territory size; LaMontagne 2007). Therefore we also tested the prediction that population density in the year of birth would have a negative effect on cohort-specific survival and reproduction of females, and that this effect would be more pronounced when food availability was low, as increasingly reported in vertebrate populations (for review see Boyce *et al.* 2006).

Finally, long-term effects of conditions early in life can be potentially confounded with cohort-specific conditions during adulthood. For example, in a resource-pulse system such as our red squirrel–spruce system (Boutin *et al.* 2006), all cohorts do not have equal opportunities to encounter mast years during adulthood. As a consequence, we attempted to control for cohort-specific conditions during adulthood in our assessment of effects of conditions early in life on lifetime performance.

Methods

STUDY AREA

We conducted the study in south-western Yukon, Canada (61° N, 138° W), where a population of North American red squirrels has been monitored since 1989 on two 40-ha study grids separated by the Alaska Highway. All squirrels were marked with numbered ear tags and a unique colour combination of wires for identification by resighting. The fate of females was determined through live trapping, sightings and/or radiotelemetry during spring and summer. The

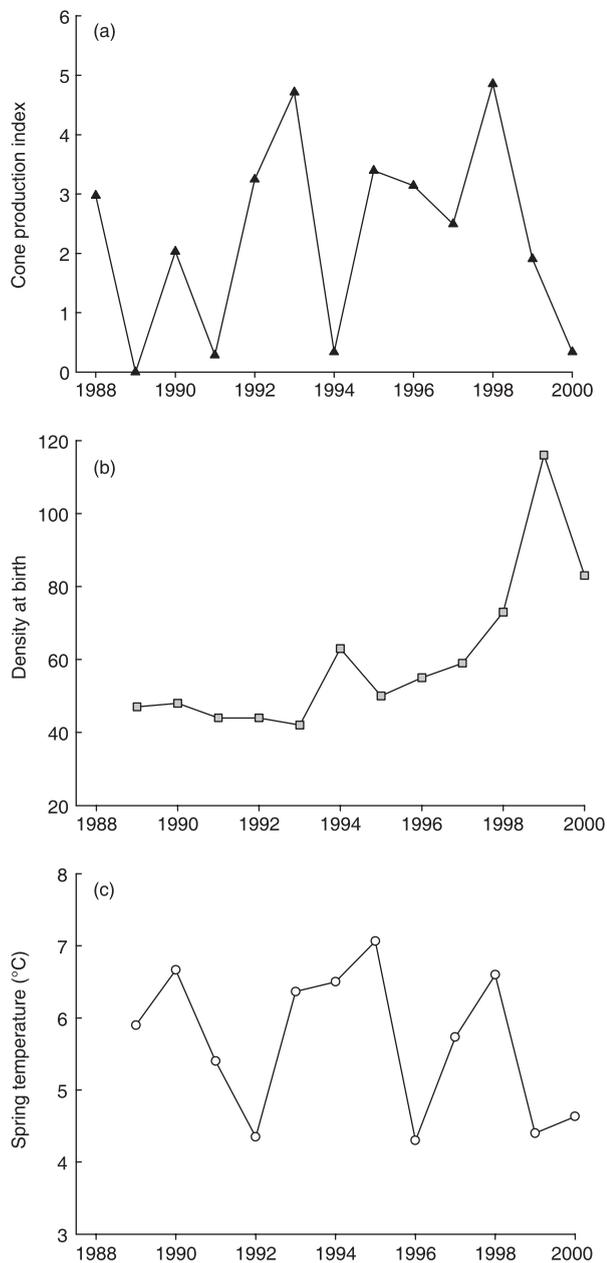


Fig. 1. Yearly variations in (a) white spruce cone production ($\ln(x+1)$ transformed index of the number of cones produced per tree; for details see LaMontagne *et al.* 2005). 1993 and 1998 correspond to mast years when cone production was high; 1989, 1991, 1994 and 2000 correspond to years of cone crop failure. (b) Density at birth (total number of squirrels owning a midden in spring on two 9-ha control areas). (c) Average temperature (measured at the Burwash Landing weather station in the Yukon) between April and June in a North American red squirrel population at Kluane, Yukon, Canada.

reproductive status of every female was monitored each year and all young produced were sexed, weighed and tagged (Berteaux & Boutin 2000; Humphries & Boutin 2000; for a detailed description see McAdam *et al.* 2007). The average dispersal distance after weaning (≈ 70 days of age) is < 100 m (Larsen & Boutin 1994; Berteaux & Boutin 2000), so most dispersal events were captured within the spatial scale of our study area, and young were followed from birth to death.

