Survival costs of reproduction vary with age in North American red squirrels

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The costs of reproduction are expected to be higher under unfavourable conditions, so that breeding in years of low food supply should have important costs. In addition, the costs of reproduction may be contingent on the age of individuals, and young growing and old senescent individuals should suffer higher costs than the prime-age ones. We tested these predictions by investigating the costs of reproduction as a function of food availability and age in female North American red squirrels using the long-term data on survival and reproduction. We found that the costs of reproduction were independent of food supply, and we did not detect any trade-off between the current and future reproduction. We also did not detect any survival cost of reproduction for the prime-age females, but found evidence for survival costs in yearlings and old (6 years or above) females with successfully breeding individuals having a lower chance of survival compared with unsuccessful or non-breeding ones. These results supported our prediction that the costs of reproduction depended on the age of female red squirrels and were higher in young growing and old senescent individuals. Our study also indicated that, in contrast to large herbivores, heterogeneity in individual quality and viability selection in red squirrels do not affect the study of trade-offs and of the age variation in life-history traits.

Keywords: age-structured population; food supply; survival; *Tamiasciurus hudsonicus*; trade-off

1. INTRODUCTION

The assumption that trade-offs occur between the life-history components is at the core of life-history theory (Roff 2002). The traditional view is that the energy available to individuals is limited so that any energy allocation to one trait reduces the allocation to another trait (Cody 1966; Williams 1966; but see Harshman & Zera (2006) for a review of other mechanisms explaining the existence of trade-offs). In particular, the allocation to current reproduction is supposed to constrain the energy available for somatic maintenance, leading to a decrease in future reproduction or survival. It has been suggested that under unfavourable environmental conditions, such fitness costs of reproduction may be more pronounced (Reznick 1985; Festa-Bianchet *et al.* 1998). Unfavourable conditions might originate from high density (Festa-Bianchet *et al.* 1998), a high level of aggressive inter-actions (Lindström 2001), low food availability (Davis *et al.* 2005; Penn & Smith 2007) or harsh weather (Tavecchia *et al.* 2005).

The costs of reproduction might also vary in relation to the age of individuals. First, reproduction by young

individuals that are still growing can negatively influence their adult size and mass, and thereby their future survival and/or reproduction (Metcalfe & Monaghan 2001). Second, physiological condition can decrease at old ages (Rose 1991) and it might be harder for senescent individuals to meet demands required by reproduction. Consequently, in age-structured populations where breeding occurs when individuals are still growing and where senescence occurs, a given reproductive effort should be more costly for young and old individuals than for the prime-age ones. For example, in human females, survival costs of breeding as a teenager or as an elder have been reported, whereas the survival costs of reproduction are generally limited in the prime-age individuals (e.g. Newcomb *et al.* 1991; Mayor 2004). Under resource limitation, the fitness costs of reproduction may occur even in prime-age humans (in both the males and females) although to a limited extent when compared with costs associated with old age (Penn & Smith 2007). Greater fitness costs of reproduction in young and old female breeders have also been reported in large herbivores (e.g. Clutton-Brock *et al.* 1982 on red deer; Tavecchia *et al.* 2005 on Soay sheep).

Age-specific variation in reproductive costs can have important evolutionary consequences. Indeed, if the costs of reproduction in mature individuals do increase with increasing age for a given reproductive effort (i.e. energetic

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allocation to reproduction), identical or even decreasing reproductive effort with age could actually correspond to an increase in reproductive investment (i.e. the fitness cost to the parents of allocating energy to their offspring; Trivers 1972; Evans 1990). Therefore, the terminal investment hypothesis (Clutton-Brock 1984), which predicts an increase in the reproductive investment with increasing age (or more accurately with decreasing reproductive value) could be supported by a constant or even decreasing reproductive effort. The study of age-specific variation in the costs of reproduction is thus crucial to understanding the relationships between the reproductive allocation (or effort) and reproductive investment (*sensu* Evans 1990), and thereby to find a solution to the 'general life-history problem' (i.e. to determine and understand 'the schedule of age-specific reproduction and mortality, which [...] is likely to be favoured by natural selection', Schaffer 1983, p. 418).

