Resources and Reproductive Trade-offs Affect Fitness, Life History Traits, and Sexual Selection in Red Squirrels

by

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Abstract

Animals face trade-offs throughout life between competing functions, such as between self-maintenance, reproduction, and survival. Resource allocation between these competing functions leads to different patterns of life history traits, changes in investment in reproductive effort, and different patterns of reproductive success. Reproductive investment is also influenced by environmental factors, for example by resource availability or mating opportunities. In this thesis, I test for evidence of reproductive and life history trade-offs, as well as for whether individual- and population-level resource availability affect reproduction and life history traits.

In my first chapter I tested whether there was evidence of age-related changes in reproductive success and a sexually-selected trait in male red squirrels, and in particular whether there was evidence of senescent decline in older ages. I also considered whether there was a trade-off between early-life reproduction and late-life senescence in male red squirrels by testing whether age at first reproduction affected senescent decline. Theories of the evolution of senescence predict that this trade-off exists, but are typically tested in females. I found evidence of senescence, as well as evidence that males who delay reproduction achieve higher reproductive success throughout life. However, I did not find that age at first reproduction affected senescence rate. Thus, males do decline late in life but the rate of this decline was not dependent on the timing of the onset of reproductive success.

In my second chapter I tested whether encountering a resource pulse affected life history traits. I also tested whether life history trade-offs and the fitness consequences of life history traits were affected by encountering a resource pulse called a mast year. I found that males who encountered a resource pulse as a yearling were more likely to breed. As mast years occur in the autumn but squirrels breed during the spring, this increase in reproductive effort is evidence of anticipatory reproduction in males. I also found that males achieved higher lifetime reproductive success when they encountered a mast year during their life. The fitness consequences of life history traits were also affected by encountering a mast year: males sired more pups when they bred early in life if they encountered a mast year in their lifetime, but they sired more pups when they bred late in life if they did not encounter a mast year. Encountering a mast year thus has significant consequences for fitness and for life history traits of male red squirrels.

In my third chapter I tested whether there were different siring opportunities in mast years compared with non-mast years. I then tested whether this affected male mating behaviour. I found that there were more females who produced offspring during a mast year, and that in particular there were more second litters produced during a mast year. Male mating behaviour and siring patterns differed during a mast year, during a mast year males increased their reproductive effort. Reproductive success also differed between first and late litters during mast years: in late litters, males sired pups closer to their territories, with fewer females, and sired a larger proportion of the litter. I also showed evidence that males committed infanticide during a mast year. This suggests that resource pulses influence both mating opportunities for males, as well as the fitness consequences of reproductive investment.

In my fourth chapter, I tested whether individual-level food availability was related with breeding season timing, mating behaviour, and reproductive success in male and female red squirrels. I demonstrated that there was an effect of cached cones on male reproductive success: males bred earlier, sired more pups, and sired more recruits when they had more cached cones in their midden. Males who cached more cones also had higher longevity and lifetime reproductive success. In contrast, the effect of resources on female reproductive success was weaker, as having higher cached resources was only associated with earlier breeding. There was also no effect of resources on female lifetime reproductive success.

Preface

This thesis is an original work by Jessica A. Haines. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Animal Care and Use Committee for Biosciences, “Effects of resource variability on behavioural and life history characteristics of red squirrels.”

The research conducted for this thesis forms part of an international research collaboration in the Kluane Red Squirrel Project; the lead collaborator at the University of Alberta is Dr. Stan Boutin. The chapters in this thesis were designed and written by Jessica A. Haines. The field data was collected as part of this collaboration and collaborators also contributed to refining of the chapters. These chapters have been written in the format of manuscripts to be submitted to scientific journals.

Dedication

I dedicate this thesis to my partner Josh and the rest of my family for their love and support. I particularly wish to dedicate this thesis to my new family members who were born while I wrote it: to my nieces Chloe, Penny, Victoria, and Murphy. And finally, I dedicate this thesis to my grandparents that I lost during my university degrees: to Red, Evie, and Marilyn. I wish they could be here to share in this accomplishment with me.

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Chapter 1: Introduction

"Life histories are shaped by the interaction of extrinsic and intrinsic factors, the extrinsic factors are ecological impacts on survival and reproduction, the intrinsic factors are trade-offs among life history traits and the lineage-specific constraints on the expression of genetic variation." (Stearns 2000)

An organism's lifetime is a series of allocation decisions which shape their patterns of growth, maturation, reproduction and survival; these are described as life history traits (Stearns 2000). Reproduction is costly (Reznick, Nunney & Tessier 2000), and so allocating resources into different life history traits can result in trade-offs between competing functions (Stearns 1989). For example, investing in current reproduction may necessarily detract from self-maintenance, resulting in decreased reproduction in future reproductive events and senescence in older age classes (Lemaître *et al.* 2015). Thus, the timing and magnitude of reproductive investment throughout life creates many of the between-individual differences in life histories. However, trade-offs have not been universally detected even though they are predicted by theory (Reznick *et al.* 2000). There may be individual-level differences not only in the allocation of resources to reproduction, but in resource acquisition (Van Noordwijk & de Jong 1986). Thus reproductive trade-offs are central to understanding the patterns of investment detected among and within species, but are also influenced by extrinsic factors and can be difficult to detect.

Organisms live in variable environments, and as a result the life history trait combinations that maximize fitness may differ depending on the conditions that individuals encounter. Although it is intuitive to expect animals to be able to respond appropriately to environmental or food conditions, they may be constrained in their response. For example, animals may be capital or income breeders (Stephens *et al.* 2009): capital breeders use internal resources to fuel reproduction, while income breeders use external resources to fuel reproduction; this distinction may affect whether they respond to resource availability (Reznick & Yang 1993). Individuals that use resources external to themselves may have a more immediate response to resource limitation. In contrast, individuals that use internal resources may be buffered against variation in the environment. Animals are also constrained by intrinsic trade-offs between life history traits, such as through genetic correlations, limits on development, or due to selection for certain trait combinations (Pease & Bull 1988; Stearns 2000; Ricklefs & Wikelski 2002; Réale *et al.* 2010). Because life history traits can have limited plasticity, animals may not be able to respond appropriately to all environmental conditions that they encounter. Thus, reproductive investment and timing of that investment is limited both by intrinsic constraints and ecological limits on animals, and exploring these internal and external limits on organisms is central to life history theory (Stearns 2000). In addition, males and females may be under different selection pressures, resulting in different intrinsic and extrinsic constraints on life history traits and sex-specific life history optima (Wedell *et al.* 2006).

Theory predicts that life history traits will occur in specific combinations due to these intrinsic and extrinsic limits. For example, according to the pace of life theory animals rank along a fast-slow continuum: fast animals reach age of primiparity early in life, have high fecundity, and short longevity, while slow animals have the opposite traits (Réale *et al.* 2010). Particularly novel is that this theory suggests that these patterns of life history traits are also connected with animal behaviour and physiology (Réale *et al.* 2010). For example, animals with a fast pace of life may have higher metabolic rates or certain personality syndromes, such as being more active (Careau *et al.* 2009; Montiglio *et al.* 2014). These different phenotypes may exist due to fluctuating environments that result in certain behavioural, life history, or physiological traits producing high fitness in different environments (Réale *et al.* 2010; Montiglio *et al.* 2014). Thus, variable environments not only could have consequences for life history but also for the associated behavioural and physiological traits. If this extends to effects on mating behaviour, then these patterns of selection on life history traits also have implications for sexual selection in different environments.

I studied how reproductive trade-offs and changes in mating opportunities due to fluctuating resources affect fitness, life history traits, and sexual selection in North American red squirrels (*Tamiasciurus hudsonicus*). Since 1988, the Kluane Red Squirrel Project has collected data in two study areas (Kloo and Sulphur) near Kluane Lake, Yukon. More detailed descriptions of the field methodology can be found elsewhere (McAdam *et al.* 2007). Squirrels in these populations were tagged with alphanumeric ear tags threaded with unique combinations of coloured wires. Both trapping and behaviour observations were thus used to monitor survival of individuals from March to August each year. Red squirrels defend territories centered on a food cache, called a midden; this territorial behaviour enables us to enumerate all individuals in the population. Female reproduction was assessed with regular trapping to determine when they were pregnant. Parturition date was then determined using trapping by observing weight and nipple changes. Nests were located using telemetry, all pups were counted and weighed, and tissue samples were taken to determine paternity with genetic analyses. Pups were measured again at 25 days old to calculate growth rate, then tagged to monitor their subsequent survival. Pups disperse over short distances (Berteaux & Boutin 2000), so detecting pups in the population after their first winter is a reasonable measure of recruitment into the breeding population.

Male reproductive success was estimated using genetic analyses of tissue samples collected from pups during the breeding seasons in 2003-2014. Red squirrels have a scramble competition mating system: males achieve success by mating with many females and having larger home ranges to access those females (Lane *et al.* 2009). Females come into oestrous for a single day, and mate with many males during a mating chase (Lane *et al.* 2008, 2009). In a subset of years (2003-2005, 2008, 2013-2014), Male home range area was measured by radio-collaring females to monitor attendance at mating chases and/or by locating males regularly throughout the breeding season to record their spatial location.