Red squirrels are conifer cone specialists, and support winter and spring energy requirements from a larder hoard of cones clipped from trees in late summer (Gurnell 1987). Food available for reproduction in a given year is therefore a function of cone production in the previous season (McAdam & Boutin 2003a; Boutin *et al.* 2006). In each year we counted the number of new cones in the top 3 m of between 170 and 250 trees distributed systematically throughout the study area, to estimate the annual production of spruce cones (LaMontagne, Peters & Boutin 2005). Cones were counted in July, when cones are fully formed but harvesting by squirrels has not yet begun. These counts per tree were \ln -transformed and averaged within each year to provide an index of yearly spruce cone production (Fig. 1a).

STUDY DESIGN

As we were interested mainly in long-lasting effects of conditions experienced early in life, we considered only females who survived to at least 300 days of age. Any female that survived to 300 days of age had survived her first winter and could potentially initiate reproduction (McAdam *et al.* 2007). We measured individual performance for each of 280 females as the total number of juveniles successfully weaned during their entire life (lifetime reproductive success, LRS; Clutton-Brock 1988). A high LRS can be reached either by having a long life span and/or by being highly successful at each breeding attempt. We therefore analysed the long-term effects of food availability, population density and spring temperature in the year of birth on female longevity (measured as number of years the female was alive on the study area) and female LRS adjusted for longevity (we included longevity as an independent variable: effect of longevity on LRS, $F_{1,274} = 289.87$, $P < 0.0001$). This latter variable measured the average annual reproductive success (ARS) of females. We considered only cohorts from 1989 to 2000. Recent cohorts (after 2000) were excluded because some females from these cohorts were still alive after 2005 (our last year of data) so their longevity and LRS could not be measured. No female born between 1989 and 2000 was alive after the 2005 season, so our estimates of lifetime performance were not underestimated by individuals with incomplete data.

We used two variables to describe food availability experienced early in life. The first was cone production in the autumn preceding the year of birth, which corresponds to the food available before weaning (food available to the mother during gestation and lactation, hereafter referred to as 'nestling food abundance'). The second measure of early food abundance was cone production during the year of birth. This corresponds to the food available between weaning and 1 year of age (hereafter called 'yearling food abundance'). Each year since 1987, the total number of squirrels owning middens in spring (May) was counted on the same 9-ha area on each of the study grids. We used this number (summed over the two grids) as an index of spring population density for that year (Fig. 1b). Spring temperature was measured as the average temperature between April and June recorded at Burwash Landing (Fig. 1c; monthly mean temperatures provided at <http://www.climate.weatheroffice.ec.gc.ca/climateData>).

Correlation coefficients between nestling food abundance, yearling food abundance and average spring temperature were all < 0.18 (all $P > 0.51$). Density was not correlated with yearling food abundance ($P = 0.98$) and spring temperature ($P = 0.20$), but was correlated to nestling food abundance ($r = 0.51$, $P = 0.042$). However, we presented results from type 3 tests, whereby the effect of each variable was tested after adjusting for every other variable in the

Table 1. Summary of linear models performed to test for an effect of food availability early in life (food availability between birth and weaning, Food_{nestling}; food availability between weaning and 1 year of age, Food_{yearling}), spring density in year of birth and average spring temperature in year of birth (T_{Spring}) on future performance, estimated over the lifetime (longevity and lifetime reproductive success, LRS) and on a yearly basis (yearly survival and yearly reproductive output). We controlled for the size of litter in which individuals grew up and/or for year (for analyses of yearly survival and breeding success). Variables in bold indicate significant effects. Details are given in the Methods section

Trait	Fixed effects			Percentage variance explained†
	Variables of interest*	Covariates	Random effects	
LRS	Year of birth			15.5
Longevity	Year of birth			10.6
LRS	Density + Food _{nestling} ‡ + Food _{yearling} ‡ + T_{Spring}	Litter size _{birth}		10.5
Longevity	Density + Food _{nestling} + Food _{yearling} + T_{Spring}	Litter size _{birth}		4.4
LRS	Density + Food _{nestling} + Food _{yearling} + T_{Spring}	Litter size _{birth} + Longevity		54.1
Yearly breeding success	Density + Food _{nestling} ‡ + Food _{yearling} + T_{Spring}	Age + Age ² + Litter size _{birth}	Individual	12.7
Yearly breeding success	Density + Food _{nestling} + Food _{yearling} ‡ + T_{Spring}	Age + Age ² + Litter size _{birth}	Individual, Year	25.0
Yearly survival	Density + Food _{nestling} + Food _{yearling} + T_{Spring}	Age + Age ² + Litter size _{birth}		7.8
Yearly survival	Density + Food _{nestling} + Food _{yearling} + T_{Spring}	Age + Age ² + Litter size _{birth}	Year	13.7
Mass at 1 year old	Year of birth	Birth date		31.2
Mass at 1 year old	Density + Food _{nestling} + Food _{yearling} + T_{Spring}	Birth date + Litter size _{birth}		18.1

*Variables that refer to cohort effects.