We investigated the variation in the costs of reproduction for female North American red squirrels *Tamiasciurus hudsonicus*, in a population studied since 1987 at Kluane, Yukon territory, Canada (see McAdam *et al.* (2007) for details). Red squirrels have been individually monitored from birth to death, and the age and reproductive status of nearly all females have been registered each year. Females are sexually mature at 1 year of age, but are still growing, and survival and reproductive senescence occurs from 4 years of age onwards (McAdam *et al.* 2007; Descamps *et al.* 2008a). The age-structured population of the North American red squirrels at Kluane thus offers an opportunity to test whether the reproductive costs in terms of future survival and/or reproduction are age dependent.

In addition, the squirrels are part of a typical resource-pulse system (Boutin *et al.* 2006), where the main food resource (seeds of white spruce, *Picea glauca*) exhibits yearly variation, spanning three orders of magnitude between failure and mast years (McAdam & Boutin 2003; Boutin *et al.* 2006). This temporal variation provides a rare opportunity to determine whether the costs of reproduction vary with food conditions. Red squirrels cache unopened cones in hoarding sites called middens during late summer and autumn, and then husk these cones throughout the following winter and spring to extract the seed that provides most of their energy requirements. Middens are defended year round, and food available for reproduction in the spring is determined by the abundance of cones produced in the previous year (McAdam & Boutin 2003; Boutin *et al.* 2006). The reliance on previously stored food and the defence of individual caches means that the individual females have the potential to assess the level of stored food that is available for current reproduction. However, as female squirrels do not adjust the size of their litter according to the food available from the previous autumn (Humphries & Boutin 2000; Boutin *et al.* 2006), reproduction is expected to be more costly during the years of low food availability.

Therefore, we tested the two following predictions: (i) the costs of reproduction should be higher for young (i.e. growing) and senescent females than for the prime-age ones and (ii) the costs of reproduction should be more pronounced when food availability during reproduction was low.

2. MATERIAL AND METHODS

(a) *Red squirrel population*

The study was conducted in southern Yukon, Canada (61° N, 138° W), on two 40 ha grids of white spruce forest. We report here the results for the years 1989–2005. All squirrels present on these grids were marked with numbered ear tags, and individual colour combinations of short wires twisted around the ear tags were used for individual identification from a distance. Individual fates of squirrels were determined through live trapping (Tomahawk traps), visual observations and/or radio-telemetry from March to August every year (see McAdam *et al.* (2007) for a detailed description of the study). The reproductive status of females and parturition dates were determined through mass changes, palpation for foetuses and changes in the appearance of nipples and/or lactation. We visited the nest of each breeding female soon after birth to count and sex the young, and we tagged juveniles at approximately 25 days of age. Weaning occurs at approximately 70 days of age and the average dispersal distance of weaned juveniles is typically less than 100 m (Berteaux & Boutin 2000), so that most young were monitored from birth to death.

For our study, we used the data on 309 females born between 1988 and 2003. Our last year of data for this analysis was 2005, so that the costs of reproduction on subsequent survival and reproduction for females born after 2003 could not be assessed.

(b) *Measured variables*

Previous reproductive allocation was measured as the total number of juveniles a female weaned during a given breeding season (average $= 1.05 \pm 0.04$ s.e.; range 0–7; see appendix 1 in the electronic supplementary material). Preliminary analyses indicated that there was no difference in the future breeding success and survival probabilities between females that weaned 1, 2, 3 or more juveniles. Consequently, we defined the previous reproductive allocation, hereafter called *previous success*, as a binary variable: 0 or 1 or more offspring weaned. Therefore, non-breeding females and unsuccessful females were both characterized by a reproductive allocation of zero and were termed 'unsuccessful females'. This is justified because first, it has been shown that the gestation costs are low when compared with lactation costs in mammals (Millar 1978; Thompson & Nicoll 1986; Clutton-Brock *et al.* 1989), and second, very few females of 3 years or above and no female of 6 years or above were non-breeders (Descamps *et al.* 2007).

