POPULATION ECOLOGY - ORIGINAL RESEARCH

Reproductive phenology of a food-hoarding mast-seed consumer: resource- and density-dependent benefits of early breeding in red squirrels

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Abstract The production of offspring by vertebrates is often timed to coincide with the annual peak in resource availability. However, capital breeders can extend the energetic benefits of a resource pulse by storing food or fat, thus relaxing the need for synchrony between energy supply and demand. Food-hoarding red squirrels (*Tamiasciurus hudsonicus*) breeding in the boreal forest are reliant on cones from a masting conifer for their nutrition, yet lactation is typically completed before the annual crop of cones is available for consumption such that peaks in energy supply and demand are not synchronized. We investigated the phenological response of red squirrels to annual variation in environmental conditions over a 20-year span and examined how intra- and inter-annual variation in the timing of reproduction affected offspring recruitment. Reproductive phenology was strongly affected by past resource availability with offspring born earlier in years following large cone crops, presumably because this affected the amount of capital available for reproduction. Early breeders had higher offspring survival and were more likely to renest following early litter loss when population density was high, perhaps because late-born offspring are less competitive in obtaining a territory when vacancies are limited. Early breeders were also more likely to renest after successfully weaning their first litter, but renesting predominantly occurred during mast years. Because of their increased propensity to renest and the higher survival rates of their offspring, early breeders contribute more recruits to the population but the advantage of early breeding depends on population density and resource availability.

Keywords Density dependence · Hoarding · Mast seeding · North American red squirrel · Phenology

Communicated by Jörg U. Ganzhorn.

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Introduction

Seasonal variation in the quality and availability of essential resources, such as energy or water, is one of the most important drivers of natural selection on the phasing and duration of reproduction (Baker 1938; Farner 1985; Gwinner 1986). The timing of annually recurring life cycle events is shaped, in large part, by the need to reproduce when conditions are favorable, and in many vertebrates, reproduction is timed such that peak energy supply and demand are synchronized (Lack 1954; Daan et al. 1989). Interest in the seasonal timing of annually recurring life cycle events, including migration, hibernation, and reproduction, is increasing as evidence accumulates that

phenology is advancing in many environments in response to climate change (Inouye et al. 2000; Parmesan and Yohe 2003). Despite widespread interest in climate-driven phenological shifts of migrants (Both and Visser 2001; Durant et al. 2007; Thackeray et al. 2010), less attention has been placed on the drivers of reproductive phenology in resident species and in particular, there has been a paucity of studies on resident mammals.

In temperate regions, physical forcing by changes in light and temperature drive a cycle of primary productivity that commences in spring and declines in autumn. However, the size of the annual peak in resource availability can be extremely variable and consumers have evolved a variety of attributes to buffer themselves from this stochasticity (Boyce 1979; Erikstad et al. 1998; Boutin et al. 2006). Nevertheless, unpredictable variation in resource supply that is superimposed on the predictable annual cycle of resource availability can profoundly affect population density, which, in turn, also alters access to food, particularly in territorial species (Ostfeld and Keesing 2000). To date, studies have principally focused on the capacity of animals to time their reproduction such that peak energetic demands coincide with the seasonal pulse in energy availability (Visser and Both 2005; Post and Forchhammer 2008) and on the demographic consequences of failing to match supply and demand (Miller-Rushing et al. 2010). However, the effects of past resource availability and/or population density on reproductive timing have received less attention (but see Kerby and Post 2013).

Synchrony between energy supply and demand is likely to be particularly important in 'income breeders', where concurrent intake is used to pay for a reproductive attempt (Stephens et al. 2009). However, even in income breeders, the timing of reproduction may not be driven entirely by a need to match peak resource supply and demand as earlier breeding can also provide increased opportunities for reproduction following reproductive failure or success (Crick et al. 1993; Roellig et al. 2010). Furthermore, offspring born earlier may also benefit from increased time for growth and reproduction prior to the onset of winter (Bieber et al. 2012), particularly in systems where juveniles compete to recruit into the population. Because the survival and recruitment of offspring is often density dependent, the benefits of early breeding might also vary with population density. Perhaps most importantly, the capacity of many resident species to fuel reproduction using stored resources (i.e. 'capital breeders'), either in the form of endogenous stores or cached food, can potentially extend the energetic benefits of a resource pulse, thus lessening the need for synchrony between supply and demand (Jönsson 1997). Although capital breeders likely have less need to synchronize the peak demands of reproduction with the seasonal pulse in resource availability, they may be more susceptible to carry-over effects from the size or quality of past resource pulses as reproductive success is often correlated with stored capital (Harrison et al. 2011). For example, Kerby and Post (2013) found that while the reproductive performance of income breeding caribou (*Rangifer tarandus*) decreased with phenological mismatch between consumers and resources, capital breeding muskoxen (*Ovibos moschatus*) were relatively unaffected by current breeding season resource variability, yet were sensitive to resource conditions from previous years. However, other studies suggest that capital breeders can be sensitive to conditions during the onset of breeding and reproductive phenology is not necessarily solely, or even primarily, dictated by past resource availability (Lehikoinen et al. 2011).