White spruce (*Picea glauca*) influences red squirrel reproduction and breeding timing (Boutin *et al.* 2006; Williams *et al.* 2014). Females produce more litters, more pups, and more recruits in years with high cone availability (Boutin *et al.* 2006). This does not, however, occur because of increases in energy available for reproduction. Squirrels breed in spring and cones are available until July (Fletcher et al. 2013). Red squirrels harvest and cache these cones in their midden and these resources are important for over-winter survival especially for juveniles (Larsen & Boutin 1994; LaMontagne *et al.* 2013). Thus, white spruce cone availability influences recruitment of their pups, and female red squirrels respond with anticipatory reproduction (Boutin *et al.* 2006). White spruce trees periodically produce large amounts of cones, called mast years (Lamontagne and Boutin 2009); these years are particularly influential on female reproduction because of the magnitude of resource availability in these years and thus the increased pup recruitment in those years (Boutin *et al.* 2006; Williams *et al.* 2014). The effects of masts on male reproduction has not been studied, but due to the changes in female reproduction these years will result in higher mating opportunities for males. These resource pulses thus provide an easily quantified, biologically relevant measure of resources. The number of cones produced by trees within each study area was quantified by counting the number of cones visible on one side of the crowns of marked trees located systematically throughout each study area (Lamontagne, Peters & Boutin 2005). The variation in cached cones was quantified using quadrats set up on middens as a measure of individual-level resource availability.

In my first chapter, I explored whether there was evidence of senescence, as well as whether there were trade-offs between early- and late-life reproduction. Senescence is a physiological deterioration in old age resulting in decreased reproduction and survival (Monaghan *et al.* 2008; Wilson, Charmantier & Hadfield 2008). Senescence occurs in a wide range of wild species (Jones *et al.* 2008), and persists in the wild despite having negative consequences for fitness. Senescence may be due to a connection between early-life success and late-life decline (Lemaître *et al.* 2015): genes with a positive effect on early-life reproduction may have negative effects on late-life fitness (Williams 1957). Alternatively, due to trade-offs between self-maintenance, reproduction, and other functions, deleterious damage should accumulate beyond average longevity due to decreased investment in self-maintenance (Kirkwood 1977). Thus, higher investment early in life should cause faster senescence rates late in life (Lemaître *et al.* 2015). This has been less studied in males than in females, and as males often invest in offspring quantity rather than quality they could have a higher wear and tear strategy with faster senescence than in females (Bonduriansky *et al.* 2008). In red squirrels, previous work has explored patterns of senescence in females, as well as actuarial senescence in males (Descamps *et al.* 2008). I investigated whether there is evidence of senescence in male red squirrels. I then tested whether there was evidence of a trade-off between age at first reproduction and late-life senescent decline.

In my second chapter, I tested for evidence of life history trade-offs and the effects of mast years on life history traits and trade-offs. Life history traits are limited by both external (eg. environmental) and internal (eg. genetic) constraints (Stearns 1989, 2000). Previous research on female red squirrels has shown evidence that early-breeding females have higher breeding success and shorter longevity, as well as achieve higher lifetime reproductive success (Descamps *et al.* 2006); life history traits have not been studied in males. I tested whether encountering mast years affected male life history trade-offs and lifetime reproductive success. I then tested whether encountering a mast year altered the trade-offs between life history traits, as well as the fitness consequences of those life history traits. I thus tested whether there is evidence that, like females, a resource pulse influences male life history traits.

In my third chapter, I tested whether mast years influenced mating opportunities and thus patterns of mating behaviour and paternity in red squirrels. Ecological conditions that alter the spatial or temporal distribution of mating opportunities affects sexual selection by altering the mate availability (Emlen & Oring 1977). Ecological factors such as predation, density, and weather have had demonstrated effects on the magnitude and strength of sexual selection (Chaine & Lyon 2008; Cockburn, Osmond & Double 2008; Gosden & Svensson 2008; Weese *et al.* 2010). Although shifts in sexual selection have been demonstrated, the mechanisms underlying these changes are often poorly-understood. I tested whether mast years influenced male mating behaviour and paternity. Females increase their reproductive investment in mast years (Boutin *et al.* 2006), suggesting that siring opportunities may also change in these years. This makes it an ideal system to study the effects of the environment on sexually selected traits.

In my last chapter, I investigated whether individual-level resources affected reproduction and mating behaviour. It is intuitive to predict that having access to more resources would improve success as reproductive investment is energetically demanding (Lane *et al.* 2010; Fletcher *et al.* 2012). There is evidence of a link between resources and breeding timing, litter size, and reproductive success in other species (Boutin 1990; Pelletier & McNeil 2003; Derbyshire, Strickland & Norris 2015; Kaiser *et al.* 2015), but there is also evidence to the contrary (Boutin 1990; Dawson & Bortolotti 2000; Harrison *et al.* 2010; Sim *et al.* 2015; Crates *et al.* 2016). I tested for a connection between cached cones and reproduction in male and female red squirrels. The connection between fitness and population-level cone availability has been demonstrated (Boutin *et al.* 2006) but the effects of individual-level resources and reproduction has not been previously tested. I also tested whether cached cones influenced lifetime reproductive success.

Red squirrels make ideal study species for these questions. I was able to reliably estimate life history traits, as well as both annual and lifetime measures of reproductive success. In addition, the squirrels' reliance on conifer seed and the demonstrated effects of this on female reproduction mean that their predominant source of energy can be measured. The masting of white spruce trees creates irregular resource pulses that are quantifiable and that alter mating opportunities. As well, by caching cones in a central midden I can quantify individual-level resource availability. Thus, the red squirrel system is ideal for studying the effects of reproductive trade-offs, mating opportunities, and resources on life history traits, fitness, and sexual selection.

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Chapter 2: Evidence of senescence in male red squirrels but no link between early-life reproduction and late-life decline

Introduction

Senescence is a physiological deterioration in old age that leads to decreased reproduction and survival (Monaghan *et al.* 2008; Wilson, Charmantier & Hadfield 2008). Research from wild animals is providing evidence that senescence occurs in a wide range of species (Jones *et al.* 2008). Although often studied by sampling individuals of different ages within a population, selective appearance or disappearance of individuals of a certain quality can mask detection of age-related patterns of change at the individual level (Van de Pol & Verhulst 2006; Nussey *et al.* 2008). Senescence is thus best detected using longitudinal, individual-based studies, enabling separating age-related changes into between-individual and within-individual differences (Van de Pol & Verhulst 2006; Nussey *et al.* 2008). Research such as this exploring senescence in wild animals is providing insights about the evolution of senescence and its underlying mechanisms (Wilson *et al.* 2008).

Due to sex-specific life history optima and reproductive strategies, patterns of senescence may differ between the sexes. For example, males in many species invest in offspring quantity, rather than quality, potentially leading to a high wear and tear strategy and thus rapid senescence (Bonduriansky *et al.* 2008). It is therefore essential to investigate senescence in both sexes (Lemaître *et al.* 2015). Actuarial senescence has been well-documented in both sexes, but most studies on reproductive senescence have focused on females and it is less understood in males. Where it has been studied, reproductive senescence has been documented in males of some species (Vanpé *et al.* 2007), but not others (Mason *et al.* 2012; Benowitz *et al.* 2013), suggesting that reproductive senescence in males warrants further investigation. It is also essential to investigate a diversity of traits when studying senescence in either sex (Nussey *et al.* 2008). Many studies have examined patterns of actuarial senescence, but reproductive success or sexually-selected traits may have different age-related patterns of change (Nussey *et al.* 2008; Evans, Gustafsson & Sheldon 2011). For example, males of many species have sexually-selected traits whose expression increases with age so that older age classes have higher reproductive success; this could potentially reduce the expression of senescence (Bonduriansky *et al.* 2008).

Connections between sexual selection and ageing will help further the understanding of senescence in males.

Three explanations for the evolution of senescence have been proposed (Partridge & Gems 2006; Monaghan *et al.* 2008). First, accumulation of deleterious mutations in old age occurs because the strength of selection is reduced given the small proportion of individuals alive in older age classes (Medawar 1952). Second, according to the antagonistic pleiotropy explanation, alleles that have negative effects later in life may be selected for because they have positive effects early in life (Williams 1957). Finally, the disposable soma theory suggests that there is a trade-off between self-maintenance, reproduction, and other functions: animals should not invest in self-maintenance beyond average longevity, so deleterious damage accumulates beyond that point (Kirkwood 1977). The last two hypotheses suggest a connection between early-life investment and late-life declines and there is some empirical support for this link (Lemaître *et al.* 2015). In particular, if a life history trade-off is present, higher investment early in life should cause steeper late-life declines. However, some empirical work has failed to show this link while other studies have even found a positive correlation between early- and late-life reproductive success (Lemaître *et al.* 2015). Individual differences in allocation and acquisition of resources and selective mortality can mask life history trade-offs (Van Noordwijk & de Jong 1986), suggesting that the link between early-life and late-life success could be obscured or positive even if a trade-off is present (Nussey *et al.* 2008). Trade-offs between survival and reproduction have also been shown to depend on environmental conditions (Robert *et al.* 2015). Thus, despite theory predicting a link between early-life success and senescence, the evidence is unclear and this warrants further investigation.