In order to avoid inflating the survival costs of unsuccessful breeding by including females that died prior to weaning, we only considered females that survived until the end of the breeding season for the group of unsuccessful females (i.e. survival until July for the non-breeders, and survival until their estimated weaning date for unsuccessful breeders). As such, we are considering here only the costs of reproduction after the weaning of juveniles and do not consider the potential survival costs of reproduction that occurred prior to weaning.

We tested the effect of *previous success* (0 or 1 or more weaned juveniles), *food supply* (i.e. food availability during rearing; continuous variable) and *age* (four classes; see justification below) as well as the effects of first-order interactions among these factors on subsequent survival (i.e. survival until the next breeding season), weaning success probability (i.e. probability to wean 1 or more juveniles

among females that survived until the subsequent breeding season) and the number of weaned juveniles (among females that survived and bred successfully in the subsequent breeding season). In our red squirrel population, senescence occurred at 4 years of age, but was more pronounced from 6 years of age onwards (Descamps 2006; Descamps *et al.* 2008*a*). Indeed, survival decreased by 29 per cent between 4 and 6 years of age, and by 70 per cent between 6 and 8 years of age (Descamps *et al.* 2008*a*). Therefore, age was included as a four-class variable (i.e. yearlings, 2–3 years, 4–5 years and 6 years or above).

As an index of red squirrel food abundance, we counted the number of new cones in late July–early August in the top 3 m of 170–254 marked trees systematically distributed throughout the two study areas (LaMontagne *et al.* 2005; LaMontagne & Boutin 2007). This index is highly correlated with the total cones produced per tree (LaMontagne *et al.* 2005) and it is indicative of the food available to squirrels because the cones are clipped and stored for later consumption over the winter and following spring (Smith 1968; Boutin *et al.* 2006). We used the mean number of cones counted per tree (average of log-transformed data, Boutin *et al.* 2006) as an index of the food available for reproduction in the subsequent spring (i.e. the food available for reproduction in year t corresponds to the cones produced at the end of the summer, year $t-1$). This index (hereafter referred to as the food supply) represents the between-year variation in food supply at the population level, and the variation is extreme (0–4.85; average $\pm$ s.e. $=$ 2.14 $\pm$ 0.38; see appendix 2 in the electronic supplementary material) as is characteristic of a masting system (LaMontagne & Boutin 2007). This variation has strong effects on many aspects of the red squirrel life history (Boutin *et al.* 2006). There is also a within-year spatial variation in the cone supply leading to variation in access to the cones for individual squirrels but the observed variation was far lower than year-to-year variation (LaMontagne 2007).

(c) *Statistical analyses*
For all dependent variables (survival, weaning success probability and the number of weaned juveniles), we built generalized linear mixed models based on a binomial (survival and weaning success probability) or Poisson (the number of weaned juveniles) error distribution and a logit- or log-link function using the GLIMMIX procedure of SAS v. 9 (Littell *et al.* 1996). For the models considered, the dispersion parameter c for the survival and weaning success probability was close to 1 ($\hat{c}=1.0$ and 1.3, respectively), which indicates that our analyses did not suffer from overdispersion (Burnham & Anderson 2002). For the number of weaned juveniles, the dispersion parameter ($\hat{c}=0.4$) indicated a variance of the number of weaned juveniles that was low relative to that predicted by a Poisson distribution.

Females breeding in the study area were monitored from birth to death with a yearly probability of detection that was estimated to be 1 (results not shown), so that our estimates of survival based on linear models were not biased by recapture rates of less than 1 (Nichols 1992). Our data included the repeated measurements of the same individuals at different ages (range: 1–7 observations per individual; average of 2.7). Thus, for the analyses of breeding and weaning success probabilities, we included individual identity as a random effect to take into account this non-independence and thereby the problem of pseudoreplication (Hurlbert 1984). For the survival analysis, as death occurs only once, no

pseudoreplication occurred and we did not include individual identity as a random effect (Allison 1995; see Cam & Monnat (2000) for a similar approach). The average environmental conditions experienced by the different age classes may have differed (because, for example, no female of age 6 years or above was present before 1994), so that we included a random *year* effect to adjust our analyses to yearly variations in environmental conditions. All results are reported as means $\pm$ s.e.

