ORIGINAL ARTICLE

Sex-specific effects of capital resources on reproductive timing and success in red squirrels

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Abstract

Reproduction is an energetically expensive activity for both sexes. However, if males and females differ in their annual timing of reproduction, such that peak investment for one sex occurs during a more resource-limited period, there is an opportunity for sex-specific selection to act on the acquisition of energetic resources. Both male and female North American red squirrels (*Tamiasciurus hudsonicus*) cache conifer cones, although males typically have larger caches than females. Peak energetic investment in reproduction occurs for males during the mating season in winter and early spring (when squirrels rely almost exclusively on cached resources) and for females during lactation (which can align with fresh food availability). We provide evidence that suggests sex differences in cache size are likely driven by a stronger positive connection between cached resources and components of fitness for males than for females. Specifically, males with larger caches have greater siring success than males with smaller caches, whereas for females, only early breeding females experience a positive effect of cache size on the number of recruits produced. We also show that males sire pups and females give birth earlier in the year if they have larger caches compared with squirrels of the same sex with smaller caches. Sexual selection can thus extend beyond traits directly connected to mating behavior, and can act on traits related to acquiring resources needed to fuel reproduction that are expressed months or years in advance of breeding efforts.

Significance statement

The timing and energetic requirements of reproduction are often different for males and females which could drive different life history strategies between the sexes. Red squirrels in the southwest Yukon, Canada cache white spruce cones in autumn, which serve as their primary food source until fresh food becomes available during summer. We measured the size of squirrel caches and subsequently monitored their reproduction to test whether the influence of stored food differs for males and females. We confirmed that males have larger caches than females and show that this is likely driven by a stronger positive association of cache size and components of fitness for males than for females. These findings highlight that the strength of selection can differ on the homologous traits of males and females leading to sex-specific extended phenotypes.

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Introduction

A foundational concept in life history theory is that investment in reproduction is constrained by limited resources (Cody 1966; Roff 1992; Stearns 1992; Brown et al. 2004). Indeed, empirical studies have shown that females across a variety of taxa produce more or larger offspring when they have access to a greater amount of resources (Boutin 1990; Reznick et al. 1996; Podofillini et al. 2019; Chevallier et al. 2020). Although the connection between energy acquisition and allocation to reproduction is more often documented

for females, limited energy should similarly constrain male reproductive investment. For example, male smallmouth bass (*Micropterus dolomieu*) and Palestine sunbirds (*Nectarinia osea*) increase parental care when their own access to food is greater (duration in bass, Ridgway and Shuter 1994; increased food delivery in sunbirds, Markman 2014). In systems without male parental care, secondary sexual characteristics that enhance breeding likelihood such as weapons or ornaments are often condition dependent (Hill 1990; Holzer 2003; Körner et al 2017) which suggests that resource acquisition could influence a male's fitness through his ability to develop a phenotype that can secure more reproductive opportunities. Thus, male reproductive investment should also be sensitive to resource levels (Key and Ross 1999).

Because the timing and energetic requirements of peak reproductive investment differ for males and females in most animal systems (Hau et al. 2017), the fitness consequences of resource acquisition are likely to be sex specific. For example, in species without male provisioning, males likely allocate the greatest energetic investment to reproduction when searching or competing for mating opportunities, whereas females should maximize their allocation to reproduction later when they are fueling the development of offspring through parental care and/or provisioning (Oftedal 1985; Kenagy et al. 1989; Naya et al. 2008; Lane et al. 2009).

Within each sex, the timing of reproduction and energetic investment therein can be influenced by environmental food availability, and often has consequences for offspring success. Specifically, organisms that receive experimental food supplementation (reviewed by Boutin 1990) or experience earlier or greater food availability tend to breed earlier (Hindell et al. 2012; Schroeder et al. 2012; but see Post and Forchhammer 2008). Young that are produced earlier within a breeding season have more time to develop and secure territories compared to offspring born later, often leading to greater early-life success (Woodroffe 1995; Hall et al. 2020). Thus, selection should favor greater resource acquisition in systems wherein early reproduction is limited by resources and early-born offspring have greater success.

For capital breeding organisms that rely on stored energy (e.g., fat or cached food) to finance reproduction (Drent and Daan 1980), energy accumulation prior to breeding can have a significant influence on reproductive success (Festa-Bianchet et al. 1998; Milner et al. 2013; see also Gaillard et al. 2000). Food caching is one such mode of energy storage that may be under sex-specific selection (Vander Wall 1990). For example, male great grey shrikes (*Lanius excubitor*) with augmented caches sired more offspring (Yosef and Pinshow 1989), and male bull-headed shrikes (*Lanius bucephalus*) that retrieved more cached food improved their song tempo and, in turn, attracted more mates (Nishida and Takagi 2019). Moreover, caching behavior in these shrikes seems to be restricted to males (Yosef and Pinshow 1989, 2005).

In mammals, sex differences in food caching behavior have been observed in several species (e.g., Hodgdon and Larson 1973; Kumari et al. 1979; Jenkins 2011). For example, male arctic ground squirrels (*Urocitellus parryii*), but not females, cache plant matter in hibernacula, and it is believed this cache is used to fuel earlier emergence and physiological preparation for reproduction in males (McLean and Towns 1981). Although asymmetry in food caching between the sexes has been interpreted to be due to differential energetic costs of reproduction, a direct link between cached resources and the ensuing reproductive success of both males and females has not been drawn.

North American red squirrels (*Tamiasciurus hudsonicus*; hereafter, squirrels) are food-caching mammals that primarily consume conifer seeds contained in cones (Fletcher et al. 2013). In the southwest Yukon, both male and female squirrels defend solitary territories in which they cache cones from white spruce (*Picea glauca*) trees in a central larder called a midden (Smith 1968). There is little evidence of adult sexual size dimorphism in this population (Boutin and Larsen 1993; Stuart-Smith and Boutin 1994; Descamps et al. 2008). Instead, sex differences appear in the size of their cache of spruce cones, with males typically having caches of cones that are about 1.5 times greater than the caches of females (Donald and Boutin 2011; Archibald et al. 2013; Fisher et al. 2019). In fact, squirrels that acquire a midden that was previously owned by a male have larger caches and obtain higher lifetime reproductive success than if the previous owner was a female (Fisher et al. 2019). At the population level, spruce reproductive dynamics cause cone crops to fluctuate annually, with exceptionally large crops (masts) occurring every 4–7 years (LaMontagne and Boutin 2007; McAdam et al. 2019). Squirrels breed earlier in the year when the cone crop from the previous autumn is larger (Boutin et al. 2006; Williams et al. 2014; Lane et al. 2018), and early breeding is typically favored by selection (McAdam and Boutin 2003a; Réale et al. 2003; Lane et al. 2018). At the individual level, females supplemented with food successfully wean more offspring (Kerr et al. 2007). In addition, in a different habitat (non-masting jack pine (*Pinus banksiana*) forest of northern Alberta), females with experimentally augmented caches bred earlier than controls in 1 year of monitoring (Larsen et al. 1997). Whether this reproductive advantage is experienced by females who naturally cache more cones than their same-sex competitors and whether it may hold in the naturally more variable white spruce systems, however, is unknown. Furthermore, the influence of cache size on male reproduction has not been assessed.

Thus, while we have previously found that red squirrel reproduction is influenced by annual variation in masting, the size of the cache an individual settles on, and experimental supplementation of food, here we examined how natural variation in cache sizes relates to reproductive success

within years and among individuals for both males and females. We test the hypothesis that males have larger caches of cones than females (Donald and Boutin 2011; Archibald et al. 2013; Fisher et al. 2019) because positive directional selection on cached resources is stronger for males than for females. To evaluate this hypothesis, we first tested whether having access to more cached cones leads to (1) earlier breeding in males and/or females and (2) increased reproductive output (i.e., number of pups produced per year) and success (i.e., number of offspring surviving to 200 days of age per year) for males and/or females. Similar to other species described above, male red squirrels experience peak reproductive energetic requirements when they search for mates during late winter or spring (Lane et al. 2010), whereas females experience peak reproductive energetic requirements when producing milk for pups during late spring/summer (Fletcher et al. 2012). Because the later energetic requirements of females may occur when fresh foods are available, we predicted male reproductive success would be more strongly associated with cached resources than for females. We then tested for potential sex-specific mechanisms (e.g., male breeding home ranges, female litter size) by which cache size could affect annual reproductive success. Female red squirrels come into estrus on a single day, and mate with multiple males in a scramble competition mating system (Lane et al. 2007, 2008). Males increase home range size during the breeding season, and males that travel farther during the mating season tend to sire more offspring (Lane et al. 2009). Thus, for males, we also tested whether individuals with larger caches had larger home ranges during the breeding season. For females, we also tested whether individuals with larger caches produced larger litters, faster growing pups, or multiple litters per year (i.e., traits that could contribute to annual reproductive success).