I investigated whether there was evidence of senescence of reproductive success, a sexually-selected trait, and survival in male red squirrels. Previous research demonstrated evidence of actuarial senescence in both sexes and reproductive senescence in females (Descamps *et al.* 2008), but reproductive senescence in males has not been studied. I used long-term data on individually-marked squirrels collected by the Kluane Red Squirrel Project. For over a decade, genetic techniques were used to assign paternity to offspring in two populations. As all animals in these populations are monitored throughout their lifetime, I was also able to determine longevity of adults as well as survival of offspring into the breeding season after their birth year. I was thus able to quantify male reproductive success as the number of offspring sired and offspring recruited. Male red squirrels achieve reproductive success by having large home range areas during the breeding season and copulating with many females (Lane *et al.* 2009), and I quantified this mating behaviour by measuring home range area with field observations. I first determined whether there were age-related changes in the number of pups and recruits sired, a sexually selected behaviour, and survival in male red squirrels. I expected that male red squirrels would have increasing reproductive success, home range area, or survival early in life, peak during middle ages, and decline in old age; this age-related pattern has been widely shown in other species (Jones *et al.* 2008). I also tested for the effects of age at first reproduction in order to distinguish between within-individual changes in reproductive success and the effects of selective appearance or disappearance. Although testing for evidence of actuarial senescence was done previously (Descamps *et al.* 2008), the effects of age at first reproduction were not tested. I then determined whether there was a relationship between early-life success, quantified as age at first reproduction, and senescence rate in male red squirrels. I also tested whether there was evidence for a relationship between lifetime reproductive success and senescence rate. I expected that males who bred earlier or who had the highest lifetime reproductive success would have the fastest senescence rate due to the costs of investing in reproductive success.

Methods

Long-term Monitoring

Red squirrels have been studied as part of the Kluane Red Squirrel Project since 1988 near Kluane Lake, Yukon, in two study areas: Kloo and Sulphur (herein called KL and SU). Detailed field methods have previously been described (Humphries & Boutin 2000; McAdam *et al.* 2007; Lane *et al.* 2008). Squirrels were given unique combinations of numbered tags and coloured wires in their ears, allowing us to identify individuals over multiple years as well as from a distance. Red squirrels have distinct and separate territories centred on a food cache, which they defend with territorial rattles (Smith 1978; Dantzer *et al.* 2012). All individuals were monitored along with their spatial location and territory ownership, thus completely enumerating these populations each year with a detection probability of 1 (Descamps *et al.* 2009).

Individuals of both sexes were trapped and observed regularly from March to August each year to monitor their survival. Adult red squirrels rarely dispersed, with the exception of adult females who may bequeath territories to their offspring (Berteaux & Boutin 2000). Thus, I assumed that when a squirrel disappeared from its territory that it had died, and thus I estimated longevity based on the date they were last detected in the population. Female reproduction was monitored during this time using trapping, and they were given radio collars once they gave birth so that their offspring could be tagged in the nest. Juveniles dispersed over short distances (Berteaux & Boutin 2000). Thus, I determined whether a pup recruited based on whether it was detected in the population as a yearling the following year. I calculated age for each individual based on their birth year. When individuals were first detected as adults, for example because they established a territory too late in the autumn to be detected during regular monitoring, at their first capture they were assigned a birth year of the previous year as has been done previously (eg. Lane *et al.* 2009).

Measuring Male Reproductive Success and Behaviour

Since 2000, ear tissue samples were taken from squirrels the first time they were handled, either as pups in the nest or the first time they were trapped. Maternal identity of pups was determined based on telemetry at the nest and maternal behaviour. Paternal identity was determined using genetic analyses of these ear tissue samples. Systematic paternity assignment began in 2003 on both study sites; thus, this paper includes paternities from 2003-2014. DNA was extracted using Qiagen DNeasy Tissue extraction kits. PCR amplification was then performed on 16 microsatellite loci and genotypes were scored using GENEMAPPER software 3.5 (Applied Biosystems). On average, loci were genotyped at a proportion of 0.95 across individuals. Paternity was assigned at 95% confidence using CERVUS 2.0. Genotyping error based on matching of known mother-offspring relationships was 2%. On average 81% of the pups born in the population each year (including both pups tagged in the nest and juveniles tagged outside of the nest) were assigned sires (Table A1.1). More details about the genetic methods can be found elsewhere (Gunn *et al.* 2005; Lane *et al.* 2008). During 2003-2014 on two study areas, 1497 juveniles had sires identified through genetic analyses. Of these, 1420 (95%) were tagged in the nest, and 77 (5%) were tagged as juveniles outside of the nest. As the majority of offspring were thus tagged in the nest, where I can be confident that all pups in the litter were sampled, I was confident that the paternity assignments were representative of male reproductive success.

Using the paternity data from the genetics analysis, I calculated the number of pups that each male sired each year from 2003-2014. I then determined which pups survived overwinter until the following year, and thus was able to calculate the number of recruits that males sired from 2004-2015. I thus calculated annual reproductive success for each male as 1) the number of pups sired and 2) the number of recruits sired. As males were followed throughout their lives as part of long-term monitoring, I also calculated lifetime reproductive success by summing 1) pups and 2) recruits for each male. Using the paternity data, I also calculated the age at which males were first successfully sired pups (age at first reproduction or AFR) and the age at which they were last successful at siring pups (age at last reproduction, ALR).

Female red squirrels come into oestrous on a single day, and multiple males mate with her during that time in a mating chase (Lane *et al.* 2007, 2008). Males obtain higher reproductive success by attending more mating chases, obtaining more copulations, and having larger home ranges during the breeding season in order to locate receptive females (Lane *et al.* 2009). Mating behaviour was monitored from 2003-2005, 2008, and 2013-2014. More detailed description of the data collection during 2003-2005 and 2008 can be found elsewhere (Lane *et al.* 2007, 2008, 2009; Taylor 2012), but briefly females were radio-collared and followed during their day of oestrous. During mating chases, identities of males in attendance and during copulations were recorded along with their spatial locations. For a subset of these males and in 2013-2014, mating behaviour was monitored by radio-collaring males and locating them regularly during the mating season to record their spatial location. In all years that mating behaviour was monitored, spatial locations of males encountered by observers in the mating season while working on the study areas or when they were trapped as part of long-term monitoring were also recorded. All locations were used to calculate the area that males traveled during the mating season (herein called home range, as defined by Lane *et al.* 2009) using a 100% minimum convex polygon (MCP) as was done previously (Lane *et al.* 2009). Home range data for 2003-2005 and 2008 was calculated previously (Lane *et al.* 2007, 2008, 2009; Taylor 2012). Home range in 2013-2014 were calculated using the R version 3.1.2 (R Core Team 2014) and package adehabitatHR version 0.4.12 (Calenge 2006), and for these calculations males with 5 locations or less were excluded. MCP is influenced by the number of locations used in each calculation (Lane *et al.* 2009), so the number of locations was included as a covariate in all analyses of breeding season home range. In 2013 and 2014, data collection began in March and February of that year, respectively. Based on field observations, males began searching for mating opportunities prior to the first parturition date (unpublished data). It is unknown when they stopped engaging in mating behaviour, so data up to and including the date of the last parturition date of females on the study area was included.

Early-Life Success and Senescence Rate

I used age at first reproduction, quantified from paternity data, as my measure of early-life success. Most males began siring pups by age two (see Results for descriptive statistics), but some males sired pups for the first time at three to four years of age. I categorized age at first reproduction as one (1) or later (2).

I calculated the age at which males achieved peak reproduction in order to define the onset of senescence. Red squirrel reproductive success fluctuates depending on white spruce cone production (Boutin *et al.* 2006). In analyses where I tested whether reproductive success changed with age, I used absolute numbers of pups and recruits and accounted for annual variation in reproductive success by including a study area-year random effect in statistical models (see Statistical Analyses, below, for rationale and details). However, to calculate the age at which they achieved peak reproduction, I accounted for annual variation in reproductive success by standardizing reproductive success: I subtracted the study area-yearly mean annual number of pups sired (year-study area average). I then defined peak reproduction as the youngest age at which males reached their maximum standardized number of pups sired, as the year following peak reproduction was the youngest age at which they could undergo a senescent decline. I analyzed annual reproductive success, quantified as the number of pups sired, from peak reproduction until death in order to analyze senescence rate. I excluded annual reproductive success data from prior to peak reproduction in order to restrict the analysis to the years in which males could experience senescence. I used the number of pups sired as a measure of success rather than recruits sired as the number of pups sired provides a longitudinal measure of changes in reproductive success with a larger sample size.

Data Selection

The pedigree data for known-age individuals revealed that males never sired pups in the breeding season they were born (see descriptive statistics in Results), so I excluded any males who did not survive to their first breeding season (i.e. age one). Also, occasionally males with territories outside the study areas were trapped during the breeding season but never occupied a territory on the study areas; these males were excluded from my analyses. Analyzing reproductive output using longitudinal data enhances the ability to detect age-related changes (Van de Pol & Verhulst 2006; Nussey *et al.* 2008), so I included records from age one to death for age-related changes in reproductive success. When analyzing age-related changes in pups and recruits sired, I only included males who had sired at least one pup or one recruit during their lifetime, respectively, as males could not undergo age-related changes in the number of pups sired if they had never sired pups. Home range and survival data were also only analyzed for males who sired at least one pup during their lives as their age at first reproduction was known. Home range area was calculated from behaviour data which was only available in certain years, and so does not represent complete lifetime data. The oldest male whose home range I measured was five years old, which is younger than the data on reproductive success (see Results).