3. RESULTS
The survival of female red squirrels was a function of their age and previous success, and this effect of previous success on the survival differed among age classes (table 1; figure 1*a*; see appendix 3 in the electronic supplementary material). The survival of successful females was lower than that of the unsuccessful ones but only for yearlings (difference of 11%; figure 1*a*) and females of 6 years or above (difference of 55%; figure 1*a*). For the prime-aged individuals (2–5 year olds), successful females had a probability of survival that was similar to unsuccessful ones (figure 1*a*).

When considering only females that survived until the subsequent breeding season, the probability of breeding successfully varied with age, and was lower for young and old females (table 1; figure 1*b*). This probability was not a function of the previous success or its interaction with age (table 1; figure 1*b*). When considering only females that survived until the subsequent breeding season and that bred successfully in that season, the number of juveniles they weaned was not a function of their age, their previous success and the interaction between age and previous success (table 1; figure 1*c*).

Food supply did not affect the survival, the weaning success probability or the number of weaned juveniles, whether female red squirrels bred successfully or not in the previous breeding season (table 1).

4. DISCUSSION
(a) *Age-specific survival costs of reproduction*
The survival of female red squirrels was influenced by their previous reproductive output in an age-specific way. Indeed, successful females had lower survival than unsuccessful or non-breeding ones only as yearlings or when they were old (6 years or above), which supports the existence of the survival costs of reproduction for young and old females. The survival of the successful prime-age females (2–5 years of age) was similar to that of the unsuccessful prime-age ones, indicating that the costs of reproduction for the prime-age females, if any, were very limited. These results thus support our prediction of higher costs of reproduction for yearling and old females compared with prime-age ones.

(b) *Do young and old females experience higher costs because of a higher energetic allocation to reproduction or because of physiological constraints?*
Two non-exclusive explanations can be proposed to explain the age-dependent survival costs of reproduction that we found for young and old female red squirrels. First, the survival costs of reproduction could be higher for yearling and old females because of higher absolute

Table 1. Tests and p-values of *previous success*, *age* and *food supply* effects on subsequent survival and reproduction (weaning success and the number of weaned juveniles) for female North American red squirrels at Kluane, Yukon Territory, Canada. (*Previous success* corresponds to a two-modality variable: females that weaned 1 or more juveniles and females that did not wean any juvenile, and *age* corresponds to a four modality variable: yearling, 2–3 years, 4–5 years, 6 years or above. The results are from type 3 tests for fixed effects. For the survival analysis, n=846 observations performed on 309 individuals; for the weaning success probability analysis, n=631 observations performed on 249 individuals; for the number of weaned juveniles analysis, n=356 observations performed on 184 individuals.)

	fixed effects					random effects (estimate ± s.e.)		R^2
	previous success	age	previous success × age	food supply	previous success × food supply	year	individual	
survival	$F_{1,822}=5.42, p=0.020$	$F_{3,822}=8.10, p<0.0001$	$F_{3,822}=5.31, p=0.0013$	$F_{1,822}=0.04, p=0.84$	$F_{1,822}=0.08, p=0.78$	0.33 ± 0.20		0.19^a
weaning success probability	$F_{1,607}=0.28, p=0.60$	$F_{3,607}=4.29, p=0.0052$	$F_{3,607}=0.13, p=0.94$	$F_{1,607}=0.99, p=0.32$	$F_{1,607}=0.10, p=0.75$	0.54 ± 0.28	-0.017 ± 0.067	0.21^a
number of weaned juveniles	$F_{1,332}=0.07, p=0.79$	$F_{3,332}=0.16, p=0.92$	$F_{3,332}=0.06, p=0.98$	$F_{1,332}=0.72, p=0.40$	$F_{1,332}=0.58, p=0.45$	0.029 ± 0.017	0.0018 ± 0.024	0.13^b