Here, we investigate the factors that influence reproductive phenology of North American red squirrels (*Tamiasciurus hudsonicus*) during a 20-year span (1991–2010) in the southwest Yukon, Canada. We then examine how intra- and inter-annual variation in the timing of reproduction corresponded with the production and survival of offspring. Because their reproduction is typically complete before the current year's cone crop matures and is available for consumption, reproductive timing in red squirrels might provide insight into factors other than synchrony between energy supply and demand that influence reproductive phenology in temperate vertebrates. We predicted that breeding earlier would provide increased opportunities for reproduction following litter loss or after successfully weaning the first litter. As a food-hoarder that relies on a highly variable pulsed resource, seed masting of white spruce (*Picea glauca*), red squirrels represent a useful organism for examining the factors that influence reproductive phenology in capital breeders. Red squirrels in the boreal forest are reliant on masting conifers for most of their nutrition (Boutin et al. 2006; Fletcher et al. 2013), and variation in food abundance has profound effects on population density and competition (S. Boutin et al., unpublished data). Thus, our long-term dataset provides a means of assessing how intra-specific variation in phenology affects reproductive output under varying environmental and demographic conditions.

Earlier work in this population indicated selection for earlier breeding, driven by higher survival rates of offspring born earlier in the season (Réale et al. 2003; McAdam and Boutin 2003). However, because differential survival may be the result of competition for limited territories, we expected the benefits of early breeding to vary with population density and food availability which should both affect the strength of competition. We hypothesized that date of birth would produce competitive disparities among individuals and predicted juveniles born earlier in the year would

be more likely to recruit than juveniles born later when population density is high and territorial vacancies are limited. However, red squirrels are also capable of anticipating resource pulses and increasing reproductive output by renesting after successfully weaning their first litter (Boutin et al. 2006). Thus, we also examine whether the propensity to renest following weaning and/or after reproductive failure is affected by episodic fluctuations in cone availability and determine the demographic implications of renesting behaviour across a 20-year interval that includes four masting events.

Materials and methods

Study area and species

We studied a wild population of red squirrels near Kluane National Park (61°N, 138°W) in the southwest Yukon, Canada. The landscape has a canopy dominated by white spruce (*Picea glauca*) and a willow (*Salix* spp.) understory. During the 20-year span of the present study, the intermittent production of large cone crops by white spruce (i.e. masting) has occurred in 4 years (1993, 1998, 2005, and 2010) within the Kluane region (Krebs et al. 2012). White spruce seeds are an important food source for red squirrels at our study site (Fletcher et al. 2013); squirrels clip new spruce cones containing seeds each autumn and cache them in a larder hoard (midden) (Smith 1968; Fletcher et al. 2010). These middens form the centre of individual territories [0.2–0.5 ha] (LaMontagne et al. 2013), which are defended throughout the year (Smith 1968; Price et al. 1990). Females typically produce a single litter (mean = 3.0 pups/litter) each year following a 35-day gestation period, but will attempt a second litter after litter loss (McAdam et al. 2007) and, less frequently, following a successful litter (Boutin et al. 2006). Females appear to re-enter estrus immediately following loss of the first litter although females that attempt a second litter following a successful litter are still lactating when they conceive the second litter (Boutin et al. 2006). The environmental and endogenous factors that determine whether a female will initiate a second litter remain unclear. Juveniles emerge from the nest at age ca. 35 days and are weaned at ca. 70 days. Although most females (~74 %) do not survive to 1 year of age, those that do have a life expectancy of 3.5 years and a maximum life span of 8 years (McAdam et al. 2007).

Population monitoring

Since 1991, we have used complete enumeration to track population density, survival, reproductive output and phenology of red squirrels on two ~40-ha study grids (see details in Boutin et al. 2006; McAdam et al. 2007). All squirrels were marked with alphanumeric ear tags and given a unique colour combination of wires for visual identification. We monitored the reproductive status of every female each year and all offspring born in the population were enumerated, sexed, and ear-notched within days of birth. We subsequently ear-tagged juveniles at ca. 25 days of age, prior to first emergence from the nest. Date of parturition was estimated using a mass vs. age regression derived from known-age nestlings (S. Boutin, M. M. Humphries and A. G. McAdam, unpublished data). In cases where litters were lost prior to accessing the nest, typically within a few days of parturition, date of birth was estimated as the midpoint between the last day a female was caught pregnant and first day she was found to be lactating. We only used data from litters that were lost prior to accessing the nest when our estimated date of parturition had a minimum accuracy of 5 days [mean minimum accuracy 2.7 ± 1.4 (SD) days]. Annual population density for each grid was determined based on the number of squirrels that occupied territories within a 2-week interval each spring in May based on trapping data and behavioural observations (territorial rattle calls) of colour-marked individuals. Low mean natal dispersal distances in this population (96 m; Berteaux and Boutin 2000), combined with the poor quality of habitat surrounding the grids results in low rates of immigration onto or emigration from the study grids (McAdam et al. 2007).

Environmental conditions

We used weather data collected at Environment Canada's Burwash weather station, located 50 km from the study site (http://climate.weatheroffice.gc.ca). Due to extensive missing temperature records during the evening and nights, we used the mean daily temperature between 7 a.m. and 2 p.m. in our analyses; mean daily temperature between 7 a.m. and 2 p.m. is highly correlated ($r = 0.96$) with mean daily temperature across the entire day for the 7 years where complete data are available. We used the average ambient temperature (hereafter 'spring temperature') during February and March (the time period leading up to mating) in our analyses. We estimated the abundance of cones available each year on each study grid by counting the number of cones visible in the top 3 m of the crown for between 81 and 168 trees per grid each August. We used this index of cone abundance (log transformed) in our data analyses (see below), but also report the estimated total number of cones per tree, which was scaled up from the number of counted cones using an equation partially derived from our study site (LaMontagne et al. 2005).