†Percentage of variance explained calculated as: $1 - \frac{\sum (y_i - \hat{y}_i)^2}{\sum (y_i - \bar{Y})^2}$. \bar{Y} represents the average value for the trait considered; \hat{y}_i the predicted value for individual i ; y_i the observed value for individual i .

‡ P value between 0.05 and 0.10.

model. Therefore, after adjusting for the density at birth, a significant effect of the variable nestling food abundance (food available during the rearing period for the whole population) on individuals' demography would correspond to a significant effect of the average food available per individual during the rearing period. To test the specific prediction that the effect of spring density was more pronounced when food available to breeding females was low, we examined the first-order interaction between density and nestling food abundance.

To account for potential confounding effects of conditions during adulthood, we examined female survival ($n = 856$ observations performed on 280 females; females dead from unnatural death were not considered) and reproductive success ($n = 784$ observations performed on 280 females) within individual years and adjusted for environmental conditions of the current year in our analysis of the effect of food availability, density and spring temperature in the year of birth. We therefore included year as a random factor in our analyses. We also included female age and age² as continuous covariates to account for marked age-dependence of both survival and reproductive success in this population (females' survival and reproductive success increase and then decrease with increasing age: Descamps 2006; McAdam *et al.* 2007).

Finally, we investigated the effects of environmental conditions during the year of birth on mass at 1 year of age, to investigate potential physiological mechanisms linking conditions experienced during early development and future performance. We considered the average mass of females in March (before the onset of reproduction) of the year following birth. Data were available on 146 females born between 1989 and 2000. Birth date of females was included as covariate in our models to account for differences in age.

STATISTICAL ANALYSES

All analyses involved linear models performed with the GLIMMIX macro (for analyses of LRS, yearly survival and breeding success)

and GLM procedure (for analyses of longevity and mass) of SAS ver. 9 (SAS Institute 2004). Analyses performed in our study are summarized in Table 1. All parameter estimates are given as mean \pm SE.

During years of high yearling food abundance, female red squirrels increased the size of their litters in anticipation of future food conditions (Boutin *et al.* 2006). Therefore potential advantages provided by food availability early in life could be counterbalanced by negative effects of being born in a litter with more siblings. We thus included litter size at birth as a covariate in our analyses.

To test for long-term effects of conditions experienced early in life on longevity, we assumed a normal error distribution (graphical inspection of residuals plotted against fitted values revealed no tendency in the residuals distribution; Quinn & Keough 2002). We followed the same procedure for analysis of mass at 1 year of age. To test for long-term effects of conditions experienced early in life on LRS (ranging from 0 to 16 weaned juveniles), we used a Poisson distribution with a log-link function. In a generalized linear model with a Poisson or binomial error distribution, the dispersion parameter (c) is assumed to equal 1 (Burnham & Anderson 2002). There was evidence of overdispersion in our model ($\hat{c} = 2.88$), which was taken into account with the GLIMMIX macro by inflating the standard errors in the model by the square root of the overdispersion factor. This avoided an overly liberal statistical test.

To analyse long-term effects of conditions experienced early in life on yearly survival of squirrels, we used a binomial distribution with a logit-link function ($\hat{c} = 0.98$ with year included as a random effect and $\hat{c} = 1.00$ without). Such methodology is adequate for studying survival rates when recapture rates are close to 1 (for a similar approach see Cam & Monnat 2000), as is the case in our red squirrel population (Descamps 2006). To analyse long-term effects of conditions experienced early in life on yearly breeding success, we used a Poisson distribution with a log-link function ($\hat{c} = 1.13$ with year included as a random effect and $\hat{c} = 1.33$ without).

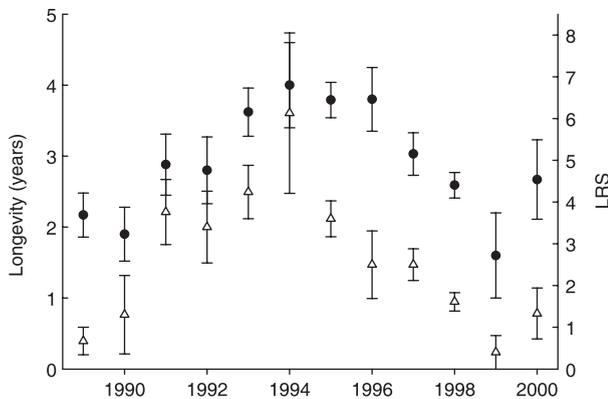


Fig. 2. Longevity (●) and lifetime reproductive success (LRS, △) of females (that survived ≥ 300 days) in a North American red squirrel population at Klwane, Yukon, Canada. Values are averages per cohort \pm SE for years 1989–2000.