[a] Max-rescaled R^2 of Nagelkerke (1991) from a logistic regression with *year* included as a fixed effect, and no individual random effect.
[b] Calculated as $1 - (\sum (y_i - \hat{y}_i)^2 / \sum (y_i - \bar{Y})^2)$, where $\bar{Y}$ represents the average number of weaned juveniles for individual i; $\hat{y}_i$ the predicted number of weaned juveniles for individual i; and y_i the observed number of weaned juveniles for individual i.
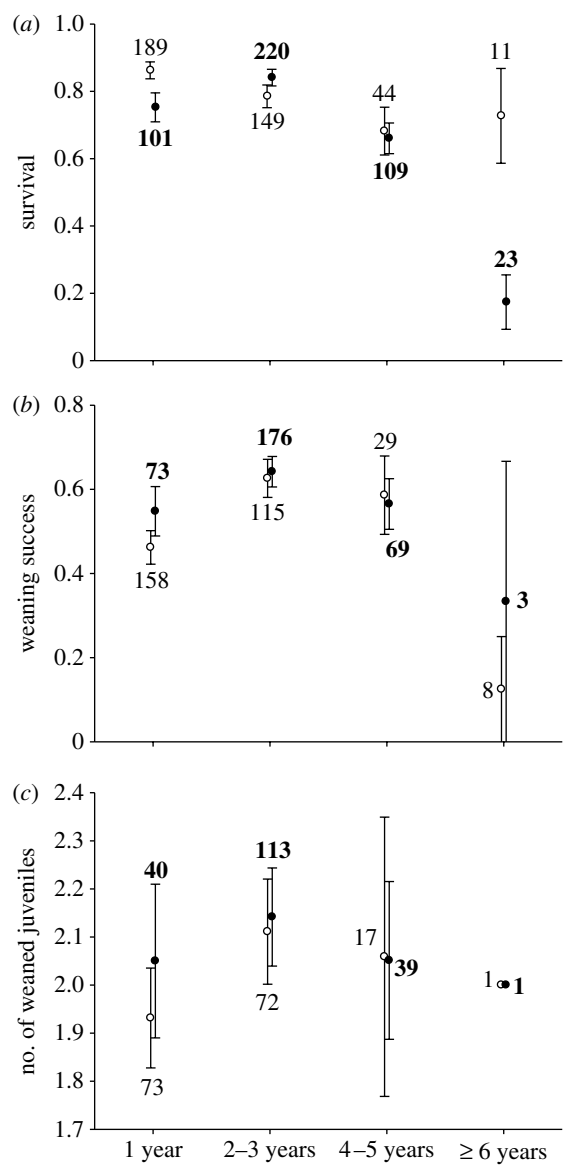

Figure 1. (a) Survival, (b) weaning success probability and (c) number of weaned juveniles according to the age and reproductive success in the previous year for female North American red squirrels at Kluane, Yukon Territory, Canada from 1989 to 2005. Filled circles represent those females that bred successfully (1 or more weaned juveniles) in the previous season whereas open circles represent females that did not wean any juvenile. Numbers indicate the sample size in each age class for each category of previous reproductive outcome (bold numbers are for females that weaned 1 or more juveniles).

energetic allocation to reproduction (i.e. higher reproductive effort). Second, the survival costs of reproduction could be higher for yearlings and old females because of an increase in the survival costs for a given energetic allocation owing to a lower physiological efficiency and/or additional competing energy requirements of growth (for young) or repair (for old). A previous study in this red squirrel population indicated that the reproductive allocation by yearlings was lower than that of prime-age females (Descamps et al. 2007). Higher survival costs of reproduction for yearlings compared with the prime-aged individuals were thus probably the consequence of higher relative costs: for a given energy allocation to reproduction, breeding is more costly for

yearlings probably because they are still growing and it may be harder for them to deal with the high energetic demands required for lactation.