Data analysis

Statistical analyses were performed using SAS 9.3 (SAS Institute, Cary, NC). For each variable of interest, we used a multimodel inference approach to explore a suite of candidate models and selected among models using Akaike's information criterion (Akaike 1973). A complete rationale for this approach is provided by Burnham and Anderson (2002). For each set of candidate models, we calculated the Akaike weights (W_i) for each model, which indicates the approximate probabilities that model i is the best model in the set of models considered; the relative likelihood that model i is better than model j is W_i/W_j (Burnham and Anderson 2002). Our indices of spruce cone production, population density, and date of parturition were right skewed therefore we log transformed these values prior to analysis; for our index of cone production, we $\ln(x + 1)$-transformed cones counted per tree prior to averaging within a grid or year. The index of cone abundance in the previous year was highly correlated with spring population density (Pearson correlation coefficient $r = 0.69$) and we therefore never include both parameters in the same model. Current and previous year's index of cone production were not correlated ($r = -0.06$; $p = 0.68$). Date of parturition was standardized within each year when used as an independent variable. We used the maximum likelihood method for linear mixed models (LMMs) and employed a Laplace approximation for generalized LMMs (GLMMs).

We used LMMs with year and identity of the mother included as random effects (random intercepts) to investigate the factors that affect date of parturition in first litters. Fixed effects at the annual level included previous and current year's cone indices, population density, and spring ambient temperature (as a single mean value). We also included quadratic effects of maternal age as reproductive output and offspring quality in red squirrels is known to be lower in young and old females (McAdam et al. 2007; Descamps et al. 2008). We ran all combinations of fixed effects with the exception of never including population density and previous year cone index in the same model. We did not include female body mass as a fixed effect in our models because some early breeding females were pregnant when they were first caught and females gain mass during pregnancy. We explore how much of the variation in date of parturition attributed to the random year effect can be explained by our fixed effects using the pseudo r^2 method of Raudenbush and Bryk (2002).

We used GLMMs with a logit link and binomial distribution to investigate the factors influencing the probability that a female would have a second litter when her first litter was lost early in lactation (before the second nest check at 25 days post-parturition) or after successfully weaning her first litter. First nests that were lost within 25 days of parturition due to death/disappearance of the mother were excluded from analysis. Year and identity of the mother were included as random effects. We ran all combinations of the following fixed effects: current year cone index, population density, date of parturition, and age of mother (MA). We also ran models with interactions between current year's cone abundance index and date of parturition, and between density and date of parturition.

We used GLMMs to investigate the factors affecting the likelihood that a juvenile born in the first litter would survive and recruit into the population the following spring (i.e. be detected in the population in the year following birth). We included year and litter identification as random effects and litter size as a fixed effect in all models. Other fixed effects included current year's cone index, population density, date of parturition, sex, age of the juvenile (in days) at first nest check and a quadratic effect of maternal age. We then repeated this analysis for juveniles born in renesting attempts except maternal age was included as a linear parameter, rather than a quadratic, based on our initial examination of model fit.

Finally, we used GLMMs with a Poisson distribution and log link to examine what parameters influence the total number of recruits produced per reproductive female each year. We included year and maternal identity as random effects and litter size as a fixed effect in all models. Other fixed effects included current year's index of cone abundance, population density, date of parturition and a quadratic effect of maternal age. We also included interactions between population density and date of parturition, and between current year's cone abundance index and parturition.

Results

Cone abundance and reproduction

Cone abundance varied more than 2 orders of magnitude during the course of this study (Fig. 1). The mean number of cones produced per tree across both grids during the 4 mast years was 988 (range of annual means, 595–1,368) whereas mean cone production per tree during non-mast years was an order of magnitude lower (mean, 97; range of annual means, 3–390 cones/tree). From 1991 to 2010, five hundred and thirty females gave birth to 3,421 squirrels in 1,122 first litters; on 194 occasions, females gave birth to a second litter after weaning their first litter ($n = 40$ occasions) or following litter loss prior to weaning ($n = 154$ occasions). During the 20 years of study, 878 juveniles successfully recruited into the population. Across all years, 20 % of recruits originated from secondary litters (i.e. renests); 36 % of recruits in mast years were from renests
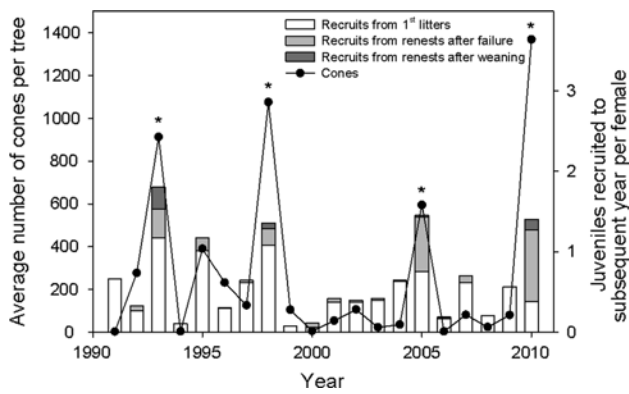
Fig. 1 Average number of white spruce cones produced per tree across two study grids in the southwest Yukon and number of juveniles per reproductive female red squirrel that successfully recruited to the population in the subsequent year. Recruits from renesting events accounted for 36 % of total recruits from mast years (*asterisks*) and 8 % of recruits from non-mast years (20 % across all years)

Fig. 2 Mean (±SE) annual date of parturition for North American red squirrels versus grid-wide average index of white spruce cone abundance in the prior year in the southwest Yukon, Canada. Data and regression line shown here does not control for age effects

Table 1 Summary of the 90 % confidence set [cumulative Akaike weights (W_i) = 0.90] of linear mixed models (LMMs) that best explain date of parturition in red squirrels at our study site from 1991 to 2010

Model	ΔAIC_c	W_i	Evidence ratio
β_0, PC, MA, MA^2	0	0.45	–
β_0, PC, C, MA, MA^2	1.4	0.22	2.0
β_0, PC, T, MA, MA^2	1.4	0.22	2.0

All models included year and maternal identity (ID) as random effects. Fixed effects included previous year's index of cone abundance (*PC*), current year's index of cone abundance (*C*), population density (*D*), spring temperature (*T*), and a quadratic effect of maternal age (*MA*)

AIC_c Corrected Akaike information criterion

whereas only 8 % of recruits in non-mast years were from renests (Fig. 1).