For analyses of yearly survival and breeding success, year was included as a random factor to take into account yearly environmental variations that occurred during adulthood. For the analysis of yearly breeding success, we also included female identity as a random effect to account for the repeated measures of individual females. We specified the compound symmetric matrix structure, which assumes that correlation was equivalent for all pairs of measurements made on the same individual. This structure assumes that individuals differ in performance and keep that individual value throughout their life. This allowed us to account for pseudoreplication (*sensu* Hurlbert 1984) generated by repeated observations of breeding success for a given female in different years. For the yearly survival analysis no pseudoreplication occurred because death occurs only once, so we did not include squirrel identity as a random effect (Allison 1995; for a similar approach see Cam & Monnat 2000).

Results

LIFETIME DEMOGRAPHIC PERFORMANCE

Cohort-specific LRS (number of weaned juveniles) varied significantly, ranging from 0.4 ± 0.4 (1999 cohort) to 6.1 ± 1.9 (1994 cohort; effect of the year of birth on LRS: $F_{11,268} = 4.49$, $P < 0.0001$; Fig. 2). Longevity (years) also varied significantly among cohorts, ranging from 1.6 ± 0.6 (1990 cohort) to 4.0 ± 0.6 (1994 cohort; effect of year of birth on longevity: $F_{11,268} = 2.98$, $P = 0.0009$; Fig. 2), as did LRS corrected for longevity (effect of longevity: $F_{1,267} = 243.37$, $P < 0.0001$; effect of year of birth: $F_{11,267} = 2.96$, $P = 0.0010$).

We did not find a significant interaction effect of nestling food availability and density at birth on LRS ($F_{1,273} = 1.18$, $P = 0.28$) or longevity ($F_{1,273} = 0.06$, $P = 0.81$) of females, so this interaction was not included in further analyses. LRS was not significantly influenced by nestling food abundance (slope on a log scale: 0.087 ± 0.051 , $F_{1,274} = 2.86$, $P = 0.092$), yearling food abundance (slope on a log scale: -0.077 ± 0.044 , $F_{1,274} = 3.09$, $P = 0.080$), or spring temperature in the year of birth (slope on a log scale: 0.15 ± 0.09 , $F_{1,274} = 2.43$, $P = 0.12$). However, LRS decreased with increasing density at birth

(slope on a log scale: -0.027 ± 0.005 , $F_{1,274} = 27.36$, $P < 0.0001$) and increased with increasing natal litter size (slope on a log scale: 0.20 ± 0.08 , $F_{1,274} = 7.15$, $P = 0.0079$; average LRS for females born in litters of size one to five were 0.7 ± 0.7 , 2.6 ± 0.5 , 2.5 ± 0.3 , 3.4 ± 0.4 and 3.1 ± 0.8 , respectively).

These effects on LRS could act through longevity, ARS or both. Squirrel longevity was not related to nestling food abundance ($F_{1,274} = 0.82$, $P = 0.37$), yearling food abundance ($F_{1,274} = 0.08$, $P = 0.78$), average spring temperature in the year of birth ($F_{1,274} = 0.49$, $P = 0.49$) or litter size at birth ($F_{1,275} = 0.82$, $P = 0.37$), but decreased with increasing density at birth (slope: -0.026 ± 0.008 , $F_{1,274} = 11.13$, $P = 0.001$). ARS (LRS adjusted for longevity) decreased with increasing density at birth (slope on a log scale: -0.014 ± 0.004 , $F_{1,273} = 11.77$, $P = 0.0007$), and with increasing yearling food abundance (slope on a log scale: -0.095 ± 0.032 , $F_{1,273} = 9.00$, $P = 0.0029$); and increased with increasing litter size (slope on a log scale: 0.19 ± 0.06 , $F_{1,273} = 10.21$, $P = 0.0016$). ARS was not significantly affected by nestling food abundance ($F_{1,273} = 0.64$, $P = 0.52$) or average spring temperature ($F_{1,273} = 1.31$, $P = 0.19$). These results indicate that density at birth influenced both reproductive success and longevity, whereas yearling food abundance and litter size at birth influenced female reproductive success but not longevity.