The situation is not so clear for old females. Indeed, over the entire breeding season, old females exhibit the highest energetic allocation to reproduction (Descamps *et al.* 2007). Their allocation during the lactation period is similar to the prime-age females, but old females have a higher probability of breeding twice within the same season and of bequeathing their territory to their juveniles at weaning (Descamps *et al.* 2007). Bequeathal has no survival cost (Berteaux & Boutin 2000), as does breeding twice within the same season (S. Descamps & S. Boutin 2008, unpublished results). Consequently, it seems unlikely that the higher costs of reproduction observed for old females compared with the prime-aged ones were only due to their higher energetic allocation. A decrease of physiological efficiency caused by senescence is more likely to be involved, so that a given energy allocation to reproduction is more costly for old squirrels than the same energy amount allocated by the prime-aged ones.

(c) *No trade-off between current and future reproduction*

We found that the weaning success, as well as the number of weaned juveniles, in a given year was not influenced by the previous weaning success of females or the interactions between this previous weaning success and age or food supply. Our study did not support the hypothesis of a trade-off between the current and future reproduction, even under unfavourable environmental conditions. This suggests that the costs of reproduction in our population mainly affected the survival abilities of individuals, but those that managed to survive had no 'memory' of their previous reproduction (i.e. there was no lasting effect of current reproduction on future reproduction).

The under-dispersion of the number of weaned juveniles ($\hat{c} = 0.4$) could explain, at least partly, the absence of evidence for differences among groups of females for this particular cost measure. In addition, our sample size for the oldest age class was low, so the statistical power to detect any effect of the interaction between the reproductive status and age on reproductive traits was very low. However, considering that the average number of weaned juveniles produced by females was very similar whether they were successful or not in the previous year (i.e. there was no trend in favour of the cost of reproduction hypothesis; see figure 1*b*,*c*), it seems very unlikely that under-dispersion of the number of weaned juveniles or low sample sizes for older age classes could explain the absence of any apparent trade-off between the current and future reproduction.

(d) *Cost of reproduction and environmental conditions*

Reproduction was not more costly under unfavourable environmental conditions (i.e. low food supply during reproduction). Two explanations can be proposed. First, the costs of reproduction may be independent of food supply (i.e. the cone availability). This would mean that the differences in energy availability during the breeding season, and thus the energetic costs of reproduction, were not related to variations in the fitness costs of reproduction. However, according to Harshman & Zera (2006), when

studying the costs of reproduction, 'an emerging unifying theme is the overriding importance of metabolism (anabolism and catabolism) and hormonal regulation as key players'. Individual metabolism and hormonal regulation are linked to the energy intake, and thus the food supply. It thus seems unlikely that the fitness costs of reproduction can be totally unaffected by the variation in food availability during the breeding season.

Second, female red squirrels may adjust their reproductive effort to match the environmental conditions. Food available during reproduction corresponds to the cones stored by the female from the previous autumn (Boutin *et al.* 2006), so that the food availability during reproduction is highly predictable. Previous studies in this red squirrel population showed that females do not adjust their litter size to this current food availability (Humphries & Boutin 2000; Boutin *et al.* 2006), so that we expected higher fitness costs of reproduction when the food supply was low. However, the litter size represents only one component of reproductive effort (Descamps *et al.* 2007), and may remain constant while the total reproductive effort decreases. For example, females could decrease their energy allocation to their offspring by decreasing their milk production and feeding rate. In such a situation, the litter size may not be affected by the food availability during rearing, but juvenile mass, size or early survival would decrease under low conditions of food availability. It has been observed in this population that nestling growth rate of juveniles decreased with decreasing cone availability during rearing (McAdam & Boutin 2003; Boutin *et al.* 2006), and that females raised during the years of low cone availability were of lower quality than those raised in the years of large cone abundance (Descamps *et al.* 2008*b*). Thus, mothers' allocation to reproduction decreased in the years of low food availability, even if the litter size did not vary with the food availability during reproduction. In the years of unfavourable environmental conditions, female red squirrels did not jeopardize their future survival or reproduction, but rather decreased their reproductive effort and consequently the quality of their offspring, as observed in large herbivores (e.g. Festa-Bianchet & Jorgenson 1998; Réale *et al.* 1999). This leads to no association between the variations in cone production and the costs of reproduction.

