

Best squirrels trade a long life for an early reproduction

Sébastien Descamps^{1,2}, Stan Boutin³, Dominique Berteaux^{1,*}
and Jean-Michel Gaillard²

¹*Chaire de Recherche du Canada en Conservation des Écosystèmes Nordiques et Centre d'Études Nordiques, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, Québec G5L 3A1, Canada*

²*Unité Mixte de Recherche 5558 Biométrie et Biologie Evolutive, Université Claude Bernard Lyon I, 43 boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France*

³*Department of Biological Sciences, CW405, Biological Sciences Center, University of Alberta, Edmonton, Alberta T6G 2E9, Canada*

Age at primiparity plays a crucial role in population dynamics and life-history evolution. Long-term data on female North American red squirrels were analysed to study the fitness consequences of delaying first reproduction. Early breeders were born earlier, had a higher breeding success and achieved a higher lifetime reproductive success than females who delayed their first reproduction, which suggests a higher quality of early breeders. However, early breeders had similar mass when tagged, and similar number of food caches available at one year of age as late breeders. Nevertheless, we found evidence of survival costs of early primiparity. Early breeders had a lower survival between one and two years of age than late breeders and a lower lifespan. Our study points out that two reproductive tactics co-occurred in this population: a tactic based on early maturity at the cost of a lower survival versus a tactic based on delayed maturity and long lifespan. High quality individuals express the most profitable tactic by breeding early whereas low quality individuals do the best of a bad job by delaying their first reproduction.

Keywords: survival cost of reproduction; phenotypic quality; lifetime reproductive success; *Tamiasciurus hudsonicus*

1. INTRODUCTION

The age at which females first reproduce can greatly affect individual fitness and population dynamics (Cole 1954; Stearns 1992). Early primiparity should be selected for because it reduces the period during which animals risk dying before reproducing (Cole 1954; Bell 1980). Nevertheless, females often delay their first reproduction well after physiological maturity in a large number of species, suggesting that reproducing early in life may be costly (Williams 1966; Gadgil & Bossert 1970; Bell 1980; Stearns 1992). Delaying the first reproduction could be compensated for by increased survival and/or future reproductive success which should offset the lost benefits of reproducing early (Curio 1983).

In mammals, few studies have addressed the demographic consequences of changing age at first reproduction, and most of these have focused on large iteroparous mammals (e.g. Reiter & Le Boeuf 1991 on elephant seal; Saether & Heim 1993 on moose; Festa-Bianchet *et al.* 1995 on bighorn sheep; but see Neuhaus *et al.* 2004 on Columbian ground squirrels). In natural populations of small mammals (less than 5 kg, *sensu* Bourlière 1975), the breeding status of females is difficult to assess and nests are hard to find (Slade 1995). However, the population growth rate of

small mammal populations is highly sensitive to changes in age at primiparity (Dobson & Oli 2001; Oli *et al.* 2001).

Physiological and environmental conditions determining survival and reproductive success of individuals may vary a lot within a population (McNamara & Houston 1996). Such heterogeneity among phenotypic quality can mask the costs of early breeding when the probability to breed early is skewed toward high quality individuals (van Noordwijk & de Jong 1986). The idea that individual heterogeneity plays a crucial role in the detection of some trade-offs has recently gained importance (e.g. Pärt 1995; Forslund & Pärt 1995; Dobson *et al.* 1999; Cam & Monnat 2000; Cam *et al.* 2002, 2004; Golet *et al.* 2004). It is now becoming clear that controlling for potential phenotypic differences between early and late breeders is required to interpret reliably the fitness consequences of age at primiparity.

We used long-term data (16 years) collected on a North American red squirrel population to study the fitness consequences of delaying the first reproduction. Red squirrels are physiologically capable of giving birth at one year old (Rusch & Reeder 1978; Becker *et al.* 1998) but less than 50% of females do so at Kluane, Yukon (this study). Such variations of the age at primiparity and the detailed knowledge of individual life histories of squirrels in this population gave us a unique opportunity to study the consequences of early reproduction on fitness in a small mammal population.