ANNUAL DEMOGRAPHIC PERFORMANCE

There was no significant interaction effect of nestling food abundance and density at birth on yearly breeding success ($F_{1,775} = 0.84$, $P = 0.36$) or survival ($F_{1,847} = 0.07$, $P = 0.80$) of females, and this result was unchanged if year was included as a random effect ($F_{1,759} = 0.11$, $P = 0.74$ for breeding success; $F_{1,833} = 0.23$, $P = 0.73$ for survival). We thus removed this interaction from subsequent analyses. Yearly breeding success of females increased until 4 years of age and then decreased (slopes for age and age² on a log scale, respectively: 0.81 ± 0.11 , $F_{1,776} = 50.84$, $P < 0.0001$ and -0.11 ± 0.02 , $F_{1,776} = 37.47$, $P < 0.0001$). Thus, after controlling for female age, we found significant negative effects of density at birth (slope on a log scale: -0.017 ± 0.003 , $F_{1,776} = 24.75$, $P < 0.0001$), yearling food abundance (slope on a log scale: -0.091 ± 0.028 , $F_{1,776} = 10.47$, $P = 0.0014$) and a significant positive effect of litter size at birth (slope: 0.17 ± 0.05 , $F_{1,776} = 10.52$, $P = 0.0013$) on yearly breeding success. Nestling food abundance ($F_{1,776} = 2.80$, $P = 0.096$) and spring temperature in the year of birth ($F_{1,776} = 2.04$, $P = 0.15$) did not significantly influence breeding success of females. Therefore the analyses of yearly breeding success (not corrected for yearly variations) led to similar results to the ARS analyses.

When year was included as a random factor ($z = 2.16$, $P = 0.015$) to account for differences among females in the conditions they experienced as adults, the yearly breeding success of females still increased until 4 years of age and then decreased (slopes for age and age² on a log scale, respectively: 0.87 ± 0.11 , $F_{1,761} = 57.14$, $P < 0.0001$ and -0.11 ± 0.017 , $F_{1,761} = 42.37$, $P < 0.0001$). After adjusting for year and age, the effect of density at birth ($F_{1,761} = 2.33$, $P = 0.13$) was not

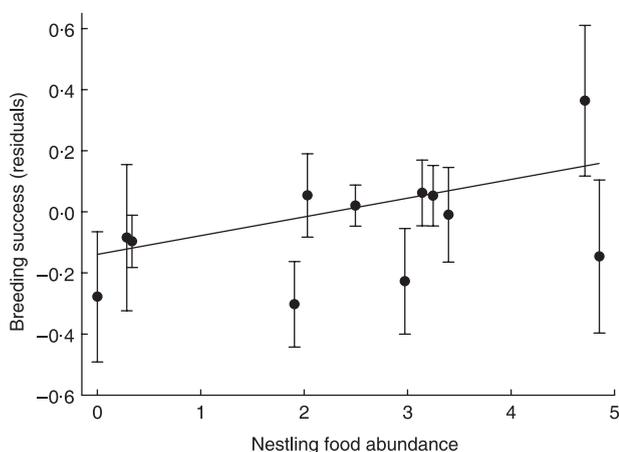


Fig. 3. Breeding success of female North American red squirrels as a function of nestling food abundance, Kluane, Yukon, Canada. Values are averages \pm SE of residuals from a linear model with year (random effect), age, age², yearling food abundance, spring temperature, density and litter size at birth. We considered only squirrels that survived ≥ 300 days from cohorts 1989–2000.

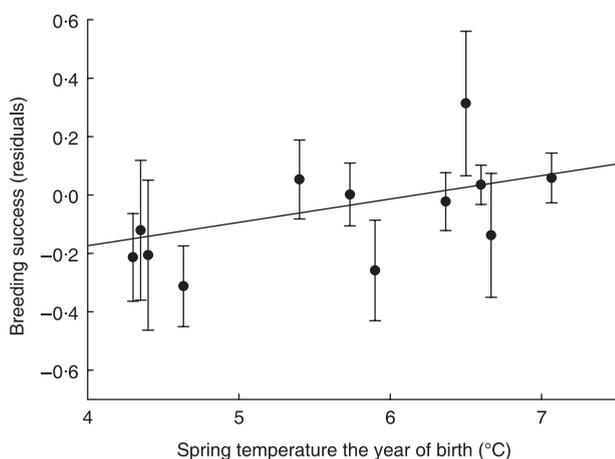


Fig. 4. Breeding success of female North American red squirrels as a function of average spring temperature during the year of birth (average between April and June, °C), Kluane, Yukon, Canada. Values are averages \pm SE of residuals from a linear model with year (random effect), age, age², yearling and nestling food abundance, density and litter size at birth. We considered only squirrels that survived ≥ 300 days from cohorts 1989–2000.

significant, and the effect of yearling food abundance was negative and nearly significant (slope on a log scale: -0.059 ± 0.030 ; $F_{1,761} = 3.82$, $P = 0.051$). Nestling food abundance (slope on a log scale: 0.070 ± 0.032 ; $F_{1,761} = 4.85$, $P = 0.028$; Fig. 3) and spring temperature in the year of birth (slope on a log scale: 0.15 ± 0.05 ; $F_{1,761} = 4.13$, $P = 0.043$; Fig. 4) were significant and positively influenced the yearly breeding success of females during their lifetime. Finally, natal litter size positively influenced future yearly breeding success of females (slope on a log scale: 0.12 ± 0.06 ; $F_{1,761} = 9.29$, $P = 0.0024$). Therefore, at each reproductive attempt, a female

born after a cone crop failure (nestling food abundance ≈ 0) produced, on average, 0.2 fewer weaned young than a female born after a mast year (large nestling food abundance). Similarly, an increase of 2.8 °C (the maximum difference between average spring temperatures observed from 1989 to 2000) during spring in the year of birth led to an increase of ≈ 0.2 weaned young per reproductive attempt.