(e) *Age variation in breeding tactics*

In North American red squirrels, longevity is a key determinant to lifetime fitness (McAdam *et al.* 2007), so that females are expected to invest in their reproduction in a way that minimizes negative impacts on longevity. For example, litter size manipulations resulted in reduced offspring growth and survival, but had no effect on maternal survival (Humphries & Boutin 2000). Furthermore, female red squirrels sometimes bequeath their territory to one of their offspring, but only when the survival costs to the dam are low (Berteaux & Boutin 2000). Thus, it appears that red squirrels typically engage in a conservative reproductive strategy where reproductive allocation is adjusted to avoid the survival costs (as reported in large mammals, see Gaillard & Yoccoz (2003) for a review). By contrast, the results of this study indicate that females of 6 years of age and older adopt an alternative breeding tactic (i.e. old females

sacrifice their survival for their reproduction) probably because of low residual reproductive value.

If longevity is the key to success in the red squirrels (McAdam *et al.* 2007), why do 1-year-old females breed, considering that they incur an 11 per cent survival cost of reproduction at that age? A previous study in this red squirrel population (Descamps *et al.* 2006) showed that females breeding for the first time at 1 year of age achieved on average a higher lifetime reproductive success than females delaying their first reproduction, despite a lower survival probability between 1 and 2 years of age. In addition, only high-quality females seemed to be able to breed at 1 year of age, whereas others delayed their first reproduction to 2 or 3 years of age (Descamps *et al.* 2006). Consequently, breeding at 1 year of age is a risky breeding tactic that is potentially highly beneficial for high-quality females. Such high benefits are likely to explain why some females breed as yearlings, despite high survival costs.

(f) Cost of reproduction and individual heterogeneity

Individual heterogeneity in survival and reproductive parameters is often observed in free-ranging populations (e.g. Cam *et al.* 2002; Nussey *et al.* 2008). A variety of genetic, maternal and environmental factors can lead to variation among individuals within a population. For example, in the Kluane red squirrel population, it has been shown that the individual traits vary with territory quality (LaMontagne 2007), year of birth (Descamps *et al.* 2008b) or characteristics of the mothers (McAdam *et al.* 2002; Descamps *et al.* 2008a) Such individual heterogeneity has to be accounted for when studying trade-offs and/or age-specific change in the life-history traits (Vaupel & Yashin 1985; Cam *et al.* 2002; Van de Pol & Verhulst 2006; Nussey *et al.* 2008).

High-quality individuals are likely to have both higher survival and higher reproductive abilities, resulting in positive covariation among life-history traits when trade-offs (i.e. negative relationships) are expected (see Cam *et al.* (1998) and Weladji *et al.* (2008) for examples). Such positive covariations do not mean that trade-offs do not exist but rather that individual heterogeneity in quality is pronounced enough to mask any trade-off (Van Noordwijk & de Jong 1986). In addition, individual heterogeneity in quality within a population can affect viability (*sensu* Fisher 1930), resulting in an increasing proportion of high-quality individuals with above average survival and/or reproduction in older age classes. Consequently, when considering age-specific variation in survival or reproduction at the population level, the viability selection generated by individual heterogeneity in quality can hide any decline due to senescence.

In female red squirrels, we still found that the costs increased with increasing age, despite such potential effects of individual heterogeneity in quality. As in previous studies in this red squirrel population (Descamps *et al.* 2007, 2008a), we obtained the same results when including or not including a random individual effect (i.e. when taking individual heterogeneity into account or not). Moreover, including the age at last reproduction, to take into account the selective disappearance of low-quality individuals (as suggested in Van de Pol & Verhulst 2006), did not affect our results (results not presented). This indicates that, in contrast to large herbivores (Nussey *et al.* 2008), the

variation in individual quality and viability selection is not a major issue in our red squirrel population. To determine why heterogeneity in individual quality masks trade-offs or age variation in life-history traits in some populations/species and not in others, and thus to determine the importance of individual heterogeneity in shaping individual life-history trajectories will need further (comparative) analyses.

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