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# Predators, energetics and fitness drive neonatal reproductive failure in red squirrels

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## Summary

**1.** Neonatal reproductive failure should occur when energetic costs of parental investment outweigh fitness benefits. However, little is known about the drivers of neonatal reproductive failure in free-ranging species experiencing continuous natural variation in predator abundance and in the energetic and fitness costs and benefits associated with parental investment.

**2.** Long-term comprehensive studies are required to better understand how biotic, abiotic and life-history conditions interact to drive occurrences of reproductive failure in the wild.

**3.** Using 24 years (1987–2011) of reproductive data from a northern boreal population of North American red squirrels in south-western Yukon, we examined the effects of predator abundance, energetics (resource availability, ambient temperature and litter size) and fitness benefits (probability of overwinter juvenile survival and maternal age) on occurrences of neonatal reproductive failure (494/2670 reproductive attempts; 18·5%).

**4.** Neonatal reproductive failure was driven by a combination of predator abundance, and the energetic and fitness costs and benefits of parental investment. The abundance of mustelids and maternal age was positively related to the occurrence of neonatal reproductive failure. High energy costs associated with a combination of low resource availability and cold ambient temperatures or large litters, corresponded to increased occurrences of neonatal reproductive failure. However, the strength of these relationships was influenced by variation in juvenile overwinter survival (i.e. fitness benefits).

**5.** We provide evidence that predation pressure is an important driver of neonatal reproductive failure. In addition, we found a trade-off occurs between resource-dependent energetic and fitness costs and benefits of raising the current litter to independence.

**Key-words:** environmental drivers, life-history, lifetime fitness, parental investment predation risk, reproductive failure, survival

## Introduction

Parental investment theory states that individuals should invest in their offspring only to the extent that the investment increases the parents' lifetime fitness (Trivers 1972; Clutton-Brock 1991). This amount of investment is dependent on two components: (i) the survival and future reproductive potential of the offspring and (ii) the parent's own expected reproductive success in future breeding attempts (Clutton-Brock 1991; Gross 2005). Thus, a greater parental investment in a current reproductive attempt should increase the offspring's reproductive value through increased survival and growth, but decrease the parent's future reproductive success. However, there is a limit to how much a parent can increase investment in their young (Schubert *et al.* 2009). If the current reproductive attempt requires a level of parental investment that either exceeds physiological and energetic capacity or crosses a cost-benefit threshold of current and lifetime fitness optimization, the probability of reproductive failure should increase (Clutton-Brock 1991; Gross 2005). Neonatal reproductive failure (from here on referred to as reproductive failure) has important implications for both

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the individual and the population. For an individual, reproductive failure represents a loss of energy and resources already invested in the reproductive attempt (Bronson 1985; Clutton-Brock 1991), as well as a potential reduction in lifetime fitness (Trivers 1972). Within a population, reproductive failure can result in a slowed or negative population growth (Millar & McAdam 2001; Wilson & Martin 2012).

Factors known to influence current parental investment and which ultimately may drive reproductive failure include litter size (Humphries & Boutin 2000; Guerra & Nunes 2001; McGuire & Bemis 2007), litter age (McGuire & Novak 1984), resource availability (Smith 1977; Rachlow & Bowyer 1998; Schubert *et al.* 2009), thermal conditions (Johnson & Speakman 2001; Schubert *et al.* 2009; Paul *et al.* 2010), and predation and predation risk (Rachlow & Bowyer 1998; Norrdahl & Korpimaki 2000; Jaatinen, Ost & Lehikoinen 2011). Although each factor may independently influence parental investment, occurrences of reproductive failure are likely associated with an energetic and fitness bottleneck imposed by a combination of conditions such as low energy availability, high energetic costs, and diminished fitness returns. Consistent with this, increased occurrences of reproductive failure have been found to occur under low food availability and harsh climate conditions (Clark & Wilson 1981; Post & Forchhammer 2008; Schubert *et al.* 2009), under low food availability with large litter sizes (Schubert *et al.* 2009), and under high predation risk (Laurenson 1994). Increased predator presence in an ecosystem may reduce juvenile survival and thus fitness, but also elevates parental energetic costs associated with intensified maternal defence of juveniles, nest attendance and vigilance (Laurenson 1994; Connell 1998; Jaatinen, Ost & Lehikoinen 2011).

Most studies that have investigated occurrences of, and processes that influence reproductive failure have focused on only one or a few environmental or life-history drivers (e.g. Neuhaus 2000; Post & Forchhammer 2008), and many are tested in laboratory settings where other conditions are maintained at levels optimal for reproduction (e.g. Perrigo 1987; Paul *et al.* 2010). As a result, we know that each of the above drivers play an important role in reproductive failure. However, a gap exists in our knowledge of how each driver contributes to reproductive failure when all drivers naturally vary simultaneously, and whether one driver is more important than others. Studies of reproductive failure in free-ranging populations are few (e.g. Rachlow & Bowyer 1998; Hamel, Cote & Festa-Bianchet 2010) and difficult due to the innumerable variables influencing the energetic and fitness costs and benefits associated with parental investment. Thus, long-term data sets that include natural range of variations of key drivers are important in determining whether patterns of reproductive failure support theoretical trade-offs between energetic and fitness costs and benefits of parental investment in wild populations.