Results were very similar when considering only females ≥ 2 years of age ($n = 520$ observations performed on 193 females; effect of density at birth: $F_{1,497} = 2.65$, $P = 0.10$; effect of yearling food abundance: $F_{1,497} = 2.04$, $P = 0.15$; effect of nestling food abundance: $F_{1,497} = 7.40$, $P = 0.0068$; effect of average spring temperature in the year of birth: $F_{1,497} = 5.05$, $P = 0.025$; effect of litter size at birth: $F_{1,497} = 8.43$, $P = 0.0038$), indicating that the effects of nestling food abundance, spring temperature in the year of birth, and natal litter size were not only due to effects on performance at 1 year of age, but corresponded to actual long-lasting effects of early environmental conditions on lifetime reproductive output. However, the effect of yearling food abundance on breeding success disappeared when considering only females ≥ 2 years old.

Yearly survival of squirrels decreased from 2 years of age onwards (slope on a logit scale for age and age² effects, respectively: 0.30 ± 0.20 , $F_{1,848} = 2.19$, $P = 0.14$ and -0.10 ± 0.03 , $F_{1,848} = 10.07$, $P = 0.0016$), but was not influenced by food abundance, temperature or litter size experienced early in life (nestling food abundance: $F_{1,848} = 1.75$, $P = 0.19$; yearling food abundance: $F_{1,920} = 0.05$, $P = 0.83$; spring temperature in year of birth: $F_{1,848} = 0.64$, $P = 0.42$; litter size at birth: $F_{1,848} = 0.49$, $P = 0.48$). However, survival of females decreased significantly with increasing density at birth (slope on a logit scale: -0.023 ± 0.006 ; $F_{1,848} = 14.62$, $P = 0.0001$).

When year was included as a random factor ($z = 1.86$, $P = 0.031$), we still found that survival decreased after 2 years of age (slopes for age and age² on a logit scale, respectively: 0.22 ± 0.21 , $F_{1,834} = 1.10$, $P = 0.30$; -0.09 ± 0.03 , $F_{1,834} = 7.63$, $P = 0.0059$). When we controlled for age and year, annual survival was not affected by nestling ($F_{1,834} = 1.72$, $P = 0.19$) or yearling ($F_{1,834} = 0.04$, $P = 0.83$) food abundance, spring temperature in the year of birth ($F_{1,834} = 0.26$, $P = 0.61$) or litter size at birth ($F_{1,834} = 0.01$, $P = 0.92$). However, annual survival decreased with increasing density (slope on a logit scale: -0.018 ± 0.008 , $F_{1,834} = -4.57$, $P = 0.033$; Fig. 5), but this result was heavily influenced by a single cohort (1999) that experienced very high density. The effect of density is no longer significant ($P = 0.10$) if the 1999 cohort is removed from the analysis. Also, the effect of density at birth on survival tended to disappear when considering only females ≥ 2 years old ($P = 0.093$), which indicated that the main effect of density at birth on survival of females was between 1 and 2 years of age.

MASS AT 1 YEAR OF AGE

Mass of females at 1 year of age (g) averaged 235.5 ± 1.8 and varied significantly among cohorts, ranging from 214.2 ± 4.1 (1999 cohort) to 243.3 ± 2.7 (1991 cohort; effect of year of

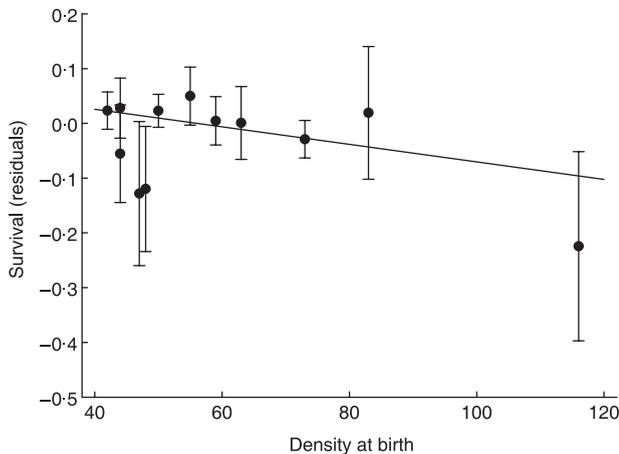


Fig. 5. Survival of female North American red squirrels as a function of density at birth (total number of squirrels owning a midden in spring on two 9-ha control areas), Kluane, Yukon, Canada. Values are averages per cohort \pm SE of residuals from a linear model with year (random effect), age, age², yearling and nestling food abundance, spring temperature and litter size at birth. We considered only squirrels that survived ≥ 300 days from cohorts 1989–2000.