Environmental effects on reproductive phenology

On average, females gave birth to their first litter on 3 May (mean of annual averages), although mean parturition date varied widely between years (range of annual means, 2 April–6 June). The 90 % confidence set of models for date of first litter parturition was made up of three models (Table 1). The most parsimonious model indicated females give birth earlier following a year with a high cone index (Fig. 2) and timing of parturition was affected by maternal age with yearlings and older females (>4 years old) breeding later than prime-age females (2–4 years). Pseudo r^2-values indicated that the top model accounted for ~52 % of the annual variation in date of parturition (i.e. 52 % of the variation acc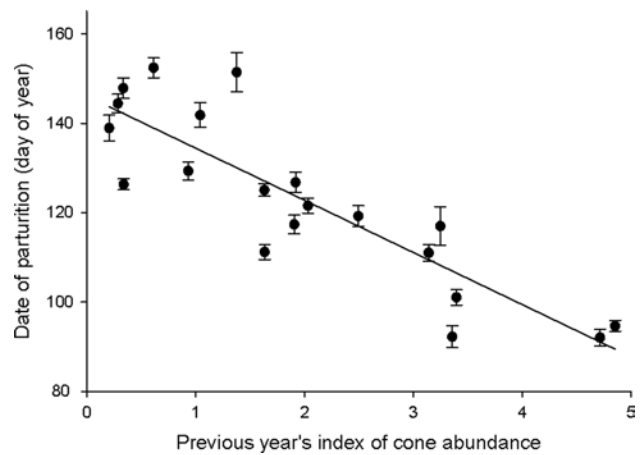ounted for by the random year effect in the null model), 25 % of the variation at the level of mother identification and 9 % of the residual variance. Based on evidence ratios, this model had twice as much empirical support as either a model that also included an effect of current year's cone index or a model that included an effect of spring temperature. Model-averaged parameter estimates and their 95 % confidence intervals are shown in Table A1.

Probability of renesting

Over the 20 years of study, females gave birth to a second litter on 52 % of occasions after their first litter was lost within 25 days of giving birth (110 of 217 litters); an additional 44 females gave birth to a second litter after losing their first litter during late lactation (i.e. when their pups were >25 days old but had not yet weaned). Overall, 76 % (53 of 70) of females that lost their litters in the first 25 days post-parturition renested during mast years, whereas only 39 % (59 of 147) renested during mast non-years. The 90 % confidence set of models for renesting after early litter loss was made up of four models (Table 2). The most parsimonious model had 45 % of model weight and included a positive effect of current year's cone abundance index [estimate, 0.57; 95 % confidence interval (0.32, 0.82)], a quadratic effect of MA with lower likelihood of renesting in the youngest and oldest females [MA^2, −0.18 (−0.32, −0.05); MA, 1.39 (0.39, 2.38); Fig. 3], and an interaction between population density and date of parturition [density, −1.31 (−2.33, −0.29); date of parturition, 0.33 (−0.58, 1.25); interaction, −1.38 (−2.63, −0.13)]. The likelihood of renesting decreased with increasing population density, but the rate of decline was higher for females that gave birth later (Fig. 4). The weight of evidence for this model was

Table 2 Summary of the 90 % confidence set (cumulative $W_i = 0.90$) of GLMMs that best explain the likelihood of renesting after loss of the first litter within 25 days of parturition

Model	ΔAIC_c	W_i	Evidence ratio
β_0, C, MA, MA^2, D, DP, $D \times DP$	0	0.45	–
β_0, C, MA, MA^2, D, DP	1.0	0.28	1.6
β_0, C, MA, MA^2, D, DP, $C \times DP$	3.1	0.10	4.7
β_0, C, D, DP, $D \times DP$	3.5	0.08	5.7

All models included year and maternal ID as random effects. Fixed effects included current year's C, D, DP (measured as day of year), a quadratic effect of MA, and interactions between D and DP ($D \times DP$) as well as C and DP ($C \times DP$). For other abbreviations, see Table 1
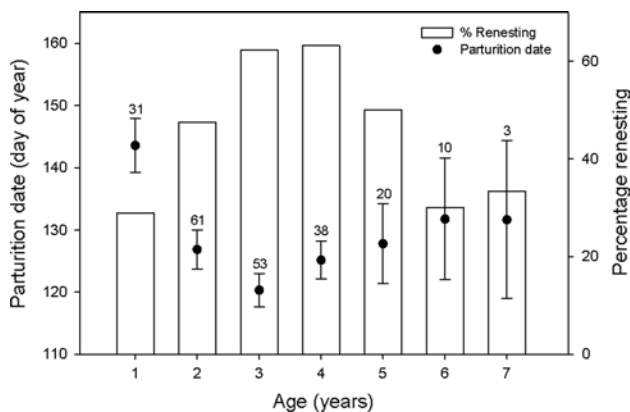