In the present study, we used a 24-year data set to examine the relative importance of these potential energetic and fitness drivers of reproductive failure in a wild population of red squirrels (*Tamiasciurus hudsonicus*). We used three groups of models to predict the effects on the occurrence of reproductive failure: (i) effects directly related to energetic costs, including resource availability, ambient temperature and litter size; (ii) effects directly related to parental fitness benefits including probability of juvenile overwinter survival and maternal age; (iii) effects related to predation risk and/or direct predator-caused mortality. We hypothesize that reproductive failure is a response to an imbalance between high energetic costs and low fitness benefits in combination with occurrences of nest predation. We predict that the occurrence of reproductive failure will increase when predation risk is increased, energetic costs are high, and fitness benefits of maternal investment are reduced (Table 1). Our multifactor approach also allowed us to assess interactions between drivers of reproductive failure. We predict that an energetic bottleneck associated with a combination of high energetic costs and low resources will influence the strength of the main effects. Specifically, ambient temperature and litter size should have stronger influences on reproductive failure when resource availability is low than when resource availability is high.

## Materials and methods

### STUDY SITE AND SPECIES

A free-ranging population of red squirrels (*Tamiasciurus hudsonicus*) in south-western Yukon, Canada (61°N, 138°W) has been the focus of a long-term individual-based monitoring study since 1987. This population experiences highly seasonal climatic conditions along with high interannual fluctuations in resource availability (McAdam *et al.* 2007) and predator abundance (Boutin *et al.* 1995; O'Donoghue *et al.* 2001) causing interannual variation in population density (Dantzer *et al.* 2012). Over 24 years, all squirrels in the population were tagged with unique identifications (Monel no. 1; 5 digits). The study used eight sites (approximately 40 ha) located adjacent to a 10 km stretch of the Alaska Highway. Three of the 8 sites were operational from 1987 to 2011, one site from 1987 to 1991, one site from 1991 to 1995, one site from 1991 to 2011, and two sites from 2006 to 2011.

General population trapping and monitoring methodologies are described elsewhere (McAdam & Boutin 2003b; McAdam *et al.* 2007), but a brief description and specifics concerning this study are described here. Within this population, red squirrels breed in the spring with average parturition date varying between years in response to resource availability (Williams *et al.* 2013). Starting as early as mid-February and continuing through the breeding season, all females were regularly trapped using Tomahawk livetraps to determine and monitor reproductive

**Table 1.** Predictions of the main effects of predators, energetic and fitness cost and benefit traits on the occurrence of neonatal reproductive failure in red squirrels

| Category | Description | Rationale | Literature | Prediction |
|---|---|---|---|---|
| Predator | Mustelid abundance | Known nest predators of squirrel pups presence also influences energetic and fitness categories | Norrdahl & Korpimaki (2000), Kerr & Descamps (2008) | Increasing probability of reproductive failure with increasing predator abundance |
| Energetic | Food resources | Influences energy available to invest in parental care and self | Bronson (1985), Bronson & Marsteller (1985), Perrigo (1987) | Increasing probability of reproductive failure with decreasing resource availability |
| | Ambient temperature | Influences energy required to maintain thermoregulation of mother and litter | Schneider & Wade (1991), Zhang & Wang (2007), Zhao (2011) | Increasing probability of reproductive failure with decreasing temperature |
| | Litter size | Influences energy required for lactation and parental care | Guerra & Nunes (2001), Paul *et al.* (2010) | Increasing probability of reproductive failure with increasing litter size |
| Fitness | Juvenile overwinter survival | The probability of juvenile recruitment influences the expected fitness returns of successfully weaning a litter | MacColl & Hatchwell (2004) | Increasing probability of reproductive failure with decreasing probability juvenile overwinter survival |
| | Maternal age | Energy allocation for reproduction should vary in relation to age of individual and senescence | Descamps *et al.* (2008) | Increasing probability of reproductive failure with increasing maternal age |

status through weight change and nipple condition. Within 5 days of parturition, females were confirmed to be lactating, and a radiotransmitter collar (model PD-2C, 4g; Holohil Systems Limited, Carp, ON, Canada) was attached to the female to facilitate location of her nest. We entered the nest twice during lactation, once during early lactation, between day 0 and 7 days post-partum and once prior to pup emergence, between day 25 and 30 days post-partum. When temporarily removing pups from their natal nest, we used the squirrel's entrance causing no structural damage to the nest. On each nest entry, the pups were counted, weighed and sexed. During the second entry, unique alphanumeric ear tags were attached. Following nest disturbance, females frequently move litters to another nest within their territory (Kerr & Descamps 2008). In this population, nests are usually built of grass and bark in the branches of white spruce (59%; *Picea glauca*), but are also built within hollows of witches' broom (*Chrysomyxa arctostaphyli*) infecting spruce trees (30%), in tree cavities (7%) and underground (4%) (E. K. Studd, unpublished data). Lactating females keep all pups in the same nest, so any pup that was not found in the nest or found dead during the second entry and was not seen postemergence was recorded as having died during lactation. In the event that a female was located to a nest containing no juveniles on one or repeated occasions, females were live captured once within 5 days to assess lactation status and nipple condition. Females confirmed to no longer be lactating, and for which no untagged emerged juveniles were subsequently observed within their territory, were classified as having experienced reproductive failure. For this study, any litter in which at least one pup survived to the second nest entry was recorded as a successful reproductive attempt. As such, our definition of reproductive failure was based on litter success from birth until approximately 1 month of age for the first reproductive attempt of the year. We use initial litter size as a measure of energetic cost as Paul *et al.* (2010) found that energetic costs of lactation and food intake were dependent on litter size in Siberian hamsters (*Phodopus sungorus*). Maternal age was calculated for all squirrels born in the study sites as 0 for the year of birth. For any squirrel that was initially caught as an adult, we assumed an age of 1 at first capture.