birth: $F_{9,136} = 2.71$, $P = 0.0062$). Interaction between density at birth and nestling food availability did not affect the mass at 1 year of age ($F_{1,138} = 2.22$, $P = 0.14$) and was thus removed from our model. Mass of females (adjusted for birth date; $F_{1,139} = 24.91$, $P < 0.0001$) was influenced positively by yearling food abundance (slope: 3.53 ± 1.46 , $F_{1,139} = 5.85$, $P = 0.017$), and negatively by density at birth (slope: -0.33 ± 0.12 , $F_{1,139} = 7.49$, $P = 0.0070$). There was no effect of nestling food abundance ($F_{1,139} = 0.82$, $P = 0.37$), litter size at birth ($F_{1,139} = 0.56$, $P = 0.45$) or spring temperature in the year of birth ($F_{1,139} < 0.01$, $P = 0.99$).

Discussion

CONFOUNDING EFFECTS OF ADULT ENVIRONMENTS AND SILVER-SPOON EFFECTS

Lifetime reproductive success of female squirrels exhibited strong intercohort variations due to variations in both average ARS and longevity. These variations are partly connected to conditions experienced during early life, but such associations between early environment and cohort performance depended on whether or not we controlled for environment experienced during adulthood (through the inclusion of a random year effect). When conditions experienced as an adult were not controlled for, spring population density in the year of birth and yearling food abundance both negatively affected female breeding success. However, once we accounted for variation in environmental conditions experienced during adulthood, these effects were severely weakened; spring density was no longer significant and yearling food abundance was only marginally significant. These apparent effects of density at birth and yearling food abundance on breeding success therefore appear to result from correlations

between these conditions experienced early in life and other environmental conditions experienced later in life. Years of high spruce cone production occur infrequently (LaMontagne & Boutin 2007) and enhance juvenile survival (McAdam & Boutin 2003b), thereby increasing female reproductive success and population density the following spring. The reduced reproductive success of females born into cohorts experiencing high spring population density and high yearling food abundance therefore probably represents their decreased probability of experiencing a high-fitness, high-food year as an adult. The negative effect of yearling food abundance on female reproductive success also disappeared when considering only females ≥ 2 years old, suggesting that any remaining effect of yearling food was limited to females' first year of breeding.

Contrary to spring population density and yearling food abundance, accounting for environmental conditions experienced in adulthood exposed highly significant positive effects of nestling food abundance and spring temperature on ARS that were not evident when variation in reproductive success was confounded by variation in current environmental conditions. Temperature and nestling food abundance therefore had persistent influences on individual demographic performance, but these effects, when measured over the lifetime, were masked by heterogeneity in conditions experienced during adulthood. In addition, temperature and food availability affected reproduction of females, but not their survival. Thus a female born under warmer temperature and higher food availability was more successful in raising young during adulthood, but did not survive better. Also, the largest observed deviation in spring temperature between two cohorts had an effect on future reproductive output that was similar to the effect of the largest observed deviation in food availability between birth and weaning. Such findings emphasize the importance of climatic conditions during early development to future individual performance, as has been reported in large mammals and passerines (see Gaillard *et al.* 1997 on roe deer; Post *et al.* 1997 on red deer; Forchhammer *et al.* 2001 on Soay sheep; Saino *et al.* 2004 on barn swallow; Solberg *et al.* 2004 on moose; Dawson *et al.* 2005 on tree swallow).

Our study did not reveal any long-term effect on individual demographic performance of food availability between weaning and 1 year of age. It is usually found that the earlier an individual's development is affected, the stronger the effects (for review see Lindström 1999). It is thus not surprising to observe long-lasting effects of nestling food abundance, but not yearling food abundance, on squirrels' performance. This does not mean that yearling food had no long-lasting effect on individual performance, but that such effects, if any, were not strong enough to be detected.

LONG-LASTING EFFECTS OF POPULATION DENSITY ON SURVIVAL

We found a negative effect of density at birth on the LRS of females, which was partly due to an effect of density on females' longevity. Average longevity of females born in the year of lowest spring population density was more than twice

as long as the average longevity of females born in the year of highest density (3.6 years \pm 0.35 SE in 1993 vs. 1.6 years \pm 0.6 SE in 1999). The effect of density at birth on yearly survival of females remained significant after adjusting for environmental conditions experienced during adulthood, but was mainly due to only one cohort (the one that experienced the highest density at birth). Our result thus supported the existence of delayed quality effects of density at birth, as has been observed in ungulates (Forchhammer *et al.* 2001; Mysterud *et al.* 2002; Gaillard *et al.* 2003). Also, density did not interact with nestling food abundance, and our prediction of a larger effect of density under conditions of low food availability was not supported.