I completed the analysis of age-related changes in reproductive success, behaviour, and survival in two ways. First, I included all data using the restrictions discussed above, regardless of whether males were successful (Models 1-4 in Table 2.1). However, comparing model coefficients for age at first reproduction (see Results) to the data (Figures A1.1-A1.4), it was evident that the coefficients for age at first reproduction were heavily influenced by including data from prior to age at first reproduction. Thus, in order to quantify the effects of age at first reproduction on reproductive success, I also excluded data from prior to when males first successfully produced offspring (Models 5-8 in Table 2.1).

Statistical Analysis

All statistical analyses were done using R Version 3.3.0 (R Core Team 2016). Data were standardized with a mean of 0 and standard deviation of 0.5 (Grueber *et al.* 2011) using the function standardize from package arm version 1.7-07 (Gelman & Su 2015). I created a biologically plausible candidate model set manually for each analysis and used Akaike's Information Criteria corrected for small sample sizes (AICc) to find the top-ranked model (Burnham & Anderson 2002). This was calculated using the model.sel and coeffTable functions in the MuMIn package version 1.12.1 (Bartón 2016). I included any models that were ≤ 6 ΔAICc from the top candidate model as this generally will include 95% of the plausible models

(Richards 2005; Richards, Whittingham & Stephens 2011; Symonds & Moussalli 2011) and calculated model-averaged coefficients using the zero method of model averaging with the model.avg function in MuMIn (Burnham & Anderson 2002; Grueber *et al.* 2011). Mixed effects models were analyzed using the functions lmer and glmer with the lme4 package version 1.1-7 (Bates *et al.* 2014). To aid with visualization and interpretation of some results, model predictions from the top-ranked model were graphed using the R function predict. In the case of model sets with more than one top-ranked model, I used the model-averaged coefficients to generate the predictions. To generate these predictions, I set all variables to 0 (ie. the mean, as the data was standardized) except for the variables of interest. Statistical output and figures were exported using the ReporteRs package version 0.7.2 (Gohel 2014). Where I have reported descriptive statistics, I also reported ±standard deviation. I have reported the model-averaged coefficients generated by the top-ranked model sets (see Results), but the full model sets are presented in Appendix 1 (Tables A1.4-A1.5). I calculated confidence intervals as 1.96 x standard error for the model coefficients in order to determine my confidence in the estimation of the coefficients. Sample size varied for each analysis, and is indicated in the supplementary model selection tables (Tables A1.4-A1.5). Pseudo-R^2 appropriate for generalized linear mixed effects models were calculated using the R package MuMIn (Nakagawa & Schielzeth 2013; Bartón 2016); these were also presented in Appendix 1 (Tables A1.4-A1.5).

I used mixed effects models to test for age-related changes in the number of pups sired, number of recruits sired, home range area, and survival in separate model sets. I included age as a quadratic independent variable, age at first and last reproduction as covariates, and individual identity as a random effect to account for selective disappearance and appearance (Van de Pol & Verhulst 2006; Nussey *et al.* 2008). I also tested whether age effects were linear by testing a competing model with age as a linear rather than quadratic variable. To account for year and study effects, I included year-study area concatenated together as a random effect in all models analyzing age-related changes. For home range area, which was normally distributed, I used a normal distribution and standardized the data by subtracting the year-study area mean from each value. Number of pups and number of recruits were Poisson-distributed and values were not standardized by year and grid prior to including in the model sets.

To analyze senescence rate, I only included the unstandardized annual number of pups sired from age at peak reproduction onwards, excluding any males who did not live beyond peak age. I included age at first reproduction and lifetime number of pups sired as independent variables in separate models, in an interaction with the number of years after peak reproduction. This was in order to determine if either of these measures influenced the slope of age-related changes in reproductive success from peak reproduction until death. In this analysis, peak reproduction occurred at year 0. Individual ID and year-study area were included as random effects.

Results

I analyzed 628 records of annual reproductive success from 229 males, with records for males ranging from one to seven years of age (Table A1.2). Sample sizes were smaller for some analyses (see Tables A1.4-A1.5). Males who sired at least one pup in their lifetime lived an average of 2.7±1.4 years (Table A1.3). They sired an average of 2.1±2.6 pups and 0.5±1.0 recruits annually (Table A1.3). They sired an average of 5.8±5.6 pups and 1.2±1.8 recruits over their lifetimes (Table A1.3). They began siring pups at an average age of 1.5±0.6 years and recruits at an average age of 1.9±1.0 years (Table A1.3). Peak reproduction occurred at an average of 1.9±1.0 years (Table A1.3). Their last successful reproductive event occurred at an average age of 2.4±1.3 years for pups and 2.3±1.2 years for recruits (Table A1.3). Males thus sired pups and recruits for 1.9±1.1 years and 1.5±0.9 years on average, respectively (Table A1.3). Their reproductive lifespan spanned 1.9±1.1 years on average (Table A1.3). Males typically continued to breed until their last year of life, as they lived an average of 0.3±0.6 and 0.7±1.0 years after they were last successful siring pups and recruits, respectively (Table A1.3).

Age-Related Changes in Success

Males sired the most pups when they were middle-aged, such that the overall effect was a positive quadratic (model set 1, Table 2.1 and Table A1.4). Based on model predictions with other variables set to the population average, males increased annual reproductive success from 1.1 pups at age one to 2.7 pups at an age of 3.2 years when they achieved peak reproduction (Figure 2.1A). Reproductive success then declined to 0.7 pups at age six, indicating that they senesced (Figure 2.1A). There was also a quadratic effect of age on annual recruits: middle-aged males sired the most recruits (model set 2, Table 2.1 and Table A1.4). Model predictions with other variables set to the population average showed that males increased annual number of recruits sired from 0.5 recruits at age one to a peak reproduction of 0.8 recruits at 2.5 years of age, they then declined and produced 0.1 recruits at age 6 (Figure 2.1B). Although home range area also showed a quadratic pattern of change with age, the confidence intervals around the quadratic age coefficient overlapped with zero so I cannot be confident in the coefficient estimates (model set 3, Table 2.1 and Table A1.4). A quadratic effect of age on survival was among the top-ranked models, but the coefficient of the quadratic age term was small with a confidence interval that crossed zero (model set 4, Table 2.1 and Table A1.4). When the model-averaged coefficients were graphed with other variables set to the population average, the effect of age on survival was linear and negative (Figure 2.1C). Thus, there is little evidence of an early-life increase in survival but rather a linear decline in survival with age. There was a positive effect of age at last reproduction on the annual number of pups sired (model set 1, Table 2.1 and Table A1.4) and home range area (model set 3, Table 2.1 and Table A1.4), and a negative effect of age at last reproduction on the annual number of recruits sired (model set 2, Table 2.1 and Table A1.4). However, the confidence intervals of the coefficients cross zero in all cases, so I cannot be confident in these estimates.

Data exploration (Figures A1.1-A1.4) suggested that the model coefficients for age at first reproduction generated from including data prior to age at first reproduction altered the coefficients of age at first reproduction in the model output such that it was most influenced by the years in which males were unsuccessful (model sets 1-4, Table 2.1 and Table A1.4). As I were interested in the effects of age at first reproduction once males were successful at siring pups, I tested the effect of age at first reproduction using a second set of models excluding data from prior to their age at first reproduction (model sets 4-8, Table 2.1 and Table A1.4). I found support for a positive effect of age at first reproduction on annual number of pups sired, recruits sired, home range, and survival; however, the confidence intervals for the coefficients crossed zero so I could not be confident in these results (model set 5, Table 2.1 and Table A1.4).

Peak Reproduction and Senescence Rate

I found that the interaction between the number of years since peak reproduction and age at first reproduction was in the top-ranked models in my model set (model set 1, Table A1.5). However, the coefficient for the interaction term was small and the confidence intervals overlapped zero so I cannot be confident in this estimate (model set 1, Table 2.2). I also found that the interaction between lifetime reproductive success and the number of years since peak reproduction was in the top-ranked models (model set 2, Table 2.2 and Table A1.5). Model predictions suggest that there is an effect of lifetime reproductive success on senescence rate: males with a higher lifetime reproductive success senesce faster, although the effect is most evident for males who achieve the highest lifetime reproductive success relative to the population mean (Figure 2.2).

Discussion

I used long-term data on male red squirrels to investigate whether reproductive success, home range area, and survival changed with age. I found that the age-related patterns of change differed depending on the trait measured. The number of pups and recruits that males sired changed with age: young and old males sired fewer pups and recruits than middle-aged males, providing evidence of early-life improvement and late-life decline. I also showed that survival senesced, but it decreased with age with little evidence for an early-life increase. There are several explanations for an early-life increase in reproductive success (Curio 1983; Van de Pol & Verhulst 2006). Young animals may be inexperienced, have access to fewer resources, or be unable to compete with older males for mates (Curio 1983; Pelletier & Festa-Bianchet 2006). Red squirrels cache white spruce cones and feed on those cones throughout the year, particularly overwinter and during the spring breeding season (Fletcher *et al.* 2013). Juvenile red squirrels have territories with fewer cones during the caching season, and tend to cache fewer cones than adults (LaMontagne *et al.* 2013). Thus, a yearling is likely to have fewer cached cones during the breeding season compared with older individuals, potentially resulting in lower reproductive success. This pattern did not match the age-related change in survival, and it is possible that survival was affected by different selection pressures than reproductive success which resulted in different age-related patterns of change (Evans *et al.* 2011). It is also possible that because I selected males who successfully sired pups at some point in their lives, these males were higher quality and had higher survival early in life and thus showed no early-life increase in survival. Although senescence has been reported in females of this species and for both sexes in other species (Berube, Festa-Bianchet & Jorgenson 1999; Vanpé *et al.* 2007; Descamps *et al.* 2008;

Sharp & Clutton-Brock 2010; Weladji *et al.* 2010; Bouwhuis *et al.* 2012), this pattern is not universal (Bonduriansky & Brassil 2002; Mason *et al.* 2012; Benowitz *et al.* 2013). Traits may also follow different age-related patterns of change, such that senescence may not be detected in all traits even within the same individuals (Evans *et al.* 2011; Hayward *et al.* 2013). I found little evidence that home range area, a sexually-selected trait, followed a quadratic pattern of age-related change. Reproductive effort and reproductive success may follow divergent patterns. For example, male roe deer experienced reproductive senescence, but investment in sexually-selected traits depended on body size which in turn likely influenced reproductive strategies (Vanpé *et al.* 2007). Old males may undergo a physiological decline in old age leading to lower ejaculate quality while still maintaining the same level of effort (Preston *et al.* 2011) and thus a disconnect between reproductive effort and success.