### RESOURCES

Within this population, the main food source for red squirrels are the seeds of the white spruce tree which exhibits a masting pattern of seed production with large cone crops in some years and little to no cone production occurring between mast years, creating a pulse resource system (Boutin *et al.* 2006; LaMontagne & Boutin 2007; Fletcher *et al.* 2013). To determine resource availability, every year in late July/early August prior to commencement of clipping by red squirrels, white spruce cone production within the study sites was assessed on systematically chosen trees ($n$ = 248–1286 trees/year) with a minimum distance of 30 m between sample trees. All trees had a diameter at breast height >5 cm, which is the size at which a white spruce may produce cones in this area (LaMontagne & Boutin 2007). All cones visible from one side on the top 3 m of each tree were counted and used to calculate a cone index [average ln (cones per tree+1)] for each study site (LaMontagne, Peters & Boutin 2005). In any year where trees were not sampled at a study site (1990, 2004), the average of all other study sites for that year was used in the analysis. As red squirrels are larder hoarders that cache cones during autumn to support overwinter survival and reproduction in the following spring (Smith 1968; Steele 1998; LaMontagne & Boutin 2007), we used the previous year's cone index (referred to as cone index from here on) as our measure of current resources availability during the breeding season. It is unknown whether cones cached in 1 year are used for multiple years. Nevertheless, good predictability of red squirrel life-history traits by the previous year's cone index has been shown (McAdam & Boutin 2003a).

### FOOD SUPPLEMENTATION

Beginning in fall 2004–2006 (one additional site each year) and continuing through spring 2010, all squirrels on three separate sites were each provided with 1 kg of peanut butter at a feeding station on their territory every 6 weeks throughout the winter and spring. In each year, food supplementation was terminated when the female was no longer lactating. Feeding stations were located in the centre of each squirrel's territory and consisted of a 10-L sealed plastic bucket suspended from a tree approximately 10 m off the ground with a squirrel-sized hole in the side of the bucket. A 1 kg container of peanut butter was placed inside this bucket. All squirrels on these experimental sites were trapped and monitored in the same methods as described above.

### AMBIENT TEMPERATURE

Since red squirrels are diurnal and occupy insulated nests during the night, we assume that daytime temperatures experienced while active and foraging are of greater importance than daily average temperatures. For this reason, we obtained daily maximum temperatures (°C) from 1988 to 2011 from Environment Canada's National Climate Data and Information Archive (www.climate.weatheroffice.gc.ca) from the nearest weather station with all 24 years of data, located at Burwash Landing (61°N, 139°W, approximately 70 km north of study area). To determine the effect that a stretch of extreme cold would have on reproductive success, we calculated the mean 4-day temperature for every day from the daily maximum temperatures (°C). We know that the onset of endothermy is a gradual process during the development of young ground squirrels (*Spermophilus* spp.), but an ability to maintain a temperature warmer than ambient temperature is associated with the growth of hair on the dorsum (Maxwell & Morton 1975; Dolman 1980; Geiser & Kenagy 1990). In red squirrels, fine hair on the dorsum is seen at 10 days of age, and by 18 days, hairs are seen on forelimbs, shoulders and tail (Layne 1954). Thus, we assumed that by 14 days of age, squirrel pups would be capable of maintaining a body temperature above ambient temperature, and thus require less of the mother for thermoregulation. By this age, ambient temperature should begin to have less of an effect on parental care, so we selected the coldest 4-day temperature (coldest $T_a$) that occurred during the initial 14 days following parturition for each litter.

### PREDATION

Since 96% of nests were located in trees, we selected the only three arboreal species present at the study site that might predate on pups in the nests to model the effect of predator abundance; short-tailed weasel (*Mustela erminea*), least weasel (*Mustela nivalis*) and American marten (*Martes americana*). Of the three species, short-tailed weasels have been observed at the study site predating on squirrel pups (Spencer & Zielinski 1983; Kerr & Descamps 2008). Through the Kluane Ecological Monitoring Project (KEMP), species abundances were estimated from repeated snow track transects along a 25 km linear transect through the study area. Transects were completed following the first snowfall of each year and continued after each new snowfall until late spring (O'Donoghue *et al.* 2001). Weasel tracks were combined as we could not distinguish between the tracks of the two weasel species. Total transect length for a year depended on snowfall and ranged between 350 and 2100 km with a general trend of shorter transect lengths in more recent years. This method has been confirmed with lynx tracks to be an accurate estimate of true predator abundance and is assumed to be accurate for marten and weasel populations (O'Donoghue *et al.* 1997). Marten and weasel abundance were collinear ($r^2 = 0{\cdot}67$, $F = 47{\cdot}0$, d.f. = 22, $P < 0{\cdot}0001$) with similar abundances ($\text{range}_{\text{marten}} = 0\text{–}47{\cdot}84$, $\text{range}_{\text{weasel}} = 3{\cdot}15\text{–}75{\cdot}64$). We tested each separately in the model but as both had strong predictive power (weasel: $0{\cdot}03 \pm 0{\cdot}008$, $P < 0{\cdot}001$; marten: $0{\cdot}04 \pm 0{\cdot}008$, $P < 0{\cdot}001$), the sum of the two species was used as an estimate of mustelid abundance in all models.