Several non-exclusive explanations can be proposed for this long-lasting effect of density at birth. First, as an increase in density led to a decrease in territory size in this red squirrel population (LaMontagne 2007), it could have led to a decrease in the average food availability per breeding female. Second, previous studies on mice and voles showed that an increase in density, independent of food availability, could create hormonal changes that lead to a decrease in lactation efficiency of mothers with long-term effects on their offspring (Christian 1961). Third, in a territorial species such as red squirrels, an increase in density could lead to a higher number of agonistic interactions, and thus energetic expenses. Lower food availability to breeding females, and/or lactation efficiency, and/or higher number of agonistic interactions could have led to a lower energetic allocation to offspring, with long-lasting effects on their demographic performance.

ENERGY ALLOCATION TO OFFSPRING QUALITY

A recent study conducted in the same red squirrel population (Boutin *et al.* 2006) showed that females adjust the size of their litters in anticipation of the abundance of food that will be available to their offspring after weaning (yearling food abundance). Our study indicated that squirrels' demographic performance did not vary as a function of yearling food abundance (at least after 1 year old). Therefore it seems that the increased anticipatory reproductive allocation in offspring number (Boutin *et al.* 2006) does not affect the future reproductive success or survival of offspring. Specifically, in years of high cone production, females produced more offspring (Boutin *et al.* 2006), but these young did not perform better or worse as adults than young born in years of low cone production. This remained true whether or not variation in litter size was accounted for (results not shown).

In contrast, litter size did not vary in relation to nestling food abundance (Humphries & Boutin 2000; Boutin *et al.* 2006). Food availability during rearing is highly predictable because food resources for a given reproductive season correspond to cones stored the preceding summer, but females do not adjust the number of offspring produced in response to nestling food abundance (Boutin *et al.* 2006). As a consequence, in years of high nestling food abundance, females have access to more resources for an equivalent number of offspring. These large total resources during

lactation may have led to high energy allocation per offspring, leading to improved quality of offspring, which could explain the long-lasting influence of food availability during lactation on female reproductive performance that we report here. In addition, high nestling food abundance led to increased mass of offspring at weaning (Humphries & Boutin 2000; McAdam & Boutin 2003a; Boutin *et al.* 2006). Part of the long-lasting effects of environmental conditions during early life on red squirrel performance may therefore be explained by an effect on early growth or some other attribute related to nutritional stress during early development. For example, early nutrition has been shown to affect the foraging abilities of seabirds later in life (Kitaysky *et al.* 2006).

It is clear that body mass is not the only trait that is both affected by early environmental conditions and associated with adult reproductive success. Average spring temperature during the year of birth also influenced the reproductive success of squirrels later in life, but had no detectable effect on squirrel mass. In addition, litter size at birth had no effect on mass at 1 year of age, but was positively correlated to female reproductive success. These results indicate the importance of some phenotypic attributes other than mass. Similar results were reported for tree swallows, where some nests were artificially heated during the chick-rearing period (Dawson *et al.* 2005). Offspring from heated nests experienced higher survival, but this increased offspring quality appeared to be independent of any effect on their mass. Our results also contrast with studies of ungulates, which have consistently identified growth and body mass as the main phenotypic link between early environmental conditions and fitness later in life (see review by Gaillard *et al.* 2003). In red squirrels, other traits, such as immunocompetence (Lindström 1999; Owens & Wilson 1999; Saino *et al.* 2004; Ardia 2005), may have been influenced by environmental conditions experienced by individuals during early life.

PHENOTYPIC PLASTICITY OR SELECTION?

So far we have assumed that persistent effects of the early offspring environment result from phenotypic plasticity. However, viability selection on offspring growth rates has been found to be influenced by both spring temperature and nestling food abundance in the same red squirrel population (McAdam & Boutin 2003b). It is possible that aspects of future reproductive performance are influenced by components of offspring growth or some traits correlated with offspring growth rates. In this case, differences among cohorts in their reproductive performance might reflect not persistent environmental effects, but rather the results of environmentally mediated selection. This would mean that, in years of high nestling food abundance or high spring temperature, selection favoured females characterized by increased reproductive abilities (females with higher reproductive potential had a higher probability of surviving until 300 days of age). For example, McAdam & Boutin (2003b) calculated that differential survival of offspring between birth and 1 year of age resulted in maternal selection gradients (selection on maternal traits

prior to their expression) on litter size and parturition date that ranged in magnitude from 0.02 to 1.13. These results indicate that early survival of offspring can impose strong selection on maternal traits that will be expressed only later in life. The importance of environmentally mediated natural selection to cohort differences in reproductive success is currently being investigated.

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