Methods

Monitoring reproduction

We monitored a wild population of North American red squirrels from 2007 to 2015 on two ~ 40 ha study areas (KL and SU) in the southwest Yukon (61° N, 138° W; for full details of the study population, see McAdam et al. 2007; Dantzer et al. 2020). We have continuously monitored this population since 1989, but have only quantified cone cache size since 2007. All individuals received permanent aluminum alphanumeric ear tags (National Band and Tag Company, Newport, KY, USA) upon first capture. It was not possible to record data without researchers knowing animal identities because our study involved focal animals in the field. Within each study area, we marked each individual with unique color combinations of wire to permit identification from a distance for behavioral observations (Dantzer et al. 2012). Using live-trapping and behavioral observations, we monitored mating behavior, reproductive status, and survival from March to August each year. We knew birth year with certainty for 225 individuals for which we also had individual measures of food resources (see below). If squirrels were first handled as adults ($n = 103$), we assigned a minimum age of 1 (i.e., conservatively assuming a birth year of 1 year prior, following Berteaux and Boutin 2000). We used birth year to estimate age in years.

We trapped females regularly to monitor reproductive status, and determined pregnancy status through body mass gain and abdominal palpation (McAdam et al. 2007). We used telemetry of radio collared lactating females to locate nests twice: first following parturition (determined by a drop in body mass, with lactation confirmed through the expression of milk) and again when pups were ~ 25 days old. We enumerated, marked, and weighed pups at both nest visits, and tagged pups at ~ 25 days of age. We calculated the postnatal growth rate for each pup as their body mass gain between the first and second nest entry divided by the number of days between nest entries, as growth is approximately linear at this stage (McAdam et al. 2002; McAdam and Boutin 2003b). We then calculated average growth rate for each litter to use in the analysis. We assessed whether pups recruited into the population by monitoring whether they survived to 200 days old (following Larsen and Boutin 1994; Berteaux and Boutin 2000; McAdam and Boutin 2003b).

To calculate male reproductive success, and confirm female reproductive success, we analyzed a genetically determined pedigree. Briefly, we collected tissue samples from all adults and pups at first handling. For details on microsatellite loci isolation and paternity assignment, see (Gunn et al. 2005; Lane et al. 2007). We assigned loci with GENEMAPPER software 3.5 (Applied Biosystems) and then used CERVUS v. 3.0 to assign paternity with 99% confidence (Marshall et al. 1998; Kalinowski et al. 2007). We assigned maternity based on behavioral observations and telemetry when we located each nest. Genotyping error from these known mother–offspring pairs was < 1% (Haines et al. 2020). For each male and female that we had cache size data for, we then defined annual reproductive output as the total number of pups produced, and annual reproductive success as the total number of offspring who survived to 200 days of age (i.e., recruits). We used parturition dates for each litter estimated from monitoring females to determine the earliest date that males sired pups within a season by subtracting the gestation period (35 days, Lane et al. 2007) from the earliest parturition date among the pups that they sired that season.

Estimating resource availability

White spruce cones become visible in mid-summer, but squirrels do not begin harvesting them until late summer once cones have matured (Fletcher et al. 2010; Archibald et al. 2013). Squirrels cache harvested cones in middens, which are characterized by large amounts of debris from consumed cones (cone scales and rachides) as well as cones cached within the layer of cone scales or within tunnels in the ground. Midden use is traditional; squirrels cache cones in the same location on a territory even when ownership changes (Fisher et al. 2019). Rarely, a new midden is established (Price and Boutin 1993) and middens last many years (Fisher et al. 2019). Within-year habitat heterogeneity does not appear to be a strong influence on the number of cones within a midden. Specifically, there is no relationship between the number of cones on a territory and cache size during non-mast years, although squirrels that defended larger territories had larger caches of cones (LaMontagne et al. 2013). Outside of the breeding season, territory sizes do not differ between males and females (LaMontagne et al. 2013). There is considerable variation in territory sizes and the number of cones on territories among years, and spatial variation in cone production was not consistent among years (i.e., no locations that were consistently productive or unproductive; LaMontagne et al. 2013).

Cached cones cannot be assessed during most of the breeding season (in winter and early spring) due to frozen ground and snow cover that obscures the midden boundaries and covers cached cones except where squirrels dig tunnels to access their cache (Krebs et al. 2001). Thus, we used autumn estimates of cache size as our measure of individual-level resource availability for the following breeding season. We included reproductive data from breeding seasons 2008–2014 as both male and female reproduction were assessed in these years; thus, we used cache size records from 2007 through 2013. Because we monitored the survival of juveniles born in the reproductive season of 2014 to 200 days old (i.e., into 2015), the period of this study extends from 2007–2015.

We estimated cache size following Fisher et al. (2019), adapted from Larivée et al. (2010) and Donald and Boutin (2011). We counted the number of cones within 10 cm of the midden's surface in the cone scales or within 30 cm of the surface in tunnels in 30 cm × 30 cm quadrats on each midden. The number of quadrats varied, as prior to 2011 we sampled 16 quadrats. In 2011 and later we sampled 4–8 quadrats depending on midden area. We accounted for this variation by averaging the number of cones counted in all quadrats for each midden. We measured midden length and width to the edge of the scale pile (for newly established middens lacking scale accumulation, we delineated edges as locations of cached cones). We calculated midden area

assuming an elliptical area. We then estimated the total number of cones per midden (i.e., cache size) by multiplying the average number of cones per quadrat by the number of quadrats that would fit within the midden area. We assigned multiple middens to the ownership of a single squirrel in 13 instances out of 522 squirrel-year combinations (2.4%). For squirrels that owned multiple middens, we summed the cones in each midden to represent their combined cache size. Because the distribution of cache size was right skewed, we $\log_{10}$-transformed the data to improve normality.

Population-level cone production by white spruce varied across the years under study. The years 2010 and 2014 were determined to be mast years based on large crops relative to intervening years (McAdam et al. 2019; Dantzer et al. 2020). Thus, our dataset consisted of two mast years and five non-mast years.

Male breeding home range area

We measured male breeding season home range area during the 2013–2014 breeding seasons by locating radio collared males regularly (i.e., at least daily, but usually several times a day) to record their spatial locations. Thus, although data on cache size and reproductive output and success existed for 7 years, data for the analysis of male breeding home range area only existed for these 2 years. We also recorded a male's location each time he was trapped or observed during regular monitoring activities. We included all location data collected prior to the last siring date in that year (last parturition date minus 35 days of gestation) because mating behavior should not occur when there are no receptive females with which to breed. Using these spatial locations, we calculated breeding season home ranges for individual males for these two years using *adehabitatHR* (version 0.4.19; Calenge 2006). We excluded males with five or fewer locations per season due to the requirements of the package. The sample size (2013: $n = 51$ males; 2014: $n = 18$ males) and total number of locations in the season per male (2013: 35 ± 26.5 SD, range $= 6$–87; 2014: 36 ± 51.4, range $= 6$–173) varied annually. We used all locations to calculate the area that males traveled during the mating season (herein called "breeding season home range") using a 100% minimum convex polygon (MCP) and then $\log_{10}$-transformed the home range area for analysis. Because MCPs are influenced by the number of locations used in each calculation, we included the $\log_{10}$-transformed number of locations as a covariate in the model of area traveled following Kenward (2001) and Lane et al. (2009).

Given the variation in male search effort for mates (Lane et al. 2009), we looked for potential spatial biases in our detection of male reproductive success and of our assignment of paternities to offspring born in our study areas by comparing the number of pups sired in the core 20 ha versus

edge 20 ha of each ~ 40 ha study area. In particular, we were concerned that males on the edge of our study areas may have traveled out of the study area and sired pups that we did not quantify. However, we did not find significant spatial differences in our ability to detect male siring success or assign paternities (see Supplementary Online Material). This gives us confidence that we are capturing measures of male success evenly across space and our measures of male reproductive success were not biased by where males resided in our study areas (similar to findings for offspring survival: Kerr et al. 2007; McAdam et al. 2007).

Statistical analyses

We conducted all analyses in R Version 4.0.2 (R Core Team 2016). We used the *lme4* (version 1.1.23) and *lmerTest* (version 3.1.2, Kuznetsova et al. 2017) packages to conduct and interpret general linear mixed models, and the package *lme4* (Bates et al. 2015) to conduct generalized linear mixed models and general linear models without random effects. To account for multiple observations of individuals and annual variation, we included squirrel identity and year as random effects in all models. However, squirrel identity explained no variance in three models and was removed to allow the models to converge. This was likely because most of the squirrels represented in these datasets contributed only one observation (male earliest reproduction (58/94 squirrels); male home range size (54/60 squirrels); female number of litters (66/117 squirrels)**.** We tested the robustness of these results by randomly selecting one observation from each squirrel (i.e., no repeated measures) and reran each model 10 times on this reduced dataset and have indicated in the results when the significance level of a test was sensitive to this resampling. We note that an assumption of results from these models is that the observed patterns faithfully reflect among-individual covariance, which cannot explicitly be tested given the available data. We also attempted to include study area (KL or SU) as a fixed effect in all models as recent studies have indicated small but significant differences in reproductive success between study areas (e.g., Martinig et al. 2020); one model would not converge when fully parameterized, and we therefore removed study area from that model. We used type III sums of squares to interpret the significance of fixed effects.