### JUVENILE OVERWINTER SURVIVAL

We used the proportion of successfully weaned juveniles born in a cohort that survived overwinter to the following year to model the potential fitness benefits of successfully raising a given litter. This measure relies on the assumption that a mother has some knowledge of future conditions and what the fitness benefits are of raising a given litter. Previous research in this population has shown that squirrels are anticipatory breeders, capable of increasing reproductive output through larger litter sizes and multiple reproductive attempts prior to peak resource levels (Boutin *et al.* 2006). In one season, squirrels are able to predict resource levels of the coming autumn through some yet unknown cue (Boutin *et al.* 2006). Red squirrels in this area experience severe juvenile mortality that varies drastically between years (Fig. 1d), but those individuals that survive the first winter have a high probability of sur-

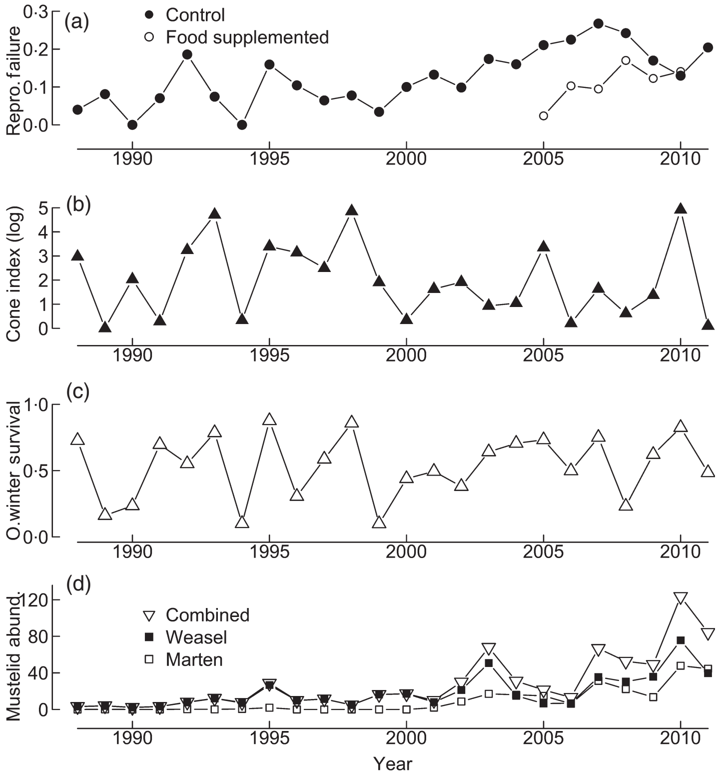

**Fig. 1.** Annual variation (a) in the proportion of neonatal reproductive failure (solid dots represents control squirrels and open circles represent food-supplemented squirrels), (b) in the average production of cones by white spruce across the study area, which is the primary food source for red squirrels, (c) in the proportion of juveniles weaned in each year that survived to the following year and (d) in combined mustelid (closed circles), short-tailed weasel (triangles) and American marten (squares) abundance (tracks/100 km) in the area.

viving to breeding (McAdam *et al.* 2007; Descamps *et al.* 2008) and thus contributing to the indirect fitness of their mother. As overwinter survival from birth is related to reproductive failure and confounded by maternal investment, only juveniles that weaned and were observed or trapped post-70 days of age were included in the baseline measure of juvenile overwinter survival. From here on, we refer to this term as overwinter survival, which represents the probability of survival to adulthood given survival to weaning.

### STATISTICAL ANALYSIS

All analyses were completed in R with package lme4 for all generalized linear mixed-effect models (R Development Core Team 2010; Barton 2011). The experimental unit for all analyses was the first reproductive attempt of the year for a female. Reproductive failure was measured as a binary response variable with each litter born within the study population recorded as a successful reproductive attempt (0) or reproductive failure (1). We used generalized linear mixed-effect models (binomial error distribution, logit link function) to evaluate predictive models of the occurrence of reproductive failure. All models included year and study site as random intercepts to control for variation between years or study sites. We created a total of nine models that included one or a combination of potential drivers of reproductive failure (Table 2). Models testing the effect of predators included mustelid abundance index (total mustelid tracks/100 km). Mustelid abundance was right skewed, so we log transformed prior to inclusion in models. All models testing energetics of parental investment included resource availability in the form of previous year's cone index and experimental food treatment (categorical; control or food supplemented), coldest $T_a$ (°C), and initial litter size (number of pups found at first nest entry). As we predicted that the effect of both coldest $T_a$ and initial litter size would be resource dependent, we tested for the following interactions: cone index and coldest $T_a$, cone index and litter size, food treatment and coldest $T_a$, and food treatment and litter size. Models testing fitness of parental investment included overwinter survival and maternal age. We tested for a quadratic response of maternal age, but it was not significant ($z = -0{\cdot}79$, $P = 0{\cdot}42$), so all models included only a linear factor. To test for trade-offs between energetic and fitness costs and benefits of parental investment, we tested for three-way interactions between the interactions in our energetic parameters (resource and temperature, and resource and litter size) and overwinter survival (Table 2). All reproductive attempts where the female died during lactation ($n = 49$) were excluded from the analysis.

All continuous explanatory variables were centred and standardized by 2 standard deviations (SD). Centring the data allows for the interpretation of the effects to be biologically relevant and for the interpretation of all main effects including those involved in interactions (Schielzeth 2010). Standardization by 2SD allows easy interpretation of strength of effects between all explanatory variables including binary variables (Gelman 2008). The standardized slopes from the models are comparable both within

**Table 2.** Generalized linear mixed effects models (binomial, logit link) of the probability of reproductive failure and the associated AIC values, ΔAIC and Akaike weights ($\omega_i$). Predator effect parameter is the annual mustelid abundance. Energetics effect parameters include previous year's cone index (CI), food treatment (F), coldest $T_a$ (T), litter size (LS) and interactions CI:T, CI:LS, F:T and F:LS. Fitness effect parameter is the proportion of a cohort of emerged juveniles surviving overwinter (JOS) and maternal age. Energetics and fitness and interactions parameters include all parameters of energetics and fitness effects as well as associated interactions between energetics and fitness parameters (JOS:CI:T, JOS:CI:LS, and JOS:F:LS). All models included random intercept effects of year and study site

| Model | AIC | ΔAIC | $\omega_i$ |
|---|---|---|---|
| Predator + Energetics + Fitness | 1975·7 | 0·0 | 0·37 |
| Predator + Fitness | 1976·1 | 0·4 | 0·30 |
| Predator + Energetics + Fitness + Interactions | 1976·3 | 0·6 | 0·28 |
| Predator + Fitness | 1980·0 | 4·3 | 0·04 |
| Predator | 1986·8 | 11·2 | 0·00 |
| Fitness | 1986·9 | 11·2 | 0·00 |
| Energetics + Fitness | 1987·1 | 11·4 | 0·00 |
| Energetics + Fitness + Interactions | 1992·8 | 17·1 | 0·00 |
| Energetics | 1996·9 | 21·2 | 0·00 |

models and between models (Schielzeth 2010). We used AIC, ΔAIC and Akaike weights ($\omega_i$) to rank the models and determine which drivers or combination of drivers best explained variation in the occurrence of NRF.