Fig. 3 Age-specific variation in the date females red squirrels gave birth (±SE) to first litters for females that lost their litters within the first 25 days of lactation and the percentage of these females that subsequently renested. Yearlings and older females gave birth later and were less likely to renest. In addition, individuals that gave birth later were less likely to renest independent of age effects (see Table 2). Values in this figure are not corrected for food and year effects

Fig. 4 A graphical representation of the predicted relationship between date of first litter parturition (standardized within each year), population density (log-transformed squirrels/ha), and the likelihood of renesting after litter loss based on our most parsimonious model. Current year's cone abundance index was held at the 20-year average and maternal age was held at 3 years to create the plot. Early nesting females are much more likely to renest when population density is high, but this difference decreases as population density decreases. The axis for population density is reversed (from high to low) to allow for easier visualization of the three-dimensional figure

1.6 times that of a simpler model that did not include any interactions, but had a negative effect of population density [−0.85 (−1.66, −0.04)] and a negative effect of date of parturition [−0.63 (−1.01, −0.25)] indicating females that gave birth later were less likely to renest. Age affected parturition date which, in turn, affects the probability of renesting. However, parturition date also affected the probability of renesting within age groups.

Renesting after successfully weaning (i.e. where young survived to at least age 70 days) was less common compared to renesting after early litter loss with renesting occurring after 5 % of first litters were weaned (40 of 750 first litters) during the 20-year span of this study. Renesting after successful weaning occurred during only 1 of 16 non-mast years (five females renested after weaning in 2006,
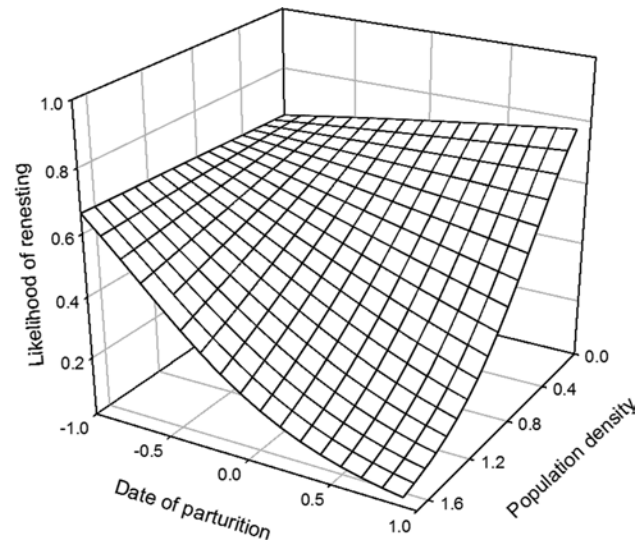
the year following a weak masting event); across all non-mast years, these five renesting events represented <1 % of all successfully weaned first litters (five of 617). In contrast, renesting after weaning the first litter occurred during all 4 mast years, although only one female (of 28) renested after weaning in 2005, the weakest of the four mast years. Across all four mast years, females renested after 35 of 133 (26 %) successfully weaned first litters. The 90 % confidence set of models for renesting after weaning was made up of four models (Table 3). The most parsimonious model had 52 % of model weight and indicated the likelihood of renesting increased with MA [estimate, 0.61 (0.19, 1.02)] and was affected by an interaction between the current year's cone abundance index and date of parturition [cones, 1.69 (0.43, 2.95); date, −1.03 (−2.44, 0.39); interaction, −0.49 (−0.98, −0.01)]. Individuals that nested earlier were more likely to renest, but this renesting only occurred during mast years, when cone abundance was high (Fig. 5). Based on evidence ratios, the most parsimonious model had 2.8 times more support than a model that also included a negative effect of population density [−0.76 (−4.78, 4.66)] and 3.1 times more support than a model that included a positive effect of cones [2.03 (0.86, 3.20)] and a negative effect of date of parturition [−2.28 (−3.33, −1.23)], but no interaction between the two.

Table 3 Summary of the 90 % confidence set (cumulative $W_i = 0.90$) of GLMMs that best explain the likelihood of renesting after weaning the first litter

Model	ΔAIC_c	W_i	Evidence ratio
β_0, C, MA, DP, C × DP	0	0.53	–
β_0, C, D, MA, DP, C × DP	2.0	0.19	2.8
β_0, C, MA, DP	2.3	0.17	3.1
β_0, C, D, MA, DP	4.1	0.07	7.9

All models included year and maternal ID as random effects. Fixed effects included current year's C, D, DP (measured as day of year), MA, and D × DP as well as C × DP. For abbreviations, see Tables 1 and 2
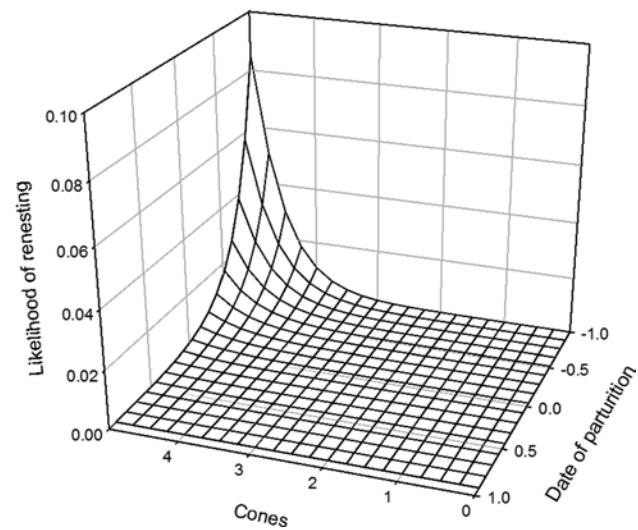