Sex and age effects on cache size

We first confirmed previous findings of a sex difference in cache size in this system (Donald and Boutin 2011; Fisher et al. 2019; see Results). Because of this sex difference, and because we expected covariates and random effects to have different fits to response variables for males and females, we chose to run separate models for males and females in subsequent analyses. Because we have previously documented

reproductive senescence in females in this population (Descamps et al. 2008), we included age as both a linear and a quadratic fixed effect to assess whether cache size shifts across squirrel age for males and females. Both linear and quadratic age terms were mean centered within each sex for analysis.

The effects of cache size on reproduction

Because our goal was to test whether selection acts on cache size more strongly for males than for females, and because selection occurs at the annual level, we focused this analysis within-years and among-individuals. To do this, we mean centered cache size within years by subtracting the annual mean from each observation (sensu Snijders and Bosker 1999). We did this for each sex independently. Mean-centered cache size measures of four males and five females were greater than 3 standard deviations below zero (Fig. 1), and we therefore removed them for the main analysis and figures. We note in the text of the Results when the inclusion of these data points would have altered the significance level of a test. We included cache size, age, age^2, and study area as fixed effects in models to assess their effects on reproductive behavior and success (full models). These full models assessed the relationships between cache size and dependent variables marginal to the effects of age (and study area). However, because age and cache size covaried, we also constructed these models without age or age^2 (reduced models) to assess the effects of cache size on reproductive variables not marginal to age effects. In other words, these reduced models assessed whether there was a relationship between cache size and reproductive variables which could be partially explained by covariation with age.

We constructed a model for each of the following dependent variables: number of pups produced per year, number of recruits produced per year, and the earliest date of birth of a litter that a female birthed or that a male sired pups within (squirrel litters exhibit multiple paternities; Lane et al. 2008). For males, we also constructed a model with breeding home range size as a dependent variable; this model also contained the number of spatial locations that the MCP was generated from as a covariate. We included year as a fixed effect rather than a random effect in this model because we had breeding home range size data from only 2 years. As such, there were relatively few squirrels with repeated measures in the area dataset (6 records of 67), leading to model convergence issues when squirrel identity was included as a random effect. We therefore ran this model with no random effects. For females, we constructed additional models with the number of pups in her first litter of the year, mean growth rate of her first litter of the year (with litter size covariate), and whether she produced a single litter or multiple litters in a year (binary). We condensed the number of litters
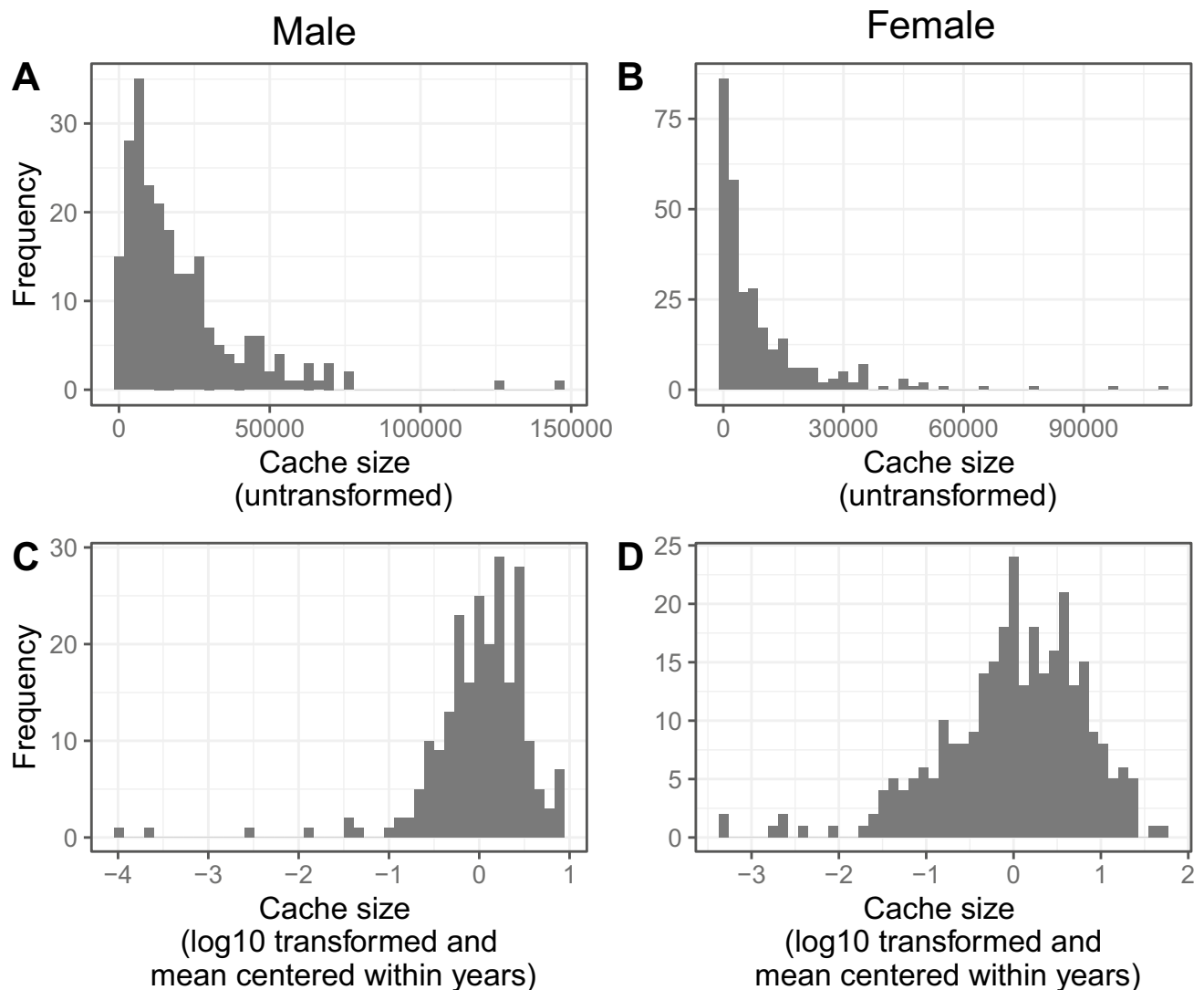
Fig. 1 Distributions of cache size estimates for **A**, **C** male ($n=229$ annual measures) and **B**, **D** female ($n=288$) North American red squirrels (*Tamiasciurus hudsonicus*). Raw data are plotted on **A** and **B**. We $\log_{10}$ transformed the data to improve normality and then mean centered the data within years (independently for each sex) which is plotted on **C** and **D**. We classified cache size estimates of four males and five females that were lower than 3 standard deviations below the mean (males $= -1.77$ on log scale, females $= -2.46$) as outliers and subsequently removed them from the dataset for analysis and plotting (see the "Methods" section)

produced in a year into a binary distribution because of the rarity of a female producing three litters ($n=7$) in a year compared to one ($n=134$) or two ($n=51$) litters per year.

Based on the results, we wondered whether the effects of cache size on reproductive output and success depended on the timing of reproduction within sexes. Therefore, we conducted an exploratory analysis to test for an interaction between cache size and the day of year of a squirrel's earliest reproduction (mean centered) on each dependent variable. We tested for these interactions in the full and reduced model structures, but report results only from the full models because the significance level of the interaction remained the same regardless of structure.

We modeled continuously distributed traits with Gaussian distributions. We modeled the number of pups produced and the number of recruits produced with Poisson distributions and log link functions. We modeled the number of litters that females produced with a binomial distribution (logit link function).

Results

Sex and age effects on cache size

We estimated red squirrels to have an average of 13,894 cones ($\pm 17,900$ SD, range 0 to 146,048) cached in their

midden, with males having more than twice as many cached cones as females (males: $19{,}733 \pm 20{,}130$, range 0 to $146{,}048$, $n = 229$ annual measures; females: $9281 \pm 14{,}356$, range 0 to $109{,}973$, $n = 288$; $t_{329} = 6.9$, $p < 0.001$). We found no effect of study area on the number of cached cones of either sex (male: $t_{122} = -0.5$, $p = 0.616$; female: $t_{167} = -0.5$, $p = 0.596$). The cache size of males increased until age five and then leveled off (linear age effect: $t_{193} = 3.9$, $p < 0.001$; quadratic age effects: $t_{153} = -2.6$, $p = 0.009$; Fig. 2A). A partial regression line suggests the cache size of females increased to a lesser degree to age four and then declined towards late life (linear age effects: $t_{256} = 2.9$, $p = 0.004$; quadratic age effects: $t_{233} = -2.5$, $p = 0.015$; Fig. 2B), although the residuals suggest cache size increases from ages 1 to 2, then level off until age 4 after which few data points exist.

The effects of cache size on reproduction

Females and males that had larger caches bred earlier in the year (female estimate: -4.9 ± 1.5 SE, male estimate: -9.5 ± 4.2 SE; Fig. 3A, D; Table 1). For example, for a squirrel with a cache size of the third quartile compared to the first quartile (and a median age (3 years old) on grid KL), a male is predicted to sire offspring 4.4 days earlier and a female is predicted to birth offspring 3.3 days earlier. In the reduced model structure, these predictions increased to 5.3 days earlier for males and 4.8 days earlier for females. This effect, however, was not significant for males in the full model ($t_{123} = -1.7$, $p = 0.088$) or for males in the reduced model when outliers ($n = 4$) were retained in the analysis ($t_{128} = -1.5$, $p = 0.146$). When we randomly sampled one observation for each male to remove repeated observations, the effect of cache size on siring timing in the full model was

significant in 80% of tests and nonsignificant in 20% (highest $p = 0.2$). Males with larger caches sired more pups than males with smaller caches (Table 1; Fig. 3B). For example, a male with a cache size of the third quartile (and median age on grid KL) is predicted to sire 0.40 more pups than a male with a cache size of the first quartile (median number of pups sired per male = 2). We did not find evidence of a relationship between male cache size and the number of recruits produced nor breeding season home range size (Table 1; Fig. 3). In subsequent exploratory analyses, we found no evidence of an interaction between cache size and first siring date on the number of pups, number of recruits, nor breeding season home range for males (all $p \geq 0.689$).

In the initial models, we did not find a relationship between the cache size of females and the number of pups produced, number of recruits, litter size, number of litters, or pup growth rate (Table 1). However, in subsequent exploratory analyses, the number of recruits that a female produced increased with cache size for females that began reproducing early (cache size*first parturition date interaction, coefficient = -0.24 ± 0.11 SE, $z = -2.1$, $p = 0.033$); this effect of cache size on reproductive success diminished for females that began reproducing in the middle of the distribution of first parturition dates and was negative for females that began reproducing later in the year (Fig. 4A). This interaction was marginally nonsignificant if outliers ($n = 5$) were retained in the analysis ($z = -1.8$, $p = 0.078$). We found a similar trend for the growth rate of pups from first litters; females with larger caches produced faster growing pups when litters were produced early, but this relationship shifted to a negative relationship when litters were birthed later in the year (cache size*parturition date, coefficient = -0.08 ± 0.04 SE, $z = -1.9$, $p = 0.055$). We did not find an interaction of female cache size and parturition timing on the number of pups produced, litter size, or whether females produced a

Fig. 2 The number of white spruce cones (*Picea glauca*) within caches of **A** male and **B** female North American red squirrels (*Tamiasciurus hudsonicus*) increased with age for both sexes and then plateaued (male) or declined (female) towards late life. Points represent residuals from models correcting for the effects of study area, year, and squirrel identity. Points are shown with a 0.5 transparency and are jittered on the x-axis to avoid overplotting. Lines represent quadratic regressions extracted from the models (results shown in Table 1)
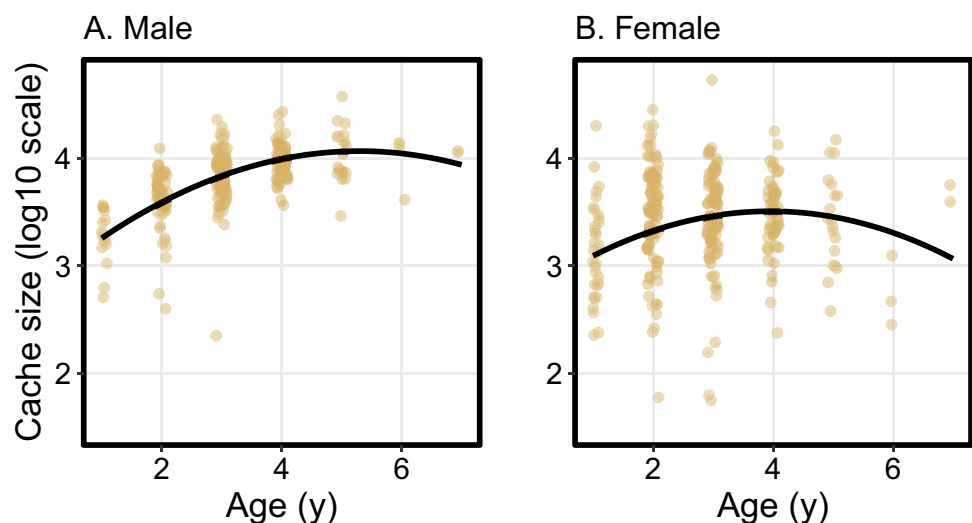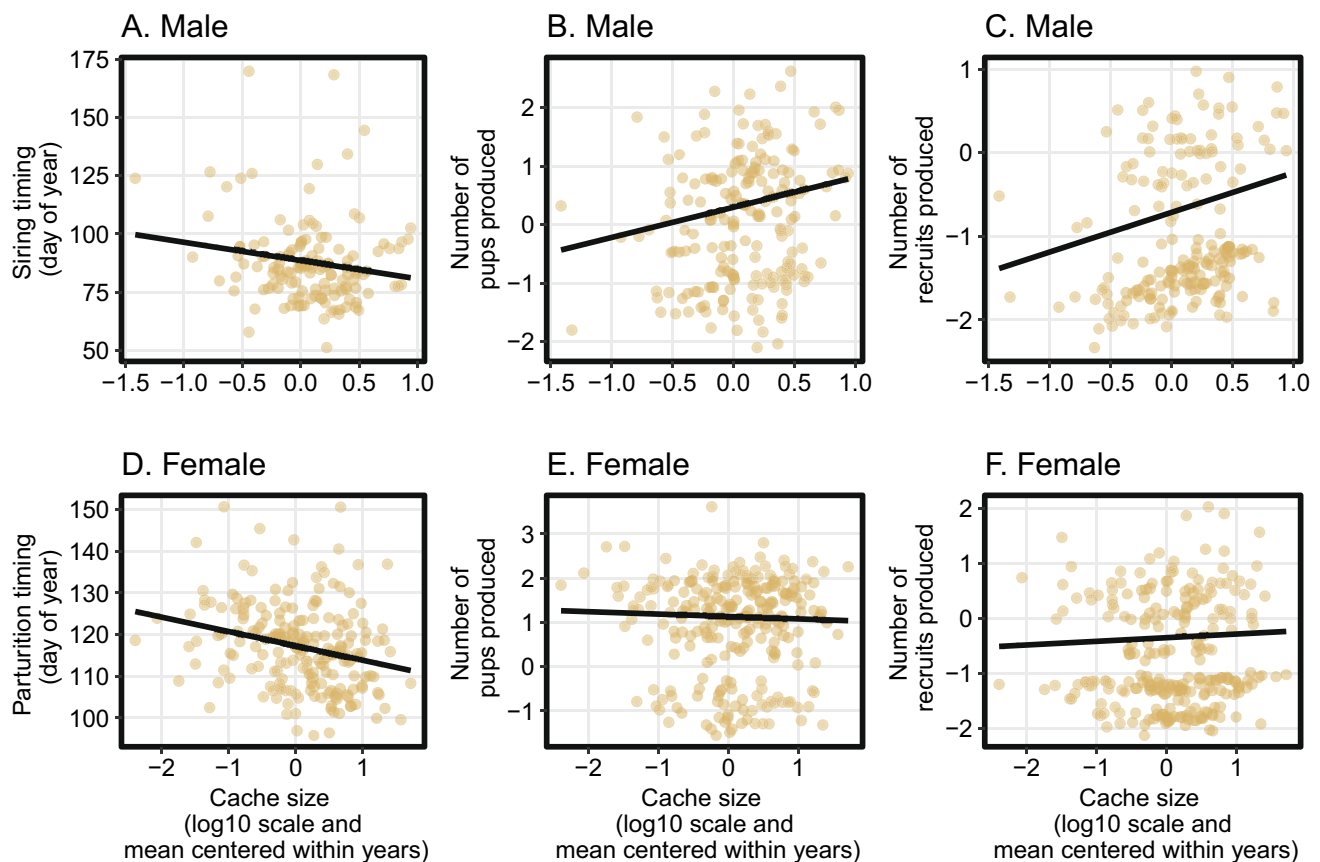
Fig. 3 The relationship between the number of cones in an individual's cache and the timing and output of reproduction for **A**–**C** male and **D**–**F** female North American red squirrels (*Tamiasciurus hudsonicus*). Cache size was $\log_{10}$ transformed and then mean centered within years. Points represent residuals from the full models reported in Table 1. Points are shown with a 0.5 transparency to avoid overplotting. Lines represent linear regressions extracted from the full models. Statistical results are reported in Table 1 and regression coefficients are reported in Supplementary Table 1

single vs. multiple litters (all $p \geq 0.104$). Regression coefficients are listed in Supplementary Table 1.

Because the relationship between cache size and reproductive output and success appeared different for males and females, we extracted and compared the 95% confidence intervals (CIs) of the slope estimates from the full model structure (without an interaction with reproductive timing) for each sex. The effect of cache size on the number of pups produced was stronger for males (estimate: 0.52, 95% CIs = (0.14, 0.89) than for females (estimate: −0.05, 95% CIs = (−0.18, 0.07) and the CIs for each estimate did not overlap. The CIs for the slope of cache size on the number of recruits produced overlapped considerably for males (estimate: 0.47, 95% CIs = (−0.16, 1.12) and females (estimate: 0.06, 95% CIs = (−0.18, 0.30). We then extracted the 95% CIs for the interaction coefficient of cache size and earliest reproduction on the number of recruits produced from our exploratory models. The 95% CIs overlapped the coefficients of this interaction for males and females (male estimate: −0.06, 95% CIs = (−0.28, 0.16); female estimate: −0.24, 95% CIs = (−0.47, −0.01).

Discussion

Asymmetrical reproductive phenologies are known to lead to differential costs among the sexes in mammalian species (Hau et al. 2017). In such situations, we might expect selection to act on male and female resource acquisition differently. Here, we show evidence of sex-specific selection that is consistent with sex differences in food cache size in red squirrels (Donald and Boutin 2011; Archibald et al. 2013; Fisher et al. 2019).

Squirrels with larger caches bred earlier than same-sex individuals with smaller caches. This mirrors among-year patterns wherein squirrels breed earlier following larger cone crops in the previous autumn (Boutin et al. 2006; Williams et al. 2014; Lane et al. 2018) and experimental findings that food supplemented females bred an average of 18 days earlier than control females (Kerr et al. 2007). Given that females that breed earlier produce offspring with higher survival under high density conditions, and are more likely to produce multiple litters in a year (Williams et al. 2014; see

Table 1 Statistical results from models assessing the effects of study area, age, age, and cache size on reproductive behavior (earliest reproduction, breeding season home range size) and output (number of offspring, number of recruits, litter size, whether there were single or multiple litters within year, and mean pup growth rate) for male (top subset) and female (bottom subset) North American red squirrels (*Tamiasciurus hudsonicus*). For each dependent variable, we assessed the effect of cache size with a fully parameterized model and a model that did not include age or age^2 (reduced model; see Methods for additional details). Females and males were analyzed in separate models. Dashes denote terms that were removed to allow model convergence. Bold face font denotes model terms with a p-value < 0.05. Regression coefficients are reported in Supplementary Table 1

| Dependent variable	n	Fixed effects					Random effect variance	
		study area	age	age^2	cache size (full model)	cache size (reduced model)	Squirrel ID	Year
Males								
Earliest reproduction	132	$t_{124}=1.1\ p=0.260$	$t_{126}=0.3\ p=0.798$	$t_{125}=-0.6\ p=0.519$	$t_{123}=-1.7\ p=0.088$	$\mathbf{t_{126}=-2.3\ p=0.025}$	–	522.1
Number of offspring	187	–	$z=-0.3\ p=0.740$	–	$\mathbf{z=2.7\ p=0.007}$	$\mathbf{z=2.8\ p=0.004}$	0.59	0.15
Number of recruits	187	$z=-1.9\ p=0.055$	$z=1.1\ p=0.268$	$z=-1.2\ p=0.225$	$z=1.5\ p=0.141$	$z=1.5\ p=0.131$	0.71	0.27
Home range size	67	$t=1.2\ p=0.255$	$t=-1.2\ p=0.218$	$t=1.0\ p=0.325$	$t=-0.3\ p=0.761$	$t=-1.1\ p=0.274$	–	
Females								
Earliest reproduction	201	$t_{104}=1.2\ p=0.250$	$\mathbf{t_{177}=-8.0\ p<0.001}$	$\mathbf{t_{171}=6.8\ p<0.001}$	$\mathbf{t_{169}=-2.6\ p=0.009}$	$\mathbf{t_{148}=-3.3\ p=0.001}$	41.7	550.5
Number of offspring	246	$z=-1.2\ p=0.212$	$\mathbf{z=4.2\ p<0.001}$	$\mathbf{z=-4.0\ p<0.001}$	$z=-0.8\ p=0.405$	$z=-0.4\ p=0.665$	0.14	0.08
Number of recruits	246	$z=-1.1\ p=0.272$	$z=1.4\ p=0.156$	$z=-1.4\ p=0.181$	$z=0.5\ p=0.620$	$z=0.7\ p=0.495$	0.23	0.37
Litter size	172	$\mathbf{t_{100}=-3.0\ p=0.003}$	$t_{162}=1.5\ p=0.148$	$t_{163}=-1.3\ p=0.210$	$t_{142}=-0.9\ p=0.346$	$t_{140}=-0.7\ p=0.480$	0.15	0.12
Single vs. multiple litters	192	$z=-0.4\ p=0.688$	$\mathbf{z=2.5\ p=0.013}$	$\mathbf{z=-2.1\ p=0.038}$	$z=0.5\ p=0.584$	$z=1.1\ p=0.293$	–	3.2
Mean pup growth rate	120	$t_{73}=-0.5\ p=0.655$	$\mathbf{t_{111}=3.1\ p=0.003}$	$\mathbf{t_{114}=-3.3\ p=0.001}$	$t_{83}=-0.6\ p=0.556$	$t_{114}=-0.2\ p=0.873$	0.00	0.01
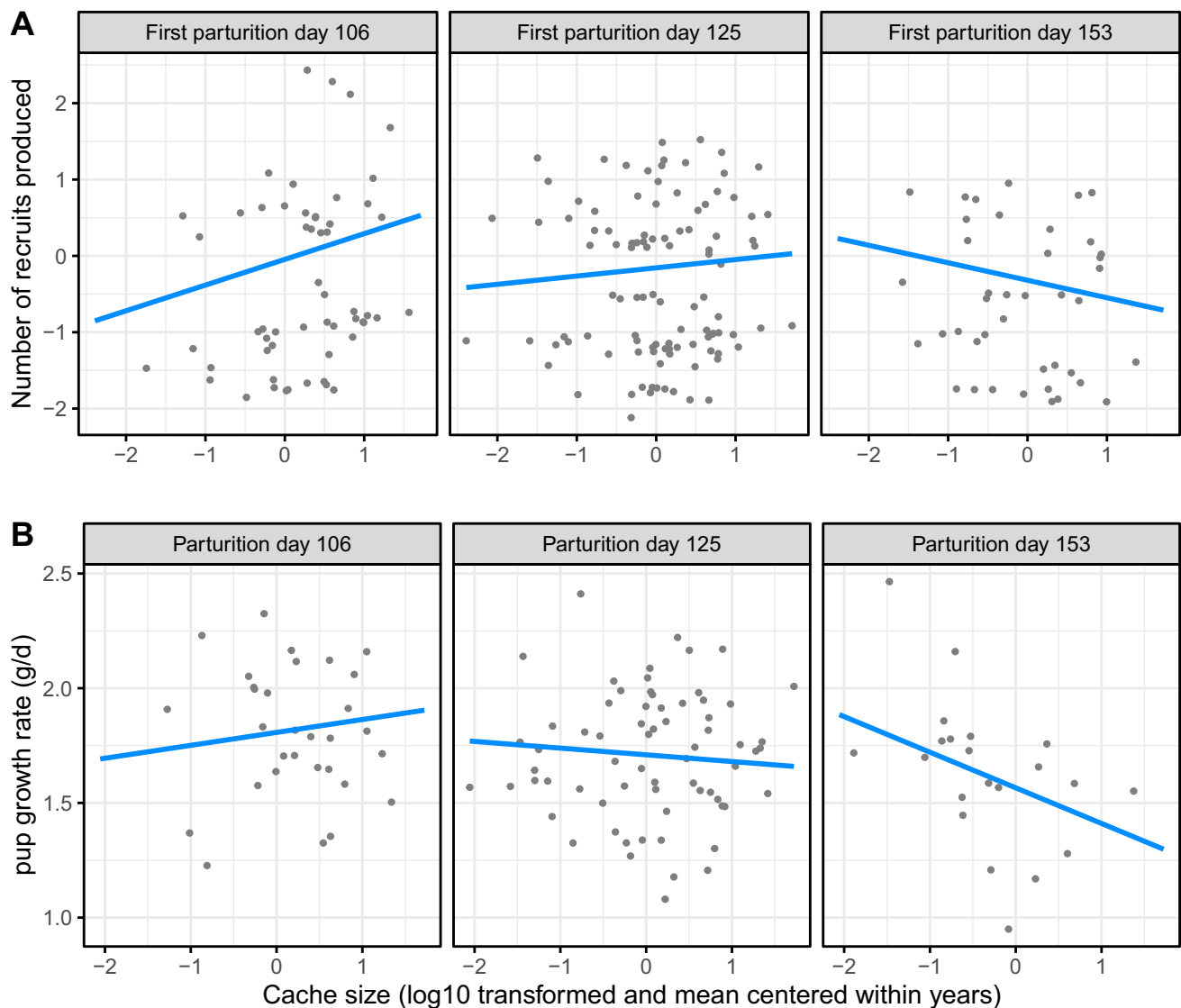
Fig. 4 The effects of the number of cones in a female North American red squirrel's (*Tamiasciurus hudsonicus*) cache and the **A** number of recruits she produced and **B** mean growth rate of the pups in her litter depending upon the timing of parturition. Lines represent linear regressions extracted from the full model structures including an interaction of cache size and parturition timing. Left panels indicate the regression line at the 10th percentile of parturition timing, middle panels represent regressions at the 50th percentile of parturition timing, and right panels indicate the regressions at the 90th percentile. Each residual is plotted only once in the panel that indicates the parturition timing the residual is closest to

also McAdam and Boutin 2003a), our phenology findings suggest individuals of both sexes with larger caches ought to experience greater reproductive success. For males, this effect of cache size on reproductive timing was only consistently significant in the reduced model, suggesting this effect may be mediated by age, and was sensitive to the inclusion/exclusion of outliers and treatment of repeated measures, but the effect for females was robust.

Males with larger caches sired more pups compared to males with smaller caches, which differed from females which exhibited no overall relationship between cache size and reproductive output. Subsequent exploratory analyses revealed that only for early breeding females were larger caches associated with more recruits compared to females with smaller caches. Although there was overlap in the 95% confidence intervals for cache size x reproductive timing interaction between males and females, we interpret these collective results to indicate that cache size is more strongly associated with the reproductive success of males than for females. This sex-specific relationship between reproductive success and resources likely results from sex differences in the timing and requirements of peak energy expenditure on reproduction. Peak energy expenditure for males is likely during the mating season in late winter when males engage

in mating chases (Lane et al. 2010), at which time cold weather may also exacerbate energetic requirements (Lane et al. 2009). During this time in the Yukon, red squirrels feed almost exclusively on cached cones (Fletcher et al. 2013). In contrast, peak energy expenditure for females is later in the year during lactation (Fletcher et al. 2012) when fresh foods (e.g., mushrooms and new cones) become available in late spring and summer (Fletcher et al. 2013). For example, ~ 50% of feeding observations before mid-May were of squirrels eating seeds from cached cones, with the remaining observations consisting of cached fungi (mushrooms/truffles) and spruce buds, each of which is less calorically dense than spruce seed (Fletcher et al. 2013). Most females in our dataset analyzed here experienced mid-lactation in early June when fresh mushrooms began to increase in frequency in feeding observations (Fletcher et al. 2013). Fresh cones can also become available as early as late June (Fletcher et al. 2013). Thus, while cached cones are still the most significant and reliable source of calories for females until sometime in July, most females have access to additional food resources during their peak energy demand. Foraging efficiency is also likely an important contributor to the patterns observed here. Males likely require a more efficient energy source to fuel high intensity mating chases, whereas females may be able to supplement their diet with less efficient fuel sources.

Our findings that sex-specific selection likely drives differences in resource acquisition between the sexes could exemplify a common pattern for animal systems (Hau et al. 2017). For example, female grey seals (*Halichoerus grypus*) begin accumulating fat earlier in the year, accumulate a greater amount, and consume more fat during the breeding season compared with males (Beck et al. 2003). Sex differences in the timing and energetic costs of reproduction are theorized to drive this differential seasonal pattern of fat accumulation and consumption, but fitness data are lacking (Beck et al. 2003). In cases where data for both fitness and resource acquisition exist, tests tend to be restricted to one sex. However, in a laboratory environment, Reddiex et al. (2013) found that male and female fruit flies (*Drosophila melanogaster*) differ in macronutrient preferences and that these sex-specific preferences maximize fitness (see also Maklakov et al. 2008 for similar results with crickets). The lack of comparable data in wild populations likely results from the difficulty of simultaneously collecting resource acquisition data at relevant time periods and fitness data for both sexes.

Another reason that comparable data is lacking is because resource acquisition is typically considered a product of temporal and spatial variance in the environment rather than a phenotype that can be shaped by natural selection (sensu Laskowski et al. 2021). While the environment is indeed likely to have large effects on available resources,

the amount of resources acquired is an expression of the phenotype that will be affected by multivariate interactions of behavior, performance, and morphological traits (Larue et al. 2022). In our system, current work to assess how red squirrel phenotypes and their heritabilities contribute to variation in resource acquisition are ongoing. Cached resources in particular represent an extended phenotype (Fisher et al. 2019), which is a trait that exists outside of their physical body (Dawkins 1978, 1982). Capital breeding organisms that fuel reproductive effort with fat (sensu Beck et al. 2003) or cached resources (as shown here) are ideally suited to compare patterns of resource acquisition and its consequences because acquisition is quantifiable and stored resources should, to some degree, be attributable to the organismal phenotype.

A putative mechanism for cache size to increase male reproductive output could be that cached resources directly provide energy that fuels greater or earlier mating effort and/or performance. However, as analyzed here, we found no connection between male cache size and breeding season home range area. It is possible that our failure to detect a relationship is a consequence of fluctuating squirrel mating behavior in the context of mast years (male home range data here are limited to one mast year and one non-mast year), or that increased effort may be concentrated within similar areas. Cache size may signal male quality to females; however, mating chases tend to be centered on the female's midden, thus restricting the opportunity of females to assess the cache size of males. Cached cones more likely serve as fuel for mate searching, a sexually selected trait in male squirrels (Lane et al. 2010). In support of this, our finding that males with larger caches sired offspring earlier in the season suggests the possibility that greater cached resources fuel earlier reproductive effort. Cached resources could also fuel males to increase the time invested into mate searching (although no relationship between male cache size and maximum length of time between successful sirings was found here; data not shown).

Given that we did not find a relationship between cache size and the number of pups that females produced, larger caches likely enable early breeding females to produce more recruits by increasing offspring quality. To support this, we found that early breeding females with larger caches produced slightly faster growing pups. Pups that grow faster usually experience greater overwinter survival (Hendrix et al. 2020) and natural selection favors mothers that produce fast growing offspring in high density environments (Dantzer et al. 2013; see also McAdam and Boutin 2003a). Experimentally supplemented females produced offspring with higher early survival despite no difference in the body size of offspring compared with offspring of non-supplemented females (Kerr et al. 2007), which suggests that maternal food resources can have a positive effect on

pup success in addition to any effect on offspring body size. Thus, mothers may improve offspring success by creating a quality environment for offspring via nest defense, as evidenced by females with high nest attendance having higher lifetime reproductive success (Westrick et al. 2020). These findings are similar to those across a variety of taxa showing that the resources available to mothers are important determinants of early-life success of offspring (Mousseau and Fox 1998; Monteith et al. 2009; Salomon et al. 2011; Warner and Lovern 2014).

Both male and female cache sizes increased with age to varying degrees and then plateaued (male) or decreased towards late life (female; similar to Fisher et al. 2019). Female reproductive effort increases with age in our population as the likelihood of breeding, the likelihood of producing a second litter within a season, and the propensity to bequeath their territory to offspring increases across lifespan (Descamps et al. 2007). Given our findings, we suggest that early life increases in reproductive effort of females may be fueled by the concomitant increase in cached resources, and that the late life decrease in the cache size of females could result from the coinciding highest reproductive effort. Additionally, females that reproduce during late life experience reduced survival (Descamps et al. 2009) which may partially result from their lower availability of cached resources. Alternatively, late life decreases in cache size, survival, and reproduction (Descamps et al. 2008, 2009; Haines 2017), which are common in wild vertebrates (Festa-Bianchet and King 2007; Gaillard et al. 2017; Lemaitre and Gaillard 2017), could reflect responses to underlying physiological senescence. Here, we focused on total cache size (newly cached cones plus stored cones from previous years), but future work that teases out caching effort (i.e., new cones only), cone consumption, and storage will be important for disentangling the causes and consequences of changes in cache size across age.

Red squirrels exhibit high variability in the timing, output, and success of reproduction among years (e.g., Boutin et al. 2006; Williams et al. 2014; Lane et al. 2018; McAdam et al. 2019), which suggests the importance of a squirrel's cache is likely to vary among years. For example, the average parturition date in the population varies by as much as ~60 days among years (Boutin et al. 2006; Williams et al. 2014), and female consumption of cached resources during mid-lactation ranges from 2 to 100% among years depending on reproductive phenology (Fletcher et al. 2013). We focused our analyses here on testing whether the importance of within-year variation in cached resources is sex specific and could explain sex differences in cache sizes. We thus analyzed a 7-year period for which we have data on the siring success of males in addition to our larger dataset of reproductive success of females (Dantzer et al. 2020). Nevertheless, future work should examine whether environmental variation at the population level, such as cone availability, spruce masting, and conspecific density, affect these within-year relationships among cache size and reproductive strategy and their consequences.

Conclusion

We show that both males and females with larger caches produced offspring earlier in the year than squirrels of their sex with smaller caches. Males with greater cache sizes sired more pups, whereas for females, cache size only positively affected components of fitness when they reproduced early in a year. We suggest that the stronger overall positive effect of cache size on reproductive success for males than for females likely contributes to males typically having larger caches than females. These results serve to expand an appreciation for factors influencing male fitness components as well as offer new perspectives on the complexities contributing to female reproductive plasticity.

Declarations

References

Archibald DW, Fletcher QE, Boutin S, McAdam AG, Speakman JR, Humphries MM (2013) Sex-specific hoarding behavior in North American red squirrels (*Tamiasciurus hudsonicus*). J Mammal 94:761–770

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using *lme4*. J Stat Softw 67:1–48

Beck CA, Bowen WD, Iverson SJ (2003) Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. J Anim Ecol 72:280–291

Berteaux D, Boutin S (2000) Breeding dispersal in female North American red squirrels. Ecology 81:1311–1326

Boutin S (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can J Zool 68:203–220

Boutin S, Larsen KW (1993) Does food availability affect growth and survival of males and females differently in a promiscuous small mammal, *Tamiasciurus hudsonicus*? J Anim Ecol 62:364–370

Boutin S, Wauters LA, McAdam AG, Humphries MM, Tosi G, Dhondt AA (2006) Anticipatory reproduction and population growth in seed predators. Science 314:1928–1930

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519

Chevallier C, Gauthier G, Lai S, Berteaux D (2020) Pulsed food resources affect reproduction but not adult apparent survival in arctic foxes. Oecologia 193:557–569

Cody ML (1966) A general theory of clutch size. Evolution 20:174–184

Dantzer B, Boutin S, Humphries MM, McAdam AG (2012) Behavioral responses of territorial red squirrels to natural and experimental variation in population density. Behav Ecol Sociobiol 66:865–878

Dantzer B, McAdam AG, Humphries MM, Lane JE, Boutin S (2020) Decoupling the effects of food and density on life-history plasticity of wild animals using field experiments: insights from the steward who sits in the shadow of its tail, the North American red squirrel. J Anim Ecol 89:2397–2414

Dantzer B, Newman AEM, Boonstra R, Palme R, Boutin S, Humphries MM, McAdam AG (2013) Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. Science 340:1215–1217

Dawkins R (1982) The Extended Phenotype. WH Freeman, Oxford

Dawkins R (1978) Replicator selection and the extended phenotype. Z Tierpsychol 47:61–7

Descamps S, Boutin S, Berteaux D, Gaillard JM (2007) Female red squirrels fit Williams' hypothesis of increasing reproductive effort with increasing age. J Anim Ecol 76:1192–1201

Descamps S, Boutin S, Berteaux D, Gaillard JM (2008) Age-specific variation in survival, reproductive success and offspring quality in red squirrels: evidence of senescence. Oikos 117:1406–1416

Descamps S, Boutin S, McAdam AG, Berteaux D, Gaillard JM (2009) Survival costs of reproduction vary with age in North American red squirrels. Proc R Soc Lond B 276:1129–1135

Donald JL, Boutin S (2011) Intraspecific cache pilferage by larder-hoarding red squirrels (*Tamiasciurus hudsonicus*). J Mammal 92:1013–1020

Drent RH, Daan S (1980) The prudent parent: Energetic adjustments in avian breeding. Ardea 68:225–252

Festa-Bianchet M, Gaillard JM, Jorgenson JT (1998) Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. Am Nat 152:367–379

Festa-Bianchet M, King WJ (2007) Age-related reproductive effort in bighorn sheep ewes. Écoscience 14:318–322

Fisher DN, Haines JA, Boutin S, Dantzer B, Lane JE, Coltman DW, McAdam AG (2019) Indirect effects on fitness between individuals that have never met via an extended phenotype. Ecol Lett 22:697–706

Fletcher QE, Boutin S, Lane JE, LaMontagne JM, McAdam AG, Krebs CJ, Humphries MM (2010) The functional response of a hoarding seed predator to mast seeding. Ecology 91:2673–2683

Fletcher QE, Landry-Cuerrier M, Boutin S, McAdam AG, Speakman JR, Humphries MM (2013) Reproductive timing and reliance on hoarded capital resources by lactating red squirrels. Oecologia 173:1203–1215

Fletcher QE, Speakman JR, Boutin S, McAdam AG, Woods SB, Humphries MM (2012) Seasonal stage differences overwhelm environmental and individual factors as determinants of energy expenditure in free-ranging red squirrels. Funct Ecol 26:677–687

Gaillard JM, Festa-Bianchet N, Delorme D, Jorgenson J (2000) Body mass and individual fitness in female ungulates: bigger is not always better. Proc R Soc Lond B 267:471–477

Gaillard JM, Garratt M, Lemaitre JF (2017) Senescence in mammalian life history traits. In: Shefferson RP, Jones OR, Salguero-Gomez R (eds) The Evolution of Senescence in the Tree of Life. Cambridge University Press, Cambridge, pp 126–155

Gunn MR, Dawson DA, Leviston A, Hartnup K, Davis CS, Strobeck C, Slate J, Coltman DW (2005) Isolation of 18 polymorphic microsatellite loci from the North American red squirrel, *Tamiasciurus hudsonicus* (Sciuridae, Rodentia), and their cross-utility in other species. Mol Ecol 5:650–653

Haines JA (2017) Resources and reproductive trade-offs affect fitness, life history traits, and sexual selection in red squirrels. Doctoral dissertation, University of Alberta, Edmonton

Haines JA, Nason SE, Skurdal AMM et al (2020) Sex- and context-specific associations between personality and a measure of fitness but no link with life history traits. Anim Behav 167:23–39

Hall JM, Mitchell TS, Thawley CJ, Stroud JT, Warner DA (2020) Adaptive seasonal shift towards investment in fewer, larger offspring: evidence from field and laboratory studies. J Anim Ecol 89:1242–1253

Hau M, Dominoni D, Casagrande S, Buck CL, Wagner G, Hazlerigg D, Grieves T, Hut RA (2017) Timing as a sexually selected trait: the right mate at the right moment. Phil Trans R Soc B 372:20160249

Hendrix JG, Fisher DN, Martinig AR, Boutin S, Dantzer B, Lane JE, McAdam AG (2020) Territory acquisition mediates the influence of predators and climate on juvenile red squirrel survival. J Anim Ecol 89:1408–1418

Hill GE (1990) Female house finches prefer colourful males: sexual selection for a condition-dependent trait. Anim Behav 40:563–572

Hindell MA, Bradshaw CJA, Brook BW, Fordham DA, Kerry K, Hull C, McMahon CR (2012) Long-term breeding phenology shift in royal penguins. Ecol Evol 2:1563–1571

Hodgdon HE, Larson JS (1973) Some sexual differences in behaviour within a colony of marked beavers (Castor canadensis). Anim Behav 21:147–152

Holzer B, Jacot A, Brinkhof MWG (2003) Condition-dependent signaling affects male sexual attractiveness in field crickets, Gryllus campestris. Behav Ecol 14:353–359

Jenkins SH (2011) Sex differences in repeatability of food-hoarding behaviour of kangaroo rats. Anim Behav 81:1155–1162

Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol 16:1099–1106

Kenagy GJ, Sharbaugh SM, Nagy KA (1989) Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. Oecologia 78:269–282

Kenward RE (2001) A Manual for Wildlife Radio-tagging. Academic Press, London

Kerr TD, Boutin S, LaMontagne JM, McAdam AG, Humphries MM (2007) Persistent maternal effects on juvenile survival in North American red squirrels. Biol Lett 3:289–291

Key C, Ross C (1999) Sex differences in energy expenditure in non-human primates. Proc R Soc Lond B 266:2479–2485