Part of the motivation of studying males is to test whether there are sex-specific ageing patterns. Although generally it is predicted that males may have higher wear and tear strategies leading to shorter longevity and faster senescence rates, sexual conflict or other sex-specific patterns of selection can cause males and females to diverge from these predictions (Promislow 2003). The divergence in ageing rates between males and females can also depend on the mating system (Clutton-Brock & Isvaran 2007). Thus, sexual dimorphism in ageing rates can be a result of many different factors and may not simply result from males having a live-fast-die-young strategy (Bonduriansky *et al.* 2008). Previous work on female red squirrels found evidence of reproductive senescence and showed that some female traits decline between five and six years of age, although some traits declined as early as age three (Descamps *et al.* 2007, 2008; McAdam *et al.* 2007). In contrast, I showed that males achieve reproductive success between two and three years of age (see Figure 2.1). This fits with the predictions that males should have an earlier onset of senescence due to a higher wear-and-tear strategy compared with females (Bonduriansky *et al.* 2008). Previous work demonstrated that actuarial senescence followed the opposite pattern: the onset of senescence was earlier in females than in males, with declines after three and seven years of age, respectively (Descamps *et al.* 2008). However, my results found little support for an early-life increase in survival in males, but rather a linear decline with age; this again supports the prediction that males senesce earlier than females. These studies included animals from different time periods: actuarial senescence was previously analyzed in males born between 1987-2001 (Descamps *et al.* 2008), whereas I included males from 2003-2015. Thus, the difference in age-related patterns of change in survival as well as the difference in the timing of the onset of senescence could be due to environmental influences impacting patterns of ageing and senescence (Bonduriansky *et al.* 2008; Wilson *et al.* 2008). Red squirrels would be ideal to further investigate this possibility as food resources influence female reproductive success and resources fluctuate annually (Boutin *et al.* 2006), thus individuals experience fluctuating resources throughout adulthood.

Of the three theories explaining the evolution of senescence, the antagonistic pleiotropy and disposable soma theories suggest a connection between early-life investment and late-life decline (Williams 1957; Kirkwood 1977). Alleles with negative effects later in life may have positive effects early in life (Williams 1957). Alternatively, animals should not invest in self-maintenance after average longevity, due to trade-offs with reproduction and other functions (Kirkwood 1977). There is some empirical support for this trade-off within species (Nussey *et al.* 2006; Preston *et al.* 2011; Lemaître *et al.* 2015). When comparing senescence rates between species, there is also evidence that faster senescence is found in species with a faster pace of life, i.e. those that have a younger age at first reproduction, higher fecundity, and shorter longevity (Jones *et al.* 2008). I found mixed support for these hypotheses. I showed that reproductive senescence began between 2-3 years of age, which coincided with an average longevity of 2.7 years in this population. This thus matches predictions about the evolution of senescence (Kirkwood 1977). I tested whether there was a connection between the age at first reproduction and annual reproductive success or the rate of senescent decline, as a measure of early-life success and found little support for these theories. However, the effect of age at first reproduction was small and the model coefficients had large confidence intervals, so I cannot be confident of these coefficients. This suggests that age-related changes are predominantly affected by within-individual changes, rather than due to selective appearance or disappearance of individuals of certain quality (Van de Pol & Verhulst 2006; Nussey *et al.* 2008). This also shows that early-life success had little effect on late-life decline, contrary to theory about the evolution of senescence. I did show, however, that males who achieved higher lifetime reproductive success also senesced faster. This was particularly evident for males who achieved the highest lifetime reproductive success relative to the average in this population. This pattern suggests that males face a trade-off: they can increase investment in achieving reproductive success but will undergo a faster decline as a result.

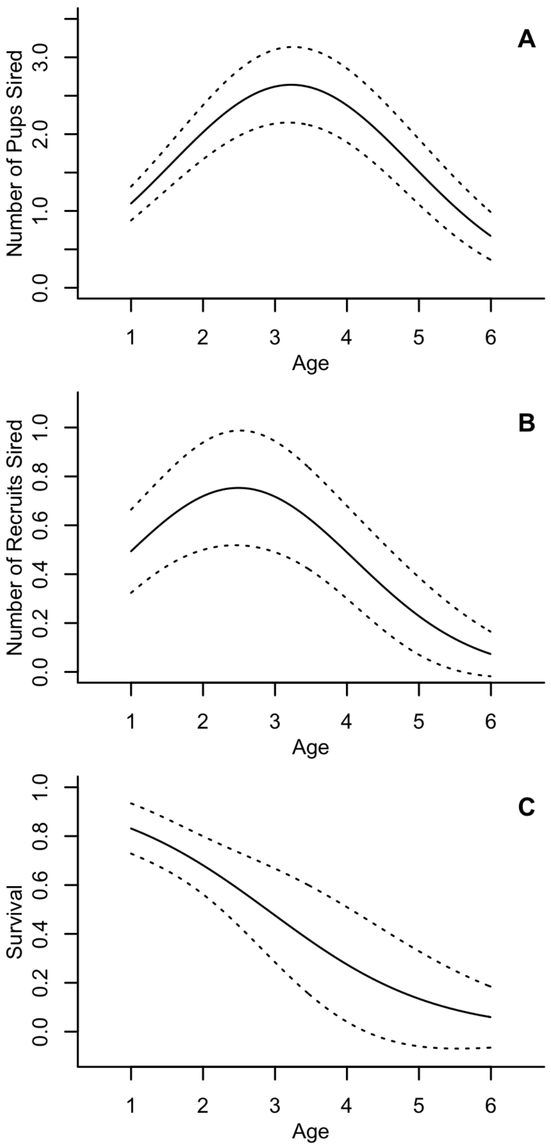

Figure 2.1. Model predictions from top-ranked models showing the effects of age on the number of pups sired (A), recruits sired (B), and survival (C). Dotted lines indicate 95% confidence intervals around model predictions. These graphs represent the model-averaged coefficients (Table 2.1) which are the top-ranked models from model selection (see Table A1.4 for full model sets). Except for age, all variables were set to 0 (ie. the mean). There is one male who lived to seven years of age, I did not include him in the graph given that he is the only individual in that age class.