* Author for correspondence (dominique_berteaux@uqar.qc.ca).

2. MATERIAL AND METHODS

(a) *Study area*

We conducted the study in the South of the Yukon territory, Canada (61° N, 138° W) from 1987 to 2003 (for a detailed description of the study, see [Bertheaux & Boutin 2000](#)). All squirrels on two contiguous control grids (approx. 40 ha each) separated by a major road were marked with numbered ear tags and a unique colour combination for identification at a distance. We trapped female squirrels weekly (Tomahawk traps) from April to August every year to determine their fate and reproductive status, through changes in mass, palpation and nipples condition. Most of the births occur from March to May, and as soon as we trapped lactating females, we found their nest by monitoring them through visual observations or telemetry. We counted and sexed pups soon after birth, tagged and weighed them at about 20–25 days of age and trapped them around weaning (70 days of age). The average dispersal distance of North American red squirrels is very low (less than 100 m, [Larsen & Boutin 1994](#); [Bertheaux & Boutin 2000](#)), and we followed most individuals from birth to death.

(b) *Study design and statistical analyses*

We considered only individuals surviving to one year of age. We called 'early breeders' the females who bred (i.e. gave birth to at least one juvenile) for the first time at one year of age (early primiparity), and 'late breeders' the females who postponed their first reproduction (delayed primiparity). Age at primiparity was known for 313 females (143 females bred at one year of age, 170 did not). Sixty-seven percent of late breeders bred for the first time at two years of age, 28% at three years of age and 5% at four years of age. The lifetime reproductive success (LRS) was measured on 279 females (134 early breeders and 145 late breeders). Analyses were carried out with SAS v. 8.00 ([SAS Institute 1999](#)).

Individuals born in a year of high food availability may experience fitness benefits throughout their lives ([Lindström 1999](#)). Such cohort variation may also influence the reproductive decisions of individuals, with high food availability or favourable weather conditions promoting early reproduction ([Boutin 1990](#); [Becker et al. 1998](#)). Thus, to account for such cohort effects that may confound the interpretation of results, we included in all analyses the year of birth as a categorical variable.

In a first step, we studied the apparent short-term effects of age at primiparity on survival between one and two years of age, and on the reproductive success at two years of age. We thus performed logistic regressions with age at primiparity and year of birth as independent variables, and survival or breeding probability at two years of age as dependent variables.

In a second step, we analysed the fitness consequences of variation in age at primiparity. Based on recent work ([Brommer et al. 2004](#)), we used the LRS as a reliable proxy for individual fitness. We defined LRS as the total number of juveniles successfully weaned during the entire life of the individual. A female can reach a higher than average LRS either by having more breeding attempts (i.e. early primiparity and/or long lifespan) and/or by being more successful at each breeding attempt (i.e. more offspring weaned per breeding attempt). We therefore looked for differences in LRS according to age at primiparity both in absolute terms (ANCOVAs with age at primiparity and year of birth as independent variables) and relative to longevity and average number of juveniles weaned per breeding attempt

(ANCOVAs with age at primiparity, year of birth and longevity or average number of juveniles weaned per breeding attempt as independent variables).

In a third step, to investigate the differences in phenotypic quality between early and late breeders, we compared their date of birth, their mass around 25 days of age (i.e. mass when tagged) and the number of hoarding sites (hereafter called 'middens') they owned at one year old at the onset of the breeding season. We thus performed ANOVAs with age at primiparity and year of birth as independent variables, and date of birth, mass or number of middens as dependent variables. For date of birth, we considered the difference (in days) between the date of birth of each female and the average date of birth for all females of the same cohort. As early born squirrels have access to more vacant territories than their later-born counterparts ([Price et al. 1990](#)), date of birth is likely to influence the quality of the territory obtained by weaned juveniles, and thereby their survival and reproductive success. Mass at weaning has been reported as a critical factor for juvenile survival in a European red squirrel population ([Wauters et al. 1993](#)). In our North American red squirrel population, mass at weaning (i.e. mass around 70 days of age) was available for relatively few squirrels. We thus used the mass when tagged (i.e. mass around 25 days of age), which was available for 302 out of our 312 females, and was correlated to the mass at weaning (S. Boutin, unpublished data). As females were not tagged exactly at the same age, we considered in our analyses the residuals of the linear regression of mass when tagged on age ($n=302$, $R^2=0.70$, $t=26.4$, $p<0.0001$). As mass and phenotypic quality of squirrels were likely to be linked to territory characteristics, we also analysed the number of middens owned by squirrels at one year of age at the beginning of the breeding season, with the assumption that it measures the quantity of cones produced per territory. Finally, to confirm the relevance of these variables (date of birth, mass and number of middens) as proxies of quality for squirrels (*sensu* [McNamara & Houston 1996](#)), we tested their effect on the LRS of females using ANCOVAs (with age at primiparity and year of birth included in the model as categorical variables).