Körner M, Vogelweith F, Foitzik S, Meunier J (2017) Condition-dependent trade-off between weapon size and immunity in males of the European earwig. Sci Rep 7:7988

Krebs CJ, Boutin S, Boonstra R (2001) Ecosystem Dynamics of the Boreal Forest: the Kluane Project. Oxford University Press, New York

Kumari PV, Khan JA (1979) Food hoarding by Indian gerbil, *Tatera indica indica* (Hardwicke). Proc Indian Acad Sci Anim Sci 88:131–135

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: tests in linear mixed effect models. J Stat Softw 82:1–26

Yosef R, Pinshow B (1989) Cache size in shrikes influences female mate choice and reproductive success. Auk 106:418–421

LaMontagne JM, Boutin S (2007) Local-scale synchrony and variability in mast seed production patterns of *Picea glauca*. J Ecol 95:991–1000

LaMontagne JM, Williams CT, Donald JL, HM M, McAdam AG, Stan B (2013) Linking intraspecific variation in territory size, cone supply, and survival of North American red squirrels. J Mamm 94:1048–1058

Lane JE, Boutin S, Gunn MR, Coltman DW (2009) Sexually selected behaviour: Red squirrel males search for reproductive success. J Anim Ecol 78:296–304

Lane JE, Boutin S, Gunn MR, Slate J, Coltman DW (2007) Genetic relatedness of mates does Not predict patterns of parentage in North American red squirrels. Anim Behav 74:611–619

Lane JE, Boutin S, Gunn MR, Slate J, Coltman DW (2008) Female multiple mating and paternity in free-ranging North American red squirrels. Anim Behav 75:1927–1937

Lane JE, Boutin S, Speakman JR, Humphries MM (2010) Energetic costs of male reproduction in a scramble competition mating system. J Anim Ecol 79:27–34

Lane JE, McAdam AG, Mcfarlane SE, Williams CT, Humphries MM, Coltman DW, Gorrell JC, Boutin S (2018) Phenological shifts in North American red squirrels: disentangling the roles of phenotypic plasticity and microevolution. J Evol Biol 31:810–821

Larivée ML, Boutin S, Speakman JR, McAdam AG, Humphries MM (2010) Associations between over-winter survival and resting metabolic rate in juvenile North American red squirrels. Funct Ecol 24:597–607

Larsen KW, Becker CD, Boutin S, Blower M (1997) Effects of hoard manipulations on life history and reproductive success of female red squirrels (*Tamiasciurus hudsonicus*). J Mammal 78:192–203

Larsen KW, Boutin S (1994) Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. Ecology 75:214–223

Larue B, Pelletier F, Festa-Bianchet M (2022) A multivariate perspective of resource acquisition behaviors in bighorn sheep. Anim Behav 184:81–87

Laskowski KL, Moiron M, Niemelä P (2021) Integrating behavior in life-history theory: allocation versus acquisition? Trends Ecol Evol 36:132–138

Lemaitre JF, Gaillard JM (2017) Reproductive senescence: new perspectives in the wild. Biol Rev 92:2182–2199

Maklakov AA, Simpson SJ, Zajitschek F, Hall MD, Dessmann J, Clissold F, Raubenheimer D, Bonduriansky R, Brooks RC (2008) Sex-specific fitness effects of nutrient intake on reproduction and lifespan. Curr Biol 18:1062–1066

Markman S (2014) Parental self-feeding effects on parental care levels and time allocation in Palestine sunbirds. PLoS ONE 9:e113890

Marshall TC, Slate J, Kruuk LEB, Pemberton JM (1998) Statistical confidence for likelihood-based paternity inference in natural populations. Mol Ecol 7:639–655

Martinig AR, McAdam AG, Dantzer B, Lane JE, Coltman DW, Boutin S (2020) The new kid on the block: immigrant males win big whereas females pay fitness costs after dispersal. Ecol Lett 23:430–438

McAdam AG, Boutin S (2003) Variation in viability selection among cohorts of juvenile red squirrels (*Tamiasciurus hudsonicus*). Evolution 57:1689–1697

McAdam AG, Boutin S (2003) Effects of food abundance on genetic and maternal variation in the growth rate of juvenile red squirrels. J Evol Biol 16:1249–1256

McAdam AG, Boutin S, Dantzer B, Lane JE (2019) Seed masting causes fluctuations in optimum litter size and lag load in a seed predator. Am Nat 194:574–589

McAdam AG, Boutin S, Réale D, Berteaux D (2002) Maternal effects and the potential for evolution in a natural population of animals. Evolution 56:846–851

McAdam AG, Boutin S, Sykes AK, Humphries MM (2007) Life histories of female red squirrels and their contributions to population growth and lifetime fitness. Ecoscience 14:362

McLean IG, Towns AJ (1981) Differences in weight changes and the annual cycle of male and female Arctic ground squirrels. Arctic 34:249–254

Milner JM, van Beest FM, Solberg EJ, Storaas T (2013) Reproductive success and failure: the role of winter body mass in reproductive allocation in Norwegian moose. Oecologia 172:995–1005

Monteith KL, Schmitz LE, Jenks JA, Delger JA, Bowyer RT (2009) Growth of male white-tailed deer: consequences of maternal effects. J Mammal 90:651–660

Mousseau TA, Fox CW (1998) The adaptive significance of maternal effects. Trends Ecol Evol 13:403–407

Naya DE, Ebensperger LA, Sabat P, Bozinovic F (2008) Digestive and metabolic flexibility allows female degus to cope with lactation costs. Physiol Biochem Zool 81:186–194

Nishida Y, Takagi M (2019) Male bull-headed shrikes use food caches to improve their condition-dependent song performance and pairing success. Anim Behav 152:29–37

Oftedal OT (1985) Pregnancy and lactation. In: Hudson RJ, White RG (eds) Bioenergetics of wild herbivores. CRC Press, Boca Raton, pp 215–238

Podofillini S, Cecere JG, Griggio M, Corti M, De Capua EL, Parolini M, Saino N, Serra L, Rubolini D (2019) Benefits of extra food to reproduction depend on maternal condition. Oikos 128:943–959

Post E, Forchhammer MC (2008) Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Proc R Soc Lond B 363:2369–2375

Price K, Boutin S (1993) Territorial bequeathal by red squirrel mothers. Behav Ecol 4:144–150

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Réale D, Berteaux D, McAdam AG, Boutin S (2003) Lifetime selection on heritable life-history traits in a natural population of red squirrels. Evolution 57:2416–2423

Reddiex AJ, Gosden TP, Bonduriansky R, Chenoweth SF (2013) Sex-specific fitness consequences of nutrient intake and the evolvability of diet preferences. Am Nat 182:91–102

Reznick D, Callahan H, Llauredo R (1996) Maternal effects on offspring quality in poeciliid fishes. Am Nat 36:147–156

Ridgway MS, Shuter BJ (1994) The effects of supplemental food on reproduction in parental male smallmouth bass. Environ Biol Fish 39:201–207

Roff DA (1992) The evolution of life histories: theory and analysis. Chapman and Hall, New York

Salomon M, Mayntz D, Toft S, Lubin Y (2011) Maternal nutrition affects offspring performance via maternal care in a subsocial spider. Behav Ecol Sociobiol 65:1191–1202

Schroeder J, Piersma T, Groen NM, Hooijmeijer JCEW, Kentie R, Lourenco PM, Schekkerman H, Both C (2012) Reproductive timing and investment in relation to spring warming and advancing agricultural schedules. J Ornithol 153:327–336

Smith MC (1968) Red squirrel responses to spruce cone failure in Interior Alaska. J Wildlife Manage 32:305–317

Snijders TAB, Bosker RJ (1999) Multilevel analysis: an introduction to basic and advanced multilevel modeling. Sage, London

Stearns S (1992) The Evolution of Life Histories. Oxford University Press, Oxford

Stuart-Smith AK, Boutin S (1994) Costs of escalated territorial defence in red squirrels. Can J Zool 6:1162–1167

Vander Wall SB (1990) Food hoarding in animals. University of Chicago Press, Chicago

Warner DA, Lovern MB (2014) The maternal environment affects offspring viability via an indirect effect of yolk investment on offspring size. Physiol Biochem Zool 87:276–287

Westrick SE, Taylor RW, Boutin S, Lane JE, McAdam AG, Dantzer B (2020) Attentive red squirrel mothers have faster growing pups and higher lifetime reproductive success. Behav Ecol Sociobiol 74:72

Williams CT, Lane JE, Humphries MM, McAdam AG, Boutin S (2014) Reproductive phenology of a food-hoarding mast-seed consumer: Resource- and density-dependent benefits of early breeding in red squirrels. Oecologia 174:777–788

Woodroffe R (1995) Body condition affects implantation date in the European badger, *Meles meles*. J Zool 236:183–188

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