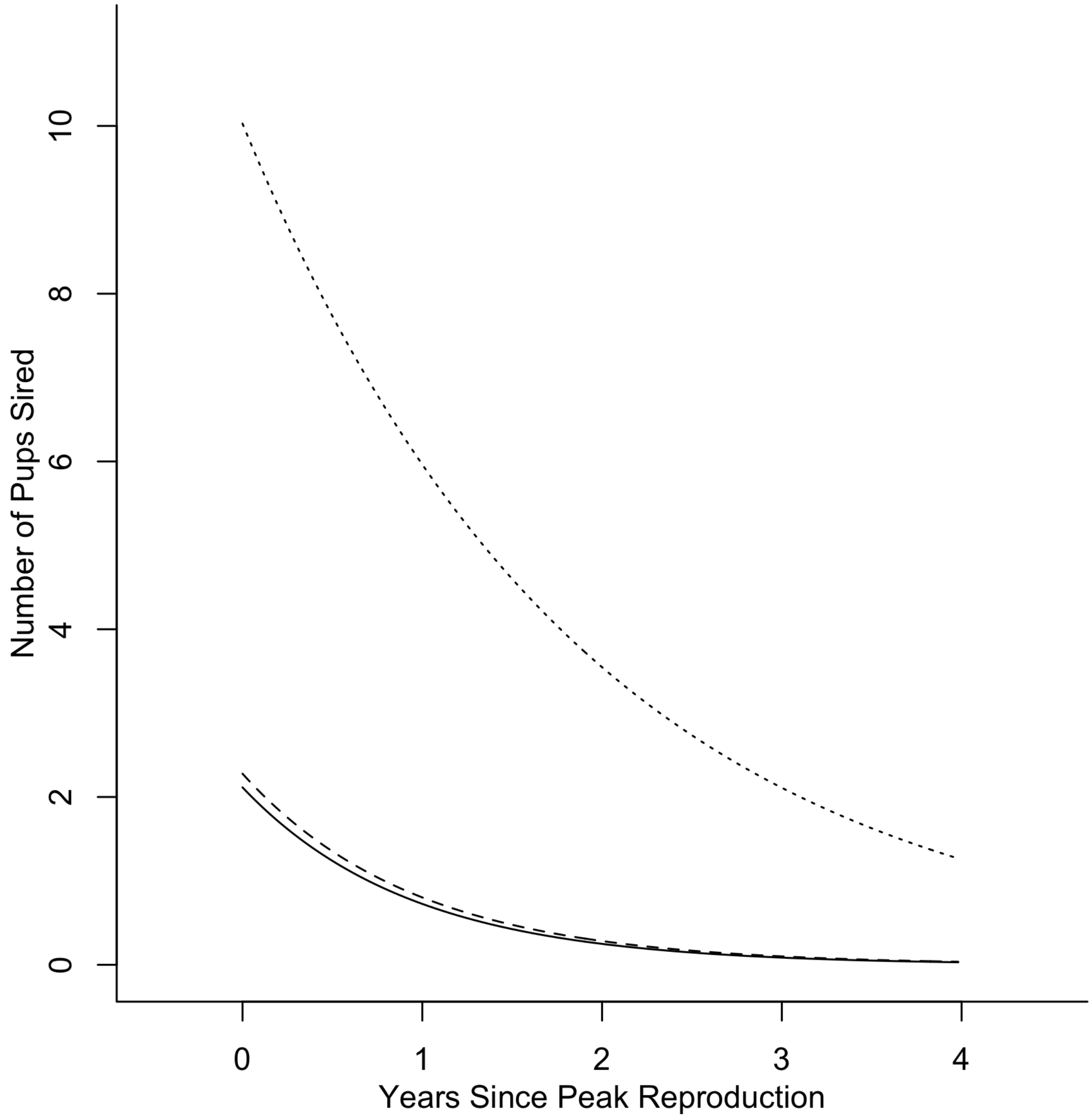

Figure 2.2. Differences in senescence rates depending on lifetime reproductive success. The solid line indicates the minimum value of lifetime reproductive success in this dataset, the dashed line represents the mean, and the dotted line represents the maximum. Model-averaged coefficients were generated following model selection (see Table A1.5 for full model sets), and the coefficients were presented elsewhere (Table 2.2). Except for years since peak reproduction and lifetime reproductive success, all variables were set to 0 (ie. the mean).

Table 2.1. Standardized coefficients (±95% confidence intervals) from the top-ranked models testing the relationship between quadratic age (Age and Age^2) and four dependent variables (Variable): annual number of pups sired (Pups), annual number of recruits sired (Recruits), annual home range area (Home Range), and survival (Survival). Models 1-4 included all males, while Models 5-8 excluded data from prior to their age at first reproduction (see Methods for more details). Model-averaged coefficients were calculated from models ≤6 ΔAICc of the top-ranked model within each model set (see full model sets with corresponding model numbers in Table A1.4). Age at first reproduction (AFR) and age at last reproduction (ALR) were included as covariates. Squirrel ID was included as a random effect in all models to account for multiple measures per individual, and Study Area-Year was included as a random effect in all models to account for annual- and study site-specific variation. Predictions using these model coefficients were presented in Figure 2.1. Coefficients with confidence intervals not overlapping zero are indicated in bold.

Model	Variable	Intercept	Age^2	Age	AFR	ALR
1	Pups	**0.80 ± 0.18**	**-1.11 ± 0.25**	**0.88 ± 0.19**	**-0.37 ± 0.21**	0.09 ± 0.23
2	Recruits	-0.30 ± 0.31	**-1.18 ± 0.60**	0.25 ± 0.35	**-0.49 ± 0.29**	-0.07 ± 0.26
3	Home Range	0.89 ± 1.25	-2.40 ± 3.99	0.28 ± 1.70	0.23 ± 1.22	0.23 ± 1.40
4	Survival	0.56 ± 0.57	-0.06 ± 0.47	**-2.12 ± 1.29**	**1.22 ± 0.74**	-
5	Pups	**0.84 ± 0.15**	-0.11 ± 0.26	**-0.38 ± 0.20**	0.21 ± 0.25	**0.51 ± 0.21**
6	Recruits	-0.15 ± 0.22	-0.05 ± 0.35	**-1.13 ± 0.37**	0.13 ± 0.33	**0.43 ± 0.33**
7	Home Range	0.90 ± 1.32	-1.86 ± 4.00	-0.54 ± 2.11	0.67 ± 1.90	0.44 ± 1.91
8	Survival	0.46 ± 0.49	**-1.01 ± 0.88**	-0.38 ± 0.53	0.01 ± 0.23	-

Table 2.2. Standardized coefficients (±95% confidence intervals) from models ≤6 ΔAICc of the top model (see Table A1.5 for full model sets with corresponding model numbers) testing whether senescence rate was affected by age at first reproduction (AFR) or lifetime reproductive success (LRS). In all cases the dependent variable was annual reproductive success, and the independent variable (Variable, with coefficient for that variable indicated by Coefficient) was included in an interaction (Interaction) with the years since the age they achieved peak reproduction (Years). I controlled for age at first reproduction (AFR) and age at last reproduction (ALR). To account for multiple measures per individual, I included a random effect of squirrel ID. As there is yearly and study area-specific variation in reproductive success, I included a random effect of study area-year. "-" indicates that the variable was not included in the model set. Predictions from these model coefficients were presented in Figure 2.2. Coefficients with confidence intervals that do not overlap zero are indicated in bold.

Model	Variable	Intercept	Coefficient	Years	Interaction	AFR	ALR
1	AFR	**0.49 ± 0.15**	-0.13 ± 0.29	**-1.36 ± 0.20**	0.03 ± 0.21	-	**1.06 ± 0.29**
2	LRS	**0.42 ± 0.12**	**1.27 ± 0.17**	**-1.71 ± 0.26**	**0.65 ± 0.29**	0.04 ± 0.14	0.18 ± 0.25

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Chapter 3: Male red squirrel anticipatory reproduction and the effects of a resource pulse on life history trade-offs and fitness

Introduction

Life history traits describe patterns of growth, maturation, reproduction, and survival (Stearns 2000), and trade-offs occur when increases in one trait result in a decrease in another (Stearns 1989; Roff & Fairbairn 2007). For example, reproduction is costly and investing in current reproduction may result in declines in future reproduction or survival (Stearns 1989; Reznick, Nunney & Tessier 2000; Roff & Fairbairn 2007). These trade-offs are the result of both internal (eg. genetic) and external (eg. environmental) influences on organisms (Stearns 1989, 2000; Roff & Fairbairn 2007). Trade-offs can limit life history trait expression, leading to limited phenotypic plasticity (Pease & Bull 1988; Stearns 1989, 2000; Ricklefs & Wikelski 2002; Bielby *et al.* 2007). For example, animals that breed early in life are predicted to also have higher fecundity and shorter longevity (Gaillard *et al.* 1989; Ricklefs & Wikelski 2002; Réale *et al.* 2010). There is some empirical support for these predictions, particularly between species (Gaillard *et al.* 1989; Bielby *et al.* 2007; Jones *et al.* 2008; Careau *et al.* 2009; Montiglio *et al.* 2014). However, empirical research has also demonstrated patterns contradictory to those predicted by theory, such as a positive link between age at primiparity and longevity or no evidence of life history trade-offs (Reznick *et al.* 2000).

Life history patterns counter to theory may arise because of the influence of extrinsic influences on life history trade-offs (Stearns 2000). Animals may differ in how they acquire resources, which can obscure trade-offs or produce positive phenotypic correlations between life history traits even when negative genetic correlations exist (Van Noordwijk & de Jong 1986; Stearns 1989; Reznick *et al.* 2000). Environmental traits may also directly alter life history traits. For example, where environmental variation affects reproductive success, theoretical models suggest that there will be selection for greater longevity and a longer reproductive lifespan (Schaffer 1974). Alternatively, when adult survival is reduced by environmental variability then there will be selection for higher investment in each reproductive event (Schaffer 1974). Thus, the environment that an organism experiences may affect the patterns of life history traits as well as whether life history trade-offs will be detected. The fitness consequences of life history traits are less clear. In some species, it has been suggested that breeding earlier leads to higher lifetime reproductive success (Descamps *et al.* 2006; Reid *et al.* 2010). However, if one life history strategy consistently leads to higher lifetime reproductive success then it is unlikely that variation in life history traits would be maintained in the population (Ellner & Hairston 1994; Roff & Fairbairn 2007). This variation in life history traits could be maintained because of genetic correlations between traits such that they cannot be simultaneously maximized even if a different trait combinations would result in higher fitness (Pease & Bull 1988; Stearns 1989, 2000; Ricklefs & Wikelski 2002; Bielby *et al.* 2007). Alternatively, different environmental traits could cause fluctuations in selection for life history traits and thus maintain variation in life history traits within a population (Ellner & Hairston 1994; Roff & Fairbairn 2007).

Pulsed resource systems are ideal for testing the effects of environmental influences on reproductive success and life history traits. Pulsed resource systems are characterized by short, intense, and infrequent resource availability (Yang *et al.* 2008). Some species respond to these resource pulses by increasing their reproductive success in subsequent years (Yang *et al.* 2008), thus using a resource pulse as a source of energy to fuel an increase in reproductive investment. In other species, the occurrence of a resource pulse triggers anticipatory reproduction in females, with reproduction timed earlier than the resource pulse such that juveniles are dispersing at the same time the excess food becomes available (Boutin *et al.* 2006; Lebl *et al.* 2010; Bergeron *et al.* 2011; Montiglio *et al.* 2014). In this case, the resource pulse does not provide energy for adult reproduction but instead increases juvenile survival and recruitment. These pulses also influence life history traits (Boutin *et al.* 2006; Montiglio *et al.* 2014). The benefit of studying pulse systems is that they are easily defined periods of resource fluctuations, thus facilitating studying their effects on life history and fitness.