All the results are reported as means \pm s.e. and correspond to predicted values from models.

3. RESULTS

Year of birth was included in all our analyses, and was significant in most of them.

(a) *Short-term effects of early primiparity on individual performance*

Early breeders had a lower probability to survive until two years of age than late breeders ($77.6\% \pm 5.2$ versus $83.5\% \pm 4.2$, $p=0.0056$). Early breeders who survived to two years of age had a higher probability to breed the next season than late breeders ($71.6\% \pm 6.3$ versus $65.1\% \pm 7.3$, $p=0.029$). When we restricted the analysis to individuals that survived to and bred at two years old, we did not find any effect of age at primiparity on the probability to breed successfully (i.e. to wean at least one juvenile) at two years of age ($77.8\% \pm 7.9$ versus $81.1\% \pm 7.6$, $p=0.12$).

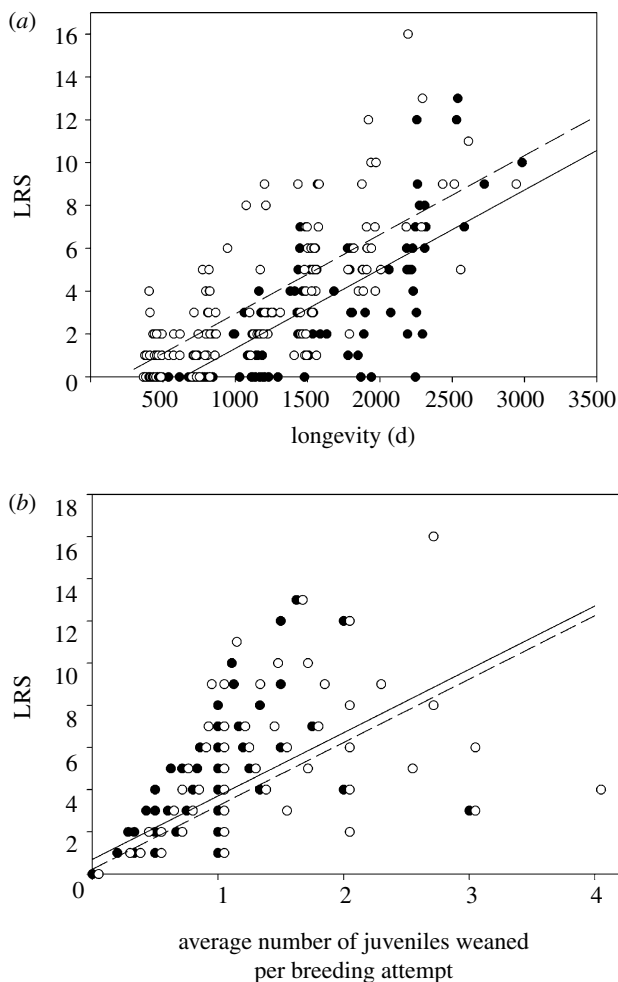


Figure 1. Lifetime reproductive success (number of weaned juveniles during the entire life) for females of a North American red squirrel population, Kluane, Yukon, Canada according to age at first reproduction and (a) longevity or (b) average number of juveniles weaned per breeding attempt (white circles and dashed lines, early breeders; black circles and solid lines, late breeders).

(b) Fitness consequences of delaying the first reproduction

Early breeders had a shorter longevity than late breeders ($1035 \text{ days} \pm 89$ versus $1245 \text{ days} \pm 89$; $F_{1,263} = 6.35$, $p = 0.012$). The average number of juveniles weaned per breeding attempt was higher for early breeders (0.97 ± 0.059 versus 0.50 ± 0.059 ; $F_{1,263} = 24.33$, $p < 0.0001$). If we considered only females who bred at least once (i.e. who gave birth to at least one juvenile), the average number of juveniles weaned per breeding attempt was still higher for early than for late breeders (1.00 ± 0.058 versus 0.76 ± 0.058 ; $F_{1,218} = 4.95$, $p = 0.027$). This difference can be partly accounted for by the larger proportion of late breeders that did not succeed in weaning one offspring compared to early breeders (19 versus 15%, respectively).

Early breeders tended to have a higher LRS than late breeders (3.0 ± 0.4 versus 2.3 ± 0.4 ; $F_{1,263} = 3.05$, $p = 0.082$), but when we considered only females who survived until two years of age, LRS of early breeders was much higher than that of late breeders (4.6 ± 0.3 versus 2.9 ± 0.3 ; $F_{1,187} = 7.14$, $p = 0.0082$). When we controlled for the positive effect of longevity ($F_{1,262} = 341.70$, $p < 0.0001$) on LRS, the difference between early

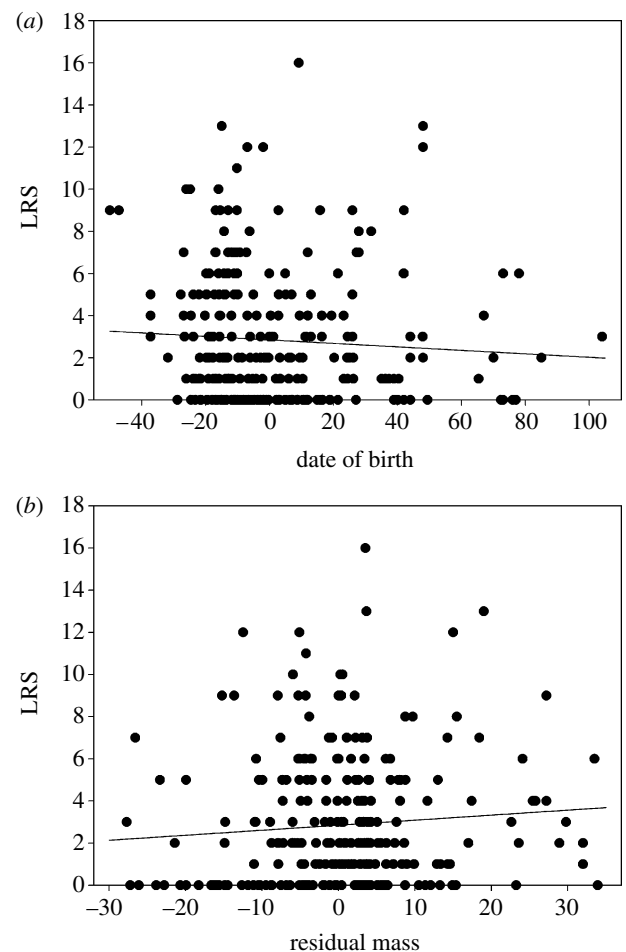


Figure 2. Lifetime reproductive success (number of weaned juveniles during the entire life) for females of a North American red squirrel population, Kluane, Yukon, Canada according to (a) their date of birth (i.e. difference in days with the average date of birth of their cohort) and (b) their mass when juvenile (i.e. residuals of the linear regression of mass when tagged on age).

and late breeders ($F_{1,262} = 29.71$, $p < 0.0001$) increased to 1.5 ± 0.3 (figure 1a). On the other hand, when we controlled for the positive effect on LRS of the mean number of juveniles weaned per breeding attempt ($F_{1,262} = 211.32$, $p < 0.0001$), late breeders had higher LRS than early breeders (difference of 0.6 ± 0.3 , $F_{1,262} = 3.96$, $p = 0.048$; figure 1b). Thus, the higher LRS of early breeders resulted from a much higher yearly weaning success (in terms of number of weaned juveniles) than late breeders, and this overcompensated for their shorter longevity.

(c) Tracking the confounding influence of individual heterogeneity

Early breeders were born 12.7 ± 2.9 days earlier than late breeders ($F_{1,296} = 19.29$, $p < 0.0001$). We found no difference in the mass when tagged (at about 25 days of age) between early and late breeders (residual values: 0.1 ± 2.1 versus -1.2 ± 2.1 ; $F_{1,286} = 1.72$, $p = 0.19$). The number of middens on females' territory at one year old was not different between early and late breeders (1.4 ± 0.1 versus 1.3 ± 0.1 ; $F_{1,205} = 0.51$, $p = 0.48$).

After controlling for the effects of age at primiparity ($F_{1,262} = 1.53$, $p = 0.22$), females born late tended to have a lower LRS than females born early (figure 2a; $F_{1,262} = 3.77$,

$p=0.053$). Similarly, mass around 25 days of age tended to have a positive effect on LRS (figure 2b; $F_{1,253}=3.09$, $p=0.080$) after controlling for the effects of age at primiparity ($F_{1,253}=2.16$, $p=0.14$). We found no effect of number of middens ($F_{1,181}=0.65$, $p=0.42$) on LRS.

4. DISCUSSION

(a) *Costs of early primiparity and individual heterogeneity*

Measuring the cost of early reproduction by comparing early and late breeders is based on a comparison between two groups in which individuals have been allocated based on unknown factors. This could potentially confound the interpretation of our results (van Noordwijk & de Jong 1986), and the most likely confounding factor is individual heterogeneity (McNamara & Houston 1996). Heterogeneity among individuals may be a consequence of cohort variation. Early primiparity is influenced significantly by year of birth, and year of birth may have long-term effects on individual life history (Lindström 1999; Beckerman *et al.* 2002). Consequently, apparent differences between early and late breeders could be a consequence of long-term or delayed cohort effects and not of costs of early primiparity. Early breeders could have a lower longevity or survival than late breeders because they were born during unfavourable years and not because of reproductive costs. In this study, all analyses included year of birth of individuals to take into account the confounding effects of cohort variation, and the differences we observed between early and late breeders were thus unlikely to represent consequences of cohort variation.

Moreover, breeding early may be a reproductive tactic used by low quality individuals with low survival probability. Such a tactic would ascertain at least some reproductive success for these low quality squirrels. The observed difference between early and late breeders would then be a consequence of the lower quality of early breeders, and not of the costs of early reproduction. In this population of North American red squirrels, our results suggest a higher quality of early breeders (see discussion below), and consequently, the difference we report on longevity between early and late breeders is likely to represent actual costs of early primiparity.

(b) *Age at primiparity and individual quality*

Early breeders were born earlier than late breeders (after correcting for cohort variation) and those who survived until two years of age achieved a higher LRS. Similar results have been found in microtines, where early born females are early breeders (Prevot-Julliard *et al.* 1999; Lambin & Yoccoz 2001) and early breeders achieve higher LRS (Ribble 1992). However, such results contrast with those found on Eurasian red squirrels for which early and late females achieved similar LRS (Wauters & Dhondt 1995). North American and Eurasian red squirrels could thus have different reproductive tactics. In Eurasian red squirrel, females rarely defend a territory at one year of age, and often behave like floaters for one or two years (Wauters & Dhondt 1989, 1992). Consequently, the proportion of one year old breeding females is very low. This difference in the spacing behaviour between Eurasian

and North American red squirrels may explain the difference we report in reproductive tactics.

In our red squirrel population, in addition to an earlier date of birth, early breeders who survived until two years of age had a higher probability to breed when two years old. They also had a higher LRS and better breeding success than late breeders. These results support the idea of heterogeneity between early and late breeders, and of a higher quality of early breeders. As females born earlier in the season may have a higher probability to access a good vacant territory (Price *et al.* 1990), their higher quality was likely to be the consequence of higher territory quality. It has been observed in North American red squirrels that a low territory quality may prevent females reaching the physiological condition required to start follicular development, and thus breeding (Becker 1993). This supports the idea that early breeders benefited from a high quality territory, thanks to an early date of birth. Similar results have been found in a Eurasian red squirrel population (Wauters *et al.* 2001), where females who bred as yearlings had higher territory quality than females who delayed their first reproduction. Such benefits early in life (i.e. a good first territory) may also have long-term effects and give fitness advantages throughout the life (i.e. 'silver spoon' effect; Grafen 1988; Wauters & Dhondt 1995).

In our study, mass when juvenile tended to affect positively fitness of females, as observed in Eurasian red squirrels (Wauters & Dhondt 1989), but we found no difference between mass of early and late breeders. This may appear surprising since body mass is an important determinant of oestrus in Eurasian and North American red squirrels (Wauters & Dhondt 1989; Becker *et al.* 1998). However, these studies considered mass of squirrels when territorial and before the onset of reproduction, which is dependent on the quality of the territory owned by females. Such data were not available in our study and we thus used mass during the juvenile stage (around 25 days of age). Juvenile mass does not reflect the quality of the territory that females got at one year of age, which may account for the absence of difference between early and late breeders that we report. If early and late primiparous females differ essentially in the quality of the territory they got after weaning (which is itself dependent on their date of birth), it is not surprising that juvenile mass was similar for early and late breeders.

As in previous studies on North American red squirrels (e.g. Berteaux & Boutin 2000), we used the number of middens per territory as a surrogate of territory quality regarding resource availability. The number of middens per territory at one year of age was similar for early and late breeders. As this measure does not take into account the quantity of cones stored per midden, the number of middens may be a poor measure of territory quality. Moreover, even if the number of middens was correlated to the quantity of cones produced per territory, the quality of a territory is likely to be a function of other factors. Quality of the food produced (e.g. McAdam & Millar 1999) or distribution of trees (e.g. Becker *et al.* 1998) within the territory may also be important determinants of territory quality and age at primiparity. We can conclude from our results that early breeders were not inferior individuals to late breeders, but detailed field measures (such as the quantity and quality of cones produced per

territory) would be needed to conclude more confidently that territories of early breeders were of higher quality than territories of late ones.

(c) Variation in age at primiparity: life history tactic or constraint?

Early breeders had a shorter lifespan than late breeders. Such survival costs of early primiparity have been observed in other mammals (e.g. Reiter & Le Boeuf 1991; Lambin & Yoccoz 2001). In our North American red squirrel population, this shorter lifespan was over-compensated by a higher reproductive activity in terms of a higher number of weaned juveniles, and early breeders who survived after their first reproduction enjoyed higher fitness than late breeders. In our squirrel population, it thus pays to breed as one year olds.

The coexistence of early and late breeders can be interpreted as the occurrence of two reproductive tactics in our population. Individuals born early in the season have the possibility to reproduce early and exhibit a high risk–high benefit tactic based on intense breeding at the costs of a shorter lifespan. On the other hand, individuals born late in the season cannot reproduce as one year olds and show a low risk–low benefit tactic based on a lower breeding intensity over a long lifespan. An alternative hypothesis explaining the existence of a delayed first reproduction despite the advantage of breeding early could be that late breeders experience a lower variability of their reproductive success or survival as observed in deer mice (Fairbairn 1977). Late breeding would thus be an alternative tactic based on a lower risk of producing no offspring at the cost of a lower average fitness. However, the variability of LRS was lower for early breeders than for late breeders (CV: 0.9 versus 1.3), which does not support this alternative hypothesis.

Differences in quality between early and late breeders indicate that passive constraints rather than active tactics drive the decision to delay primiparity (constraint hypothesis, Curio 1983), as suggested for bank voles (Prevot-Julliard *et al.* 1999). To the question ‘is a particular life-history as expressed by a given individual the optimal fitness solution for that individual or evidence of an individual doing the best it can’ (Cooch *et al.* 2002), our study showed that both answers may hold depending on the birth date. Early born squirrels express the most profitable tactic by breeding early, whereas late born squirrels do the best of a bad job by delaying their first reproduction.

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