## Results

Over 24 years, we documented 2670 reproductive attempts by 1452 female squirrels, with an annual average of 103 (range = 26–224) reproductive attempts. Of these attempts, 494 resulted in reproductive failure (Table 3). Including food supplemented and control populations, the annual average proportion of neonatal reproductive failure was 0·13 (range = 0·00–0·30) with a general trend towards higher proportions occurring in more recent years (Fig. 1a; slope = 0·009 ± 0·001, $t$ = 8·8, $P$ < 0·001). On average, 37% of females that lost their first litter attempted a second litter in the same breeding season, and approximately 75% of those females were successful on the second attempt (Table 3). Annual cone index ranged from 0 to 5·17 with three large cone crops occurring in 1993, 1998 and 2010, and a fourth occurring at three of six field sites in 2005 (Fig. 1b). Average daily temperature during rearing ranged from −23·3 to 19·8 °C. The proportion of overwinter survival averaged 0·51 but varied between years from 0·10 to 0·88 (Fig. 1c). Average mustelid abundance was 29 tracks/100 km but ranged from 0 to 125 tracks/100 km with a general increasing trend over recent years (Fig. 1d; slope = 3·7 ± 0·06, $t$ = 57, $P$ < 0·001). Average maternal age was 2·5 (range = 0–8).

### RELATIVE IMPORTANCE OF EFFECTS ON NRF

We tested nine models and compared AIC values to determine relative importance of drivers (Table 2). Predator abundance was the one driver present in all top-ranked models and was most consistently associated with reproductive failure. However, as a sole predictor, it was the 5th-ranked model with very little support (ΔAIC = 11·2, $\omega_i$ = 0, Table 2). The best models were instead those that incorporated multiple drivers of reproductive failure including interactions between the energetic and fitness costs and benefits. The two of the three models that best represented the occurrence of reproductive failure included a combination of predator abundance and energetic and fitness costs and benefits of parental investment. The third model, although more complex containing three-three-way interactions between energetic and fitness drivers was equally important (ΔAIC = 0·6, $\omega_i$ = 0·28, Table 2) as the less complex model containing the same drivers but no three-way interactions (ΔAIC = 0, $\omega_i$ = 0·37, Table 2). Only one other model had an ΔAIC < 2. This model included fitness drivers and predator abundance (ΔAIC = 0·4, $\omega_i$ = 0·30, Table 2).

### EFFECTS OF PREDATION

Reproductive failure was more likely during years of high mustelid abundance than during years of low mustelid abundance (slope = 1·2 ± 0·3, $z$ = 4·3, $P$ < 0·0001; Fig. 2;

**Table 3.** Summary of the success of the first reproductive attempt to 25 days of age during a breeding season and of the subsequent reproductive attempts. Data on control squirrels include all breeding seasons from 1988 to 2011. Food supplementation experiment includes all breeding seasons from 2004 to 2010. A reproductive attempt was included only if a litter was found during the first nest entry within 5 days of parturition. All numbers represent number of first reproductive attempts made within the population

| Outcome of 1st litter | $n$ | % | Attempted 2nd litter | % | Successful 2nd litter | % |
|---|---|---|---|---|---|---|
| Control | | | | | | |
| Reproductive success | 1701 | 82·2 | 58 | 3·4 | 48 | 82·8 |
| Reproductive failure | 369 | 17·8 | 128 | 34·7 | 92 | 71·9 |
| Total | 2070 | | 186 | 9·0 | 140 | 75·3 |
| Food supplemented | | | | | | |
| Reproductive success | 475 | 79·2 | 58 | 12·2 | 41 | 70·7 |
| Reproductive failure | 125 | 20·8 | 55 | 44·0 | 46 | 83·6 |
| Total | 600 | | 113 | 18·8 | 87 | 77·0 |

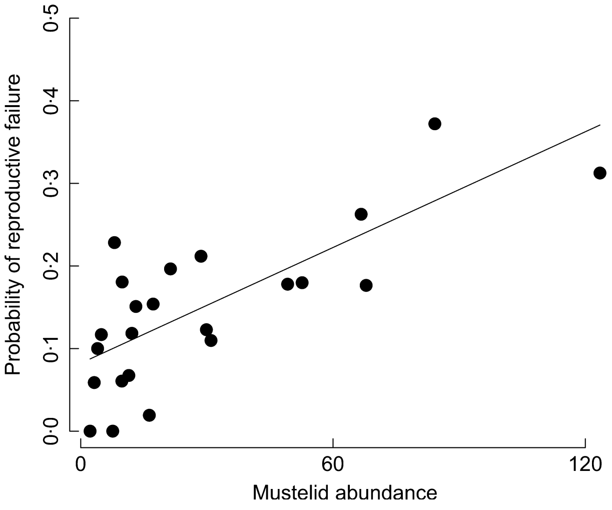

**Fig. 2.** The influence of predator abundance on the probability of neonatal reproductive failure (slope = 1·2 ± 0·3, $z = 4\cdot3$, $P < 0\cdot0001$). Dots represent the average predator index (mustelid tracks/100 km) and the proportion of reproductive attempts that experienced neonatal reproductive failure for each year (1989–2011).

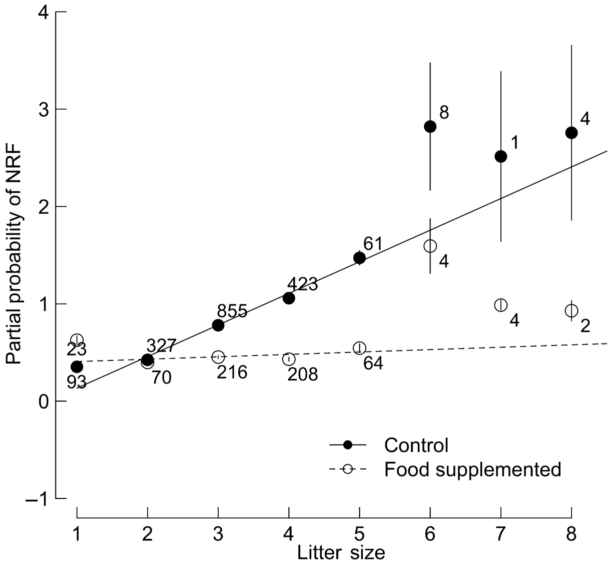

**Fig. 3.** The partial effects of litter size on the probability of neonatal reproductive failure. The effect of litter size was influenced by food treatment. Filled circles and solid line represents control squirrels. Open circles and dotted line represent food-supplemented squirrels. Numbers associated with each point is the sample size. The averaged partial residuals with standard error bars and the line are derived from GLMM of the energetics and fitness and interactions and predators (ΔAIC = 0·3, Table 3) on the occurrence of reproductive failure in red squirrels observed from 1989 to 2011.

Table S1, Supporting information). The occurrence of reproductive failure was three times more likely when mustelid abundance was high (80 + tracks/100 km) than when mustelid abundance was below 20 tracks/100 km. To ensure that the consistently low mustelid abundance from 1988 to 2002 (Fig. 1d) was not falsely driving this strong correlation, we ran an additional analysis restricted to 2002–2011 and found a similar strong correlation between mustelid abundance and reproductive failure (slope = 0·8 ± 0·2, $z = 4\cdot1$, $P < 0\cdot0001$).

### ENERGETIC EFFECTS

When resources levels (previous year's cone index) were low, reproductive failure was generally more likely than when resources were high (slope = −0·7 ± 0·3, $z = -2\cdot2$, $P = 0\cdot03$; Table S2, Supporting information). There was no main effect of food supplementation (-0·09 ± 0·2, $z = -0\cdot4$, $P = 0\cdot7$, Table S2, Supporting information), but food supplementation eliminated the effect of litter size on reproductive failure ($z = -3\cdot0$, $P = 0\cdot003$; Fig. 3; Table S4, Supporting information). On control sties, large litter sizes had higher probabilities of reproductive failure than smaller litter sizes (slope = 0·4 ± 0·14, $z = 2\cdot7$, $P = 0\cdot008$; Table S2, Supporting information). Reproductive failure was also more likely when it was cold during rearing than when it was warm (slope = −1·8 ± 0·9, $z = -1\cdot9$, $P = 0\cdot05$; Table S2, Supporting information). However, the strength of the effect of temperature on reproductive failure was influenced by a combination of cone index and overwinter survival ($z = -2\cdot3$, $P = 0\cdot02$; Fig. 4; Table S4, Supporting information). Reproductive failure was most likely when conditions included a combination of high energetic costs (cold temperatures and low resources availability) and low fitness benefits (low overwinter survival; Fig. 4a). The high probability of reproductive failure during cold temperatures decreased when conditions either included a combination of low resources and high overwinter survival (Fig. 4 g), or high resources and low overwinter survival (Fig. 4c). Although not experienced during the study, if conditions include a combination of high resource availability and high overwinter survival, reproductive failure is predicted to be more likely during cold temperatures than warm temperatures (Fig. 4i).

### FITNESS EFFECTS

Overall, reproductive failure was more likely when there was a high probability of juvenile overwinter survival and high fitness benefits, than when the probability of overwinter survival was low (slope = 1·1 ± 0·4, $z = 3\cdot1$, $P = 0\cdot002$; Table S3, Supporting information). However, the strength and direction of the effect of overwinter survival on reproductive failure was influenced by a combination of cone index and coldest $T_{\mathrm{a}}$ ($z = -2\cdot3$, $P = 0\cdot02$, Fig. 4, Table S4, Supporting information). When cone index was low and air temperatures were cold (<−10 °C), reproductive failure was more likely if overwinter survival will be low for the cohort than if overwinter survival will be high (Fig. 4a,d,g), but when cone index was high and temperatures were cold, reproductive failure was more likely if overwinter survival will be high than if overwinter survival will be low (Fig. 4c, f,i). However, when air temperatures are warm (>10 °C),

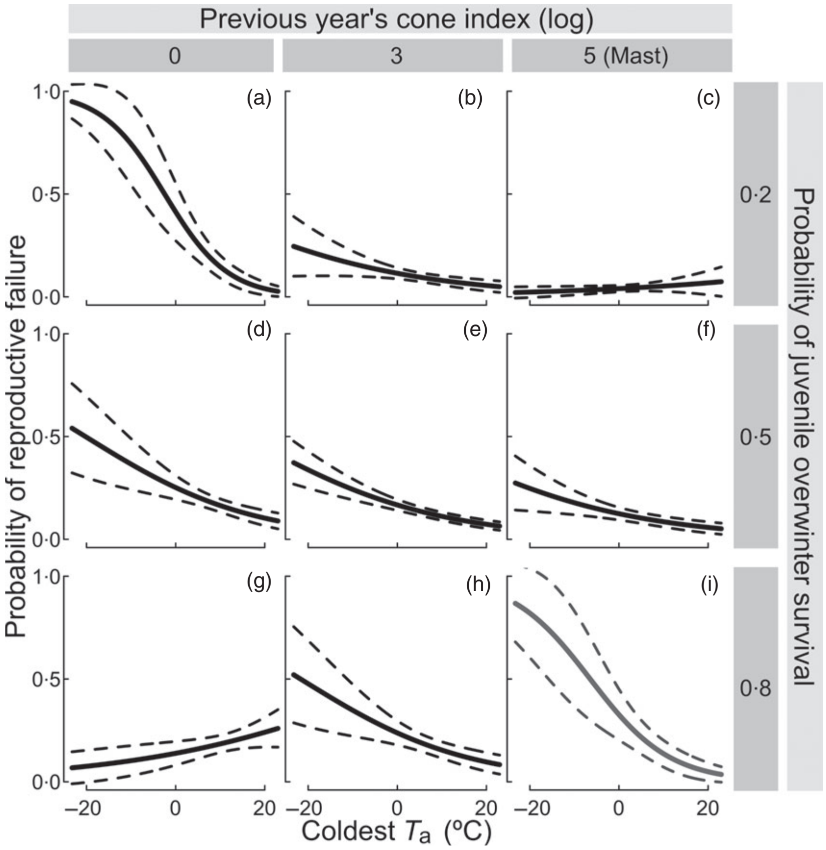

**Fig. 4.** The predicted effects of the coldest $T_a$ on the occurrence of neonatal reproductive failure at varying levels of resources (previous years' cone index; columns increasing left to right) and probability of juvenile overwinter survival (rows increasing top to bottom). Predicted effects are derived from GLMM of the energetics and fitness and interactions of parental investment and predators (($\Delta$AIC = 0·3, Table 3) on the occurrence of reproductive failure in red squirrels observed from 1989 to 2011. Black lines represent predictions under conditions that have been observed in the study. Grey lines represent predictions under conditions that have not been observed in the study but may occur in the future. All values were selected to represent the natural range for each driver that was observed during the study.

reproductive failure is least likely no matter what the cone index is or overwinter survival will be (Fig. 4). We also found that reproductive failure was more likely to occur with older females (slope = 0·30 ± 0·12, $z$ = 2·4, $P$ = 0·01) than younger females. No quadratic term of maternal age was significant.

## Discussion

Our study of the occurrence of reproductive failure in red squirrels over 24 years suggests that predation risk is an important individual driver, but more importantly confirm that trade-offs exist between maternal energetic and fitness costs and benefits. We found that predation risk, maternal age and interacting effects of food availability, overwinter survival, and coldest $T_a$ influence reproductive failure. Rates of reproductive failure have not been documented in tree squirrels but were on average double that seen in ground squirrels (10%; Spermophilus columbianus; King, Festa-Bianchet & Hatfield 1991).

### PREDATION RISK

Despite direct observations of nest predation on tree squirrels are rare with only one confirmed sighting of predation by short-tailed weasel (*Mustela erminea*) within our study population (Stuart-Smith & Boutin 1995; Kerr & Descamps 2008), red squirrels have been found to be a component of mustelid diet (Poole & Graf 1996; Bull 2000). We found evidence that mustelid abundance is a major correlate of reproductive failure. This suggests that there are likely regular occurrences of nest predation. Also predation risk may reduce perceived fitness benefits of parental investment and/or cause energetically costly changes in maternal behaviour including increased vigilance, reduced feeding and young relocation (Laurenson 1994; Kerr & Descamps 2008; Ghalambor, Peluc & Martin 2013). Squirrels are known to move their litters after disturbance which has been proposed as an antipredator defence (Kerr & Descamps 2008).

### ENERGETIC COSTS AND BENEFITS OF PARENTAL INVESTMENT

A major driver of reproductive failure is resource availability and access to energy (Bronson 1985; Thomas *et al.* 2001). With reduced resources, increased foraging time to acquire sufficient energy is required and less time and energy is available to invest in parental investment (Perrigo 1987; Schneider & Wade 1991; Schubert *et al.* 2009). Red squirrels that breed early rely primarily on capital resources (cached cones and alternatively mushrooms; Fletcher *et al.* 2013) and a decline in cone availability between 2 years produced a 65% increase in time spent foraging (Humphries & Boutin 2000). Schubert *et al.* (2009) found in mice (*Mus musculus domesticus*) that increased foraging costs led to reduction of litter sizes postparturition and reduced growth rates. We similarly found that low resource availability was associated with increased occurrence of reproductive failure. Although density can influence behaviour, the reduced reproductive failure when there are ample resources is unlikely to be related to increased territorial behaviour as there are less intrusions and squirrels spend less time in the nest when densities are high (Dantzer *et al.* 2012).

It was only when resources were low that ambient temperature affected the occurrence of reproductive failure (Table S1, Supporting information; Fig 4a,d). The response to temperature corresponds to the increased energetic costs of parental investment associated with higher thermoregulatory demands of both parent and offspring when temperatures are reduced (Maxwell & Morton 1975; Zhang & Wang 2007; Rodel, Hudson & Holst 2008; Zhao 2011). However, similarly to other small mammals (Schneider & Wade 1991; Hammond *et al.* 1994; Zhang & Wang 2007), colder temperatures have weaker effects on the occurrence of reproductive failure when resource availability is highest (Fig. 4c,f).

We found also that larger litters had a higher probability of reproductive failure but this relationship disappeared when resources were supplemented with peanut butter. This was consistent with laboratory studies on small mammals where larger litters increase the energetic costs of parental investment (Guerra & Nunes 2001; Rodel, Hudson & Holst 2008; Schubert *et al.* 2009; Paul *et al.* 2010). In some species, when there is not enough energy available to support a large litter, cannibalism, abandonment, or reduced growth rate have been shown to occur (Day & Galef 1977; Perrigo 1987; Schubert *et al.* 2009). Schubert *et al.* (2009) also found that increased access to resources decreases the required foraging time and associated energetic costs. If resources are unlimited, then increased litter sizes to a point will not push the energetic ceiling and larger litter sizes can be sustained (Humphries & Boutin 2000; Schubert *et al.* 2009).

### FITNESS COSTS AND BENEFITS OF PARENTAL INVESTMENT

Similar to other studies that have found an effect of senescence on reproduction (ex. Ericsson *et al.* 2001), we found that reproductive failure was more likely in older females. This contradicts other species that display terminal investment with no increase in failure with old age (ex. Paul, Kuester & Podzuweit 1993). However, we did not find any sign of increased reproductive failure in young females which has been shown in other mammals (ex. seals: Lunn, Boyd & Croxall 1994).

Contrary to our prediction, reproductive failure was most common when a high proportion of juveniles from a cohort will survive to the following year (Table S3, Supporting information). We believe that this pattern may be linked with occurrences of second reproductive attempts (Table 3). If conditions emerge that make the current reproductive attempt energetically costly, it might be advantageous to make the best of a bad situation by abandoning the current investment and attempting a second reproduction, especially if the energetic costs will be improved for the second attempt and there are no diminished fitness returns for doing so. Williams *et al.* (2013) found that red squirrels are more likely to rebreed if the initial breeding date is earlier (Feb–Apr) in the season rather than later (May–July). This could be due to the fact that by experiencing reproductive failure and subsequently rebreeding, a female will likely experience more favourable conditions for raising offspring including increased temperatures and greater access to fresh food (spruce buds, mushrooms and new cones) in addition to capital resources (Fletcher *et al.* 2013).

Alternatively to females abandoning their litters, infanticide by males may occur if there is a high probability that a female will rebreed and the male sired none of the current pups. It has been proposed that infanticide is a potential driver of multimale mating systems (Wolff & MacDonald 2004), like the squirrel system. Males in other mammals and squirrel species are known to commit infanticide (Wolff & MacDonald 2004; Morelli *et al.* 2009). Thus, it is likely that in years of high overwinter survival (Fig 4h,i) when the females are likely to rebreed, that the high probability of reproductive failure may be an outcome of male infanticide. There may also be infanticide by females occurring, an event observed in some rodent species. Such infanticide is predicted to be a means of reducing future competition among juveniles or as a means of increasing nutrition when resources are low (Ebensperger & Blumstein 2007), both of which could be plausible within the squirrel system.

### TRADE-OFFS IN THE TIMING OF BREEDING

In most years, red squirrels begin to produce young in mid to late winter when they have limited resource availability (Fletcher *et al.* 2013) and when temperatures regularly drop below −10 °C, both conditions that we found would increase reproductive failure. If squirrels bred later (late May–June), they would have access to the fresh resources and warmer temperatures that reduce the probability of reproductive failure. However, Williams *et al.* (2013) found that juvenile overwinter survival was dependent on current cone index, maternal age and density-dependent parturition date. They showed that in high density years, those squirrels that successfully breed earliest in a given season gain high fitness benefits with their offspring being most likely to recruit and survive overwinter. This creates a trade-off for the squirrel in the timing of breeding, the outcome of which is year- and density dependent. For any squirrel, breeding early is associated with high benefits through increased probability of recruitment, but the risk of reproductive failure is also high which in some years likely outweighs the benefits. This suggests that dependent on the characteristics of the year (ex. density: Dantzer *et al.* 2013), squirrels must find the right balance in timing of breeding in addition to other life-history traits (ex. female survival; McAdam *et al.* 2007) to increase lifetime fitness. In years following large cone production, when there are large amounts of resources and densities are high, the best strategy would be to breed early (mid-winter) to gain the fitness benefits of having their young first emerged within the population. However, in years following small or no cone production and densities are low, the best strategy would be to delay breeding until late winter so that lactation overlaps with fresh food availability (late May–June; Fletcher *et al.* 2013).

## Conclusions

Our data suggest that nest predation by mustelids is an important cause of reproductive failure in red squirrels. Although we did not measure energetic costs directly, the strong relationship between reproductive failure and environmental and life-history traits over 24 years provides evidence that parental investment and reproductive success is determined by a complex and fine balance between energetic and fitness costs and benefits. For a small mammal, expectation would be to breed when the costs are lowest; however, Williams *et al.* (2013) found that in high density years breeding when energetic costs are high is typically favoured by red squirrels. We show that risk of reproductive failure imposes a limit to how mismatched an individuals' breeding attempt can be from energetically optimal conditions and that the ultimate cost to breeding outside energetic capabilities is reproductive failure. Finally, we found that when juveniles have a high probability of surviving overwinter in a given year, or fitness benefits are high, then reproductive failure early in the breeding season during cold temperatures is high. This suggests that either females are abandoning reproductive attempts or infanticide is occurring to cause the females to recycle back into oestrous.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.** Results of the glmm model of the effects of predator drivers.

**Table S2.** Results of the glmm model of the effects of energetic drivers.

**Table S3.** Results of the glmm model of the effects of fitness drivers.

**Table S4.** Results of the glmm model of the effects of relative energetic and fitnessdrivers.