I investigated the relationships between life history traits and fitness in male red squirrels, and the influence of the environment on these traits. The Kluane Red Squirrel Project collects lifetime data on all individuals in two study populations, which I used to calculate age at first reproduction, longevity, and lifetime reproductive success. Red squirrels predominantly feed on white spruce cones, a tree that irregularly produces large amounts of cones during mast years (Lamontagne & Boutin 2007); thus, this is a resource pulse system. Female red squirrels increase reproductive investment during years of high cone production, with mast years in particular resulting in high juvenile recruitment (Boutin *et al.* 2006; Williams *et al.* 2014). As squirrels breed in late winter to spring but cones mature and can be consumed in late summer to autumn

(Fletcher *et al.* 2013), this change in reproduction is in anticipation of high juvenile recruitment rather than because females have access to more energy during reproduction (Boutin *et al.* 2006). The effects of a mast year on males has not been studied, but as females produce more litters and pups during a mast year this would provide additional mating opportunities for males. I thus investigated how mast years influenced male life history traits and fitness. I predicted that yearling males who encountered a mast year would be more likely to breed that year, similar to female red squirrels who encountered mast years (Boutin *et al.* 2006). As mast years occur irregularly every several years, males who have a longer lifespan will be more likely to encounter a mast year. Because of the higher siring opportunities in mast years due to higher female reproduction (Boutin *et al.* 2006), I predicted that encountering a mast year would result in higher lifetime reproductive success.

I then tested whether encountering a mast year influenced male life history trade-offs. I predicted that males who began breeding at an earlier age also had shorter longevities, as predicted by theory (Gaillard *et al.* 1989; Ricklefs & Wikelski 2002; Bielby *et al.* 2007; Réale *et al.* 2010) and also as previously shown in female red squirrels (Descamps *et al.* 2006). I also predicted that the strength of this relationship would depend on whether males encountered a mast year, but there are two ways in which this could affect life history trade-offs. Male mating behaviour is energetically demanding (Lane *et al.* 2010). As well, reproductive trade-offs are thought to be the result of limited resources being allocated between different functions (Stearns 1989). Thus, one prediction is that the increased reproductive investment despite no change in food availability during the breeding season in mast years would result in stronger trade-offs between life history traits because of the cost of increased reproductive effort. Alternatively, males may be better able to cope with the costs of reproduction because they will have access to more food when the cones mature during the autumn in a mast year. In this case, the trade-offs would be weaker when a male encounters a mast year. Squirrels encountering a mast year would encounter the greatest variability in resources, which is predicted to select for longer lifespan (Schaffer 1974) and which should also be associated with beginning breeding later in life (Ricklefs & Wikelski 2002; Réale *et al.* 2010). Thus, I expected that a longer longevity and a later age at first reproduction would result in the highest lifetime reproductive success; males who do not encounter a mast year would achieve higher reproductive success with the opposite traits. Given the potential influences of encountering a mast on male reproductive success because of its influences on mating opportunities, I predicted that encountering a mast would reduce the fitness benefits of these life history traits. This system provided a valuable opportunity to test the influence of the environment on life history trade-offs, as well as the fitness consequences of those life history traits.

Methods

Study Species and Long-term Monitoring

Male red squirrels were monitored in two study areas (Kloo and Sulphur) with completely enumerated populations as part of the Kluane Red Squirrel Project. The field methodology was described in more detail elsewhere (McAdam *et al.* 2007). Squirrels in these populations were tagged with unique numbers and received coloured wires in their ears for visual identification at a distance. Males and females were located regularly between March and August each year using trapping and/or behaviour observations to monitor their survival. Detection probability of squirrels in these populations was high (almost 1, Descamps *et al.* 2009). As well, with the exception of some females who bequeathed their territories to their offspring (Berteaux & Boutin 2000), adult red squirrels rarely move to a new territory. Thus the age that squirrels were last detected was a reasonable estimate of longevity.

Female reproductive status was monitored with regular trapping and their nests were located using telemetry after their pups were born. Litter size was assessed and tissue samples taken for paternity analysis (see below) at that time. Nests were relocated once pups were 25 days old so that they could be tagged. As red squirrels disperse over short distances (Berteaux & Boutin 2000), I was able to monitor recruitment into this population. A pup was considered a recruit if it was detected in the population the following spring.

Genetic Analyses for Paternity Assignment

Red squirrels have a scramble competition mating system where females mate with multiple males (Lane *et al.* 2009), so male reproductive success was determined with genetic analyses. From 2003-2014, I extracted DNA from ear tissue samples and performed PCR amplification on 16 microsatellite loci. Genotypes were scored using GENEMAPPER software 3.5 (Applied Biosystems) and assigned paternity based on CERVUS 2.0. More details on genetic analyses can be found elsewhere (Gunn *et al.* 2005; Lane *et al.* 2008; Haines et al. in prep). I then calculated the number of pups a male sired in each breeding season, as well as the number of recruits sired each year.

Life History Traits and Data Selection

I only included males with complete reproductive data, ie. males born in or after 2002 and who died by 2014, as these were the years included in the paternity analyses. I used their birth year to calculate their age in years, and I defined longevity as the age they were last detected in the population. I included in this analysis known-age males (ie. males who were born in the study sites or first captured as juveniles and thus their birth year was known) and males who recruited into the population as adults. Males who recruited as adults, likely because they dispersed too late the previous autumn to be detected during the regular monitoring season, were assigned a birth year of the previous year, as has been done previously (Lane *et al.* 2009). There was no evidence from paternity assignments that males bred in their birth year (Haines *et al*. in prep.), so I excluded all juvenile data. I defined age at first reproduction (AFR) as the youngest age that a male sired a pup. As most males sired pups at one or two years of age, I quantified age at first reproduction as yearling (0) or later (1). I used two measures of lifetime reproductive success. I first calculated the total number of pups sired throughout their lives, herein called total pups. I also calculated total number of recruits sired throughout their lives, herein called total recruits. I excluded any males who sired zero pups during their lifetime as I cannot calculate age at first reproduction for these males. Occasionally males from outside the study areas were detected when they temporarily entered the population to mate with females. I thus excluded any males who did not have a territory in the study areas during his lifetime.

Defining Mast and Non-Mast Years

White spruce trees produce cones in late summer, which then mature by early autumn when they are cached by red squirrels. Although cone production is variable, it is possible to distinguish low or moderate cone years (non-mast years) from high cone production years (called mast years, Lamontagne & Boutin 2007). White spruce cone production and in particular mast years influenced female red squirrel reproduction and life history traits: females produced more litters, more pups, and more recruits in these years (Boutin *et al.* 2006; Descamps *et al.* 2008;

Williams *et al.* 2014). Thus, the occurrence of mast years would also influence mating opportunities for males. To distinguish between mast and non-mast years, the cone production on each study site was assessed by counting cones in the top 3 metres of marked trees, which is a reliable index for total cone production (Lamontagne, Peters & Boutin 2005). I used this count to determine that mast years occurred in 2005, 2010, and 2014 (Williams *et al.* 2014 and this study). I then quantified whether a male encountered a mast year as a yearling or during his lifetime. For males who did encounter a mast year, I also determined the age at which they encountered a mast year. There were eight males who encountered two masts, but as this was a small sample size I excluded these males from calculations of the age at which they experienced a mast.

Statistical Analysis

All statistical analyses were done using R Version 3.2.4 (R Core Team 2016). In all statistical models, I included study area as a covariate. I used Poisson distribution when longevity, total pups, and total recruits were the response variables and binomial when age at first reproduction was the response. I used glm functions in R for all models. Using the function standardize from the R package arm version 1.8-6 (Gelman & Su 2015), I standardized the data with a mean of 0 and standard deviation of 0.5 (Grueber *et al.* 2011). For each analysis, I manually created a biologically plausible candidate model set, and then used model.sel and coeffTable finctions in the MuMIn package version 1.15.6 (Bartón 2016) to calculate AICc and rank models to find the top-ranked model (Burnham & Anderson 2002). When there were multiple models ≤6 ΔAICc of the top candidate model, I considered these models to be top-ranked as this generally will include 95% of the plausible models (Richards 2005; Richards, Whittingham & Stephens 2011; Symonds & Moussalli 2011). When there were multiple top-ranked models, I used the model.avg function in the MuMIn package to calculate the model-averaged coefficients using the zero method of model averaging (Burnham & Anderson 2002; Grueber *et al.* 2011). I calculated model predictions from the top-ranked model using the predict function, using model-averaged coefficients when there were multiple top models. All variables except those of interest were set to 0 (ie. the population mean) to generate these predictions. I used the predictions to generate graphs as visual representations of some results. Where raw data was plotted to aid in interpretation of model predictions, I plotted standard error bars around the mean with the package gplots version 3.0.1 (Warnes *et al.* 2016). Where descriptive statistics were presented, I included ±standard deviation in order to indicate the variability in the data. Statistical output and figures were exported using the ReportRs package (Gohel 2016). Model sets ranked by ΔAICc were presented in Appendix 2 (Tables A2.1-A2.2), and coefficients from top-ranked models were included in the Results. For each coefficient, I also calculated 95% confidence intervals by multiplying the standard error by 1.96 in order to determine to certainty of that parameter estimate. Some variables had outlying values, and to prevent them from driving the results of the statistical analysis I grouped some data together (see Results for more details).