Fig. 5 A graphical representation of the relationship between the current year's index of cone abundance, the date of first litter parturition, and the likelihood of renesting after successfully weaning the first litter based on the most parsimonious model. Only the earliest breeding females renest in years of high cone abundance

Table 4 Summary of the 90 % confidence set (cumulative $W_i = 0.90$) of GLMMs that best explain the likelihood a juvenile, born in the first litter, would survive from the time a nest was first checked within a few days of birth to the subsequent spring

Model	ΔAIC_c	W_i	Evidence ratio
β_0, FC, LS, D, C, MA, DP, Sex, D × DP	0	0.67	–
β_0, FC, LS, D, MA, DP, Sex, D × DP	1.4	0.24	2.0

All models included year and litter ID as random effects and age of juvenile at first check (FC) and litter size (LS) as a fixed effect. Other fixed effects included sex of juvenile (Sex), current year's C, D, DP (measured as day of year), MA, and D × DP as well as C × DP. For other abbreviations, see Tables 1 and 2

were more likely to survive at high population density but the advantage of early birth was not present at low population density. This model had 2.7 times more support than a model that did not include an effect of current year's cone abundance index. Effects of birth date and its interaction with population density were evident within age groups (data not shown).

Modelling results for overwinter survival of juveniles born in second litters was generally similar with higher levels of model uncertainty; the five models that make up the 90 % confidence set are shown in Table A2. The top model had 54 % of model weight and indicated survival of individuals born in second litters increased with increasing cone abundance [estimate, 0.25 (0.05, 0.44)], was higher in females [0.83 (0.38, 1.29)], and was affected by an interaction between population density and date of birth [density, −0.58 (−1.39, 0.24); date, 0.63 (0.04, 1.22); interaction, −1.15 (−1.88, −0.42)].

Female reproductive output

The number of juveniles per reproductive female that successfully recruited into the population in the year of a masting event (average of annual means, 1.8; range of means, 1.4–2.1 recruits/female) was three times higher than during low-cone years (non-masting mean, 0.6; range, 0.1–1.3 recruits/female) and the proportion of juvenile recruits that originated from secondary litters (renesting events) was higher during mast (mean proportion, 0.43; range, 0.21–0.73), compared to non-mast years (mean, 0.09; range, 0–0.47; Fig. 1).

The 90 % confidence set of models for the annual number of recruits produced per female comprised five models and is shown in Table 5. The top model had 45 % of model weight and included a positive effect of litter size [0.19 (0.11, 0.27)], a positive effect of current year cone abundance [0.16 (0.04, 0.28)], a quadratic effect of MA with the youngest and oldest females producing fewer recruits

Juvenile survival

The 90 % confidence set of models for the likelihood that a juvenile, born in the first nesting attempt, would survive overwinter comprised just two models and is shown in Table 4. The top model had 67 % of model weight and included a positive effect of current year's cone abundance index [0.22 (0.01, 0.43)], a sex effect with higher survival in females [0.76 (0.53, 0.99)], a negative effect of MA [−0.15 (−0.25, −0.04)], a negative effect of litter size [−0.17 (−0.34, 0.00)] and an interaction between birth date and population density [density, −0.92 (−1.81, −0.04); date, 0.45 (0.12, 0.78); interaction, −0.64 (−1.01, −0.27)]. This top model indicated the likelihood that a juvenile would survive to spring increased with decreasing population density and juveniles that were born earlier

Table 5 Summary of the 90 % confidence set (cumulative $W_i = 0.90$) of GLMMs that best explain the annual number of recruits (offspring that survived until the subsequent spring) produced by female red squirrels

Model	ΔAIC_c	W_i	Evidence ratio
β_0, LS, D, C, MA, MA^2, DP, $D \times$ DP	0	0.45	–
β_0, LS, D, C, MA, MA^2, DP	1.8	0.18	2.5
β_0, LS, D, C, MA, MA^2	2.2	0.15	3.0
β_0, LS, C, MA, MA^2, DP	3.5	0.08	5.8
β_0, LS, D, MA, MA^2, DP, $D \times$ DP	4.6	0.04	10.0

All models included year and maternal ID as random effects and LS as a fixed effect. Additional fixed effects included current year's C, D, DP (measured as day of year), a quadratic effect of MA, and $D \times$ DP as well as $C \times$ DP. For abbreviations, see Tables 1, 2 and 4

[MA^2, −0.04 (−0.07, −0.01); MA, 0.22 (0.00, 0.44)], and a negative interaction between date of parturition and population density [density, −0.60 (−1.00, −0.20); date, 0.08 (−0.08, 0.23); interaction, −0.18 (−0.36, −0.00)] such that the advantage of early breeding increases as population density increases (Fig. 6). The evidence for the top model was 2.5 times stronger than for a model that did not include an interaction effect and three times stronger than a model that did not include an effect of date of parturition or an interaction effect (Table 5).

Discussion

Whereas studies of income breeding temperate species revealed that reproductive timing is often responsive to spring conditions (food and/or weather) on the breeding ground (Eeva et al. 2000; Williams et al. 2013), we found that phenology in food-hoarding red squirrels was primarily dictated by the abundance of food produced during the prior year. We also found that earlier breeders had higher reproductive success, consistent with previous studies of capital and income breeders (Perrins 1970; Price et al. 1988; Rohwer and Eisenhauer 1989). Two distinct mechanisms were responsible for the higher reproductive output of earlier breeders: increased offspring survival (also reported by McAdam and Boutin 2003) and an increased propensity for early breeders to renest. However, higher survival of early born juveniles and the increased likelihood for early breeders to renest following litter loss only occurred when population density was high. In contrast, renesting after weaning the first litter occurred only in the earliest breeding females and primarily in years with a high index of cone abundance (i.e. mast years). Although the youngest and oldest females bred later than prime-age individuals, age effects alone could not explain the discrepancy in reproductive performance associated with breeding phenology.
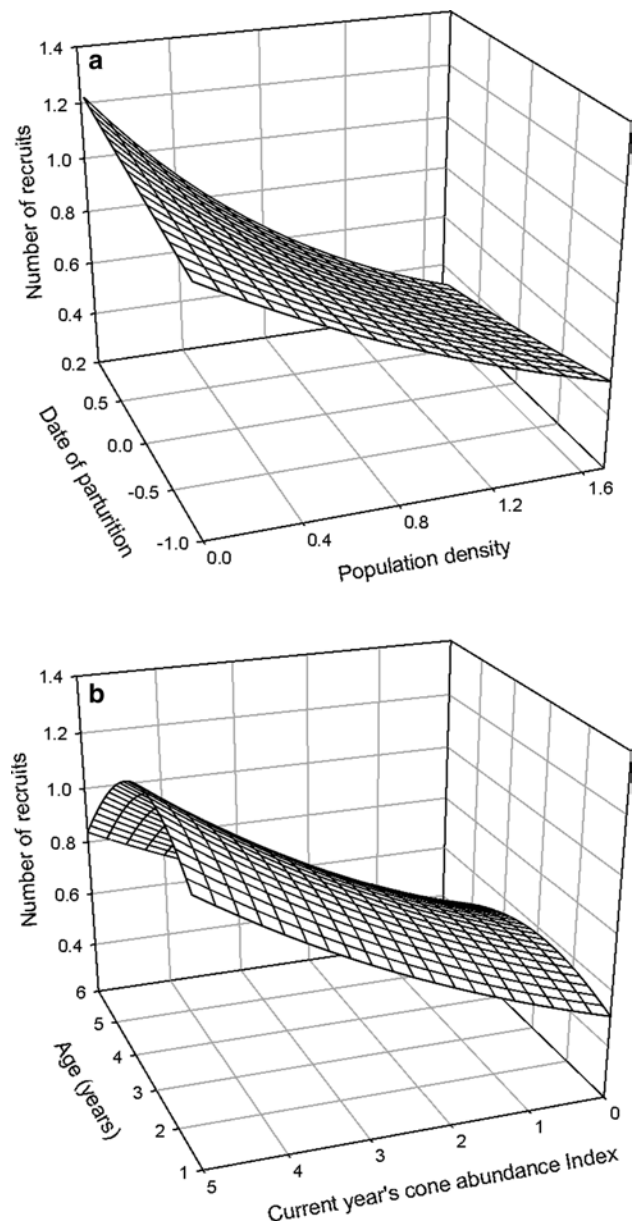

Fig. 6 A graphical representation of the relationship between **a** date of first litter parturition, population density, and the annual number of recruits (juveniles produced that survived to the subsequent spring) per reproductive female, and **b** age of the mother, current year's cone abundance index, and the annual number of recruits. **a** Current year's cone abundance index was held at the 20-year average and maternal age was held at 3 years, **b** population density held at the 20-year average and date of parturition at the standardized annual average (i.e. zero). Early breeding squirrels produce more recruits when population density is high but this advantage disappears when population density is low

Reproductive phenology in capital and income breeders

Although timing in some species can be altered due to carry-over effects from earlier life history stages, reproductive phenology in income breeding species is generally

tightly coupled to food availability when breeding is initiated (Eeva et al. 2000; Shultz et al. 2009; Williams et al. 2013). Capital breeders, in contrast, are generally thought to be buffered from conditions during the initiation of reproduction, because they can mobilize energy from either stored lipid reserves or food caches (Harrison et al. 2011). However, phenological shifts in response to ambient temperature, independent of shifts in prey availability, were previously observed in owls, with capital breeding species exhibiting greater delays in response to colder conditions (Lehikoinen et al. 2011). Because red squirrels conserve energy during the winter by drastically reducing their activity levels (Humphries et al. 2005; Fletcher et al. 2012), we anticipated they might extend their low activity phase and delay reproduction in response to colder conditions. In addition, earlier work in this study population indicated that squirrels advanced their breeding during a decade of increasing spring temperatures and increasing cone supply (Réale et al. 2003). Our current analyses, however, which are based on a dataset that is 10 years longer and explicitly examines the importance of temperature and cone supply, indicate that food availability, and not ambient temperature in spring, is the primary environmental driver of breeding phenology. Although we did not measure the size of food hoards directly, we presume that increased capital available to fuel reproduction is affecting the timing of reproduction. This presumption is supported by the finding that breeding is advanced in food supplemented squirrels (Kerr et al. 2007).

A mismatch between the timing of food availability and the peak energy demands of consumers can potentially disrupt trophodynamics resulting in depressed consumer reproduction (Visser and Both 2005; Post and Forchhammer 2008). Our results, however, indicate that capital breeding red squirrels are likely to be less responsive to spring conditions, because hoarded cones eliminate, or greatly reduce, the need for synchrony between energy supply and demand. Whether uncoupling of phenology from spring conditions is broadly applicable to capital breeders is not clear however (e.g. Lehikoinen et al. 2011; Moyes et al. 2011) and is complicated by the reality that most species do not rely exclusively on either capital or income to fuel reproduction. For example, Verreaux's sifaka (*Propithecus verreauxi*) rely on endogenous stores to fuel much of gestation and early lactation but time their reproduction such that peak energy demand during mid-lactation is synchronized with a seasonal increase in food availability, when they switch to reliance on income (Richard et al. 2000, 2002; Lewis and Kappeler 2005). Although red squirrels are generally characterized as capital breeders, Fletcher et al. (2013) recently showed that while early breeders at our study site are reliant on hoarded resources during lactation, late breeders tend to increase their consumption of 'income' by mid-lactation.

The assumption that migratory breeders attempt to match energy supply and demand also does not appear to always hold true. Dunn et al. (2011) found that timing of reproduction in an insectivorous songbird was dictated primarily by prey abundance during the initiation of reproduction rather than by timing of the seasonal peak in prey availability. Both income and capital breeders can also benefit from the increased time available for secondary nesting attempts and for growth and development of offspring that is afforded by breeding earlier. For example, by swapping clutches between early and late laying great tits (*Parus major*), Verboven and Verhulst (1996) demonstrated that advancing timing increases the likelihood of initiating a second clutch, independent of quality effects. Husby et al. (2009) further showed that great tits in the Netherlands have decreased their propensity to renest because the seasonal peak in food availability is earlier. Although this is also an example of mismatching, it does not necessarily involve a lack of synchrony between the peak in energy demand and the peak in food availability. In polyestrous seasonal breeding mammals, breeding earlier and/or reducing the length of the reproductive cycle can increase reproductive output (Roellig et al. 2010). In the common dormouse (*Muscardinus avellanarius*), for example, giving birth earlier in years of high food availability (mast years) can be advantageous because early born young can breed before the onset of winter hibernation (Bieber et al. 2012). Clearly, the proximate and ultimate drivers of reproductive phenology are rather complex and, as such, inter-specific variation in responses to climate change may not always reflect maladaptation or mismatching due to interspecific variation in the selective forces that determine phenology.

Resource- and density-dependent benefits of early reproduction

We found that offspring born earlier were at a greater advantage when population density was high, possibly because increased time for growth and development provides an advantage when competing for limited territorial vacancies. Dantzer et al. (2013) also demonstrated that females will increase investment in offspring in response to actual or perceived increases in population density; perceived density was increased using audio playbacks of red squirrel rattles. We found that females gave birth earliest in the years following a masting event, which also corresponded with the highest population densities and the lowest levels of recruitment per reproductive female (Fig. 1). Thus, early breeding in the year following a mast provides an advantage to females when juvenile competition for limited territories is highest. Density-dependent benefits of early breeding

appear to be important in other systems as well. Aloha et al. (2012) recently found that selection for earlier breeding in the pied flycatcher (*Ficedula hypoleuca*) only occurs when population density is high and there is increasing evidence for density-dependent natural selection in a variety of traits (Coltman et al. 1999). Thus, one should be careful when interpreting measures of directional selection on short time-scales, particularly in species subject to sporadic resource pulses and/or episodic population outbreaks.

That squirrels bred later when cone production in the preceding year was lower suggests that they are unable to breed as early when stored capital is lower or that delayed breeding is adaptive under these circumstances. This is likely partially explained by the fact that breeding earlier than conspecifics provides greater benefits when population density is high. However, there may also be costs to early breeding that drive the pattern of breeding later when hoarded food is reduced. One possibility is that gestation and/or lactation is more energetically costly when temperatures are lower because squirrels would face greater thermoregulatory costs with the increase in activity needed to meet energetic demands of reproduction (but see Fletcher et al. 2012). Alternatively, short intervals of bad weather may put offspring at greater risk when nesting earlier (Studd 2012). Additionally, squirrels may be delaying nesting when their food hoard is reduced so that they can utilize income, such as fresh mushrooms, to fuel some of the energetic demands of lactation (Fletcher et al. 2013). Even if squirrels have sufficient energy within their hoarded cone cache to fuel reproduction, increased use of non-hoarded items may allow them to preserve their cache to meet energetic demands during the subsequent winter.

Our models on the propensity to renest after successful weaning indicated that this predominantly occurs when the current year's index of cone abundance is high. This phenomenon was first reported by Boutin et al. (2006), who showed that American and Eurasian tree squirrels are capable of anticipating this future pulse in resource availability, as cones are not yet mature and available for consumption during the interval in which squirrels were impregnated with their second litter. Our current analyses also indicate that early breeders are more likely to renest after weaning, presumably because they have more time and/or resources to initiate a second litter. Interestingly, older females are more likely to renest after weaning during these masting events, when recruitment success is high, but typically nest later and are less likely to renest after litter loss in non-mast years.

Conclusion

Reproductive phenology in capital breeding red squirrels is advanced when the abundance of cones produced in the prior year is high. Being born earlier appears to be advantageous under high density conditions, presumably because increased time for growth and development increases competitive ability for limited territorial vacancies. The propensity to renest is also higher for females that give birth earlier and was dependent on environmental and demographic conditions, with a higher likelihood of renesting after early litter loss under high-density conditions and a higher likelihood of renesting after weaning the first litter during mast years. We suggest that the need for synchrony between energy supply and demand (i.e. reproduction) is likely to be relaxed in many food-hoarding species and postulate that their phenological response to climate change is likely to differ from that of income breeders.

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