I tested whether encountering a mast year affected life history traits and fitness, as well as whether it affected life history trade-offs. I first analyzed whether encountering a mast as a yearling affected the age at which they began breeding; I included age at first reproduction as the response and whether they encountered a mast as a yearling as the predictor. I then included whether they encountered a mast at some point in their lives as the predictor, and the following as the response in separate model sets: 1) longevity, 2) total pups, and 3) total recruits. I also included the age at which they encountered a mast as the predictor, with the following variables as the response variables in separate models: 1) longevity, 2) total pups, and 3) total recruits. Finally, I tested whether life history trade-offs and the fitness consequences of life history traits were affected by encountering a mast during their life. I included an interaction between mast year and age at first reproduction to test the effects on longevity. I then analyzed how either total pups or total recruits was affected by an interaction between mast and age at first reproduction or longevity. In models where longevity was not the response or predictor, I included it as a covariate in the model set. Although quadratic relationships could be biologically relevant for some predictor variables (eg. longevity), I found that quadratic effects were small with large confidence intervals even when in top-ranked models. Thus, I only included linear effects in my model sets. When an interaction was in the top-ranked model, I used graphs to explore the effects of the interaction. When the interaction was not in the top-ranked models or when the effect of the interaction was marginal, I excluded mast and analyzed only life history trade-offs or fitness without an interaction.

Results

I had complete lifetime data from 228 males. Squirrels began breeding at an average of 1.5 years (±0.6, range 1-4) and lived to an average of 2.7 years (±1.4, range 1-7). Only one squirrel lived until seven years of age, so he was assigned a longevity of 6 for all analyses. Males sired an average of 5.8 pups (±5.6, range 1-30) and 1.2 recruits (±1.8, range 0-12) over their lifetime. However, only two males sired greater than 6 recruits in their lifetime (one sired 11 and one sired 12); these males were assigned a total recruits value of 6 for all analyses. Of the 228 males in my analyses, 136 males encountered a mast year during their lifetime and 92 did not encounter a mast year.

My analyses demonstrated that mast years influenced life history traits (Table 3.1, Table A2.3). Males were more likely to being breeding as a yearling if they encountered a mast year in that year (Table 3.1, Table A2.3, Figure 3.1; 43 of 56 males bred as yearlings in mast years; 82 of 172 males bred as yearlings in non-mast years). Males who encountered a mast year also lived longer (Table 3.1, Table A2.3; mast years: 3.2 years ±1.5, range 1-7; other years: 2.1±1.0, range 1-4). Although the raw data suggest that there is an effect of mast year on total pups sired (mast years: 6.9±6.2 pups, range 1-30; non-mast years: 4.2±4.0, range 1-25), this effect is marginal when longevity was included as a covariate (Table 3.1, Table A2.3). This suggesting that the difference in the data was due to the difference in longevity between these two groups. Males who encountered a mast year during their lives also sired more recruits (Table 3.1, Table A2.3, Figure 3.2; mast years: 1.7±2.1, range 0-12; non-mast years: 0.6±0.9, range 0-4), even when I controlled for longevity (Table 3.1, Figure 3.2). There was a negative relationship between the age at which males encountered a mast year and the total number of pups and recruits that they sired (Table 3.1, Table A2.3).

There was evidence that encountering a mast year influenced life history trade-offs as well as the fitness consequences of life history traits (Table 3.2, Table A2.4). In analyzing longevity, an interaction between mast and age at first reproduction was in the top models explaining longevity (Table 3.2, Table A2.4). There was a positive relationship between age at first reproduction and longevity for all males, but the effect was stronger in males who did not encounter a mast year (Figure 3.3). There was an interaction between age at first reproduction and mast on the total pups sired (Table 3.2, Table A2.4): there was a negative relationship between age at first reproduction and total pups in males who encountered a mast year, while there was a positive relationship between age at first reproduction and total pups in males who did not encounter a mast year (Figure 3.4). The total number of recruits sired was affected by an interaction between age at first reproduction and mast (Table 3.2, Table A2.4). There was a negative relationship in all males, but the effect was stronger in males who encountered a mast year (Figure 3.5). An interaction between longevity and mast year was in the top-ranked models explaining the number of pups and the number of recruits sired (Table 3.2, Table A2.4). However, plotting the model predictions revealed that the interactive effect was small (Figure A2.1, Figure A2.4); I thus excluded the interaction from the analysis. There was a positive relationship between longevity and the total number of pups and total number of recruits sired (Table 3.2, Table A2.4). There was a positive relationship between the total number of pups and the total number of recruits sired (Table 3.2, Table A2.4).

Discussion

I demonstrated that experiencing a resource pulse during their lifetime influenced male life history traits and fitness. Male red squirrels were more likely to breed as a yearling if they encountered a mast year as a yearling. Red squirrels breed in the spring, but white spruce cones do not mature until late summer to early autumn. Thus, they were not responding to increased resource availability but rather to increased probability of juvenile recruitment. Previous research showed that yearling female red squirrels were also more likely to breed when they encountered a mast year (Boutin *et al.* 2006). Thus, my results suggest that, like female red squirrels, male red squirrels exhibit anticipatory reproduction in advance of a resource pulse. It is not clear whether males detect the occurrence of a mast year because females increase their reproductive effort, or because they are also sensitive to environmental cues that the females would be responding to (Boutin *et al.* 2006). I have also shown that there are fitness benefits to encountering a mast year: males encountering a mast year produced more recruits overall than males who did not encounter a mast year. Encountering a mast year did not have an effect on the total number of pups produced, suggesting that even in non-mast years males invest in achieving reproductive success, but it is the occurrence of mast years that ensures those pups survive. However, among males who encountered a mast year at some point in their lives, there was a negative relationship between the age at which males encountered a mast year and their lifetime reproductive success. This indicated that encountering a mast year early in life had the largest effect on lifetime reproductive success. Males who encountered a mast year during their lifetime also had a longer lifespan. It is likely that longer-lived males would be more likely to encounter a mast than males with short lifespans. Alternatively, during a mast year squirrels would have the opportunity to cache large amounts of cones in their middens in the fall after the breeding season, which they would then consume during the subsequent winter and breeding season (Fletcher *et al.* 2013). Hence, encountering a mast year could lead to higher survival in subsequent years. Having access to higher resources in subsequent breeding seasons may also be the reason that males who encountered a mast year early in life also achieved higher lifetime reproductive success.

I had predicted that encountering a resource pulse would not only affect life history traits, but also the trade-offs between them. I had predicted one of two patterns for the effects of encountering a mast year on life history trade-offs. Trade-offs are the product of investing limited resources among competing functions (Stearns 1989) and male mating behaviour is energetically costly (Lane *et al.* 2010). Thus, I predicted that increased reproductive effort in a mast year would result in stronger life history trade-offs in males who encountered a mast year. Alternatively, although there are no additional resources available during a mast year to provide additional energy for reproduction itself, cones are available that autumn after breeding is complete. Thus, individuals may be able to counteract additional costs associated with higher investment in mast years by consuming more resources following the breeding season; this could reduce the trade-offs between life history traits when they encounter a mast year. I found that the effect of encountering a mast year on the relationship between age at first reproduction and longevity was marginal, and thus in all individuals males who were first successful early in life also had shorter longevities. My results thus provided support that there are trade-offs between age at first reproduction and longevity, but that the trade-off is not influenced by environmental conditions. It is possible that the trade-offs between life history traits are genetically based with limited phenotypic plasticity, thus resulting in a stable pattern of life history trade-offs regardless of the environmental conditions encountered. In addition, my findings that males who sired pups early in life also had the shortest longevities, thus matching theoretical predictions. Evolutionary theory predicts that life history traits will be correlated along a continuum, with fast individuals having early primiparity and short lifespans (Gaillard *et al.* 1989; Bielby *et al.* 2007). Previous research on female red squirrels also found support for this pattern, as females with early primiparity also had the shortest longevity (Descamps *et al.* 2006). Thus, similar to other empirical research (Gaillard *et al.* 1989; Bielby *et al.* 2007; Jones *et al.* 2008; Careau *et al.* 2009), my research supports these patterns.

My results suggested that some life history traits resulted in higher lifetime reproductive success, but that some patterns depended on whether males encountered a mast year during their lifetime. Male red squirrels who encountered a mast year had higher lifetime reproductive success by beginning to sire pups at a younger age. In contrast, there was a positive effect of age at first reproduction on lifetime reproductive success in males who did not encounter a mast year. Variation in life history traits could be maintained within the same population due to fluctuations in environmental conditions that create fluctuating selection for certain life history traits (Ellner & Hairston 1994; Roff & Fairbairn 2007). Changes in resource availability alter mating opportunities due to increased reproductive investment by females (Boutin *et al.* 2006). My results suggest that these fluctuations in mating opportunities could create fluctuating selection for age at first reproduction in male red squirrels, potentially explaining some of the variation in age at first reproduction in this population. Alternatively, if males did not encounter a mast year when young they may delay breeding in order to avoid potential costs of reproduction, and thus increase their chances of encountering a mast year. Female red squirrels who bred earlier achieved higher lifetime reproductive success, and this pattern has been found in other species as well (Descamps *et al.* 2006; Reid *et al.* 2010). However, it is difficult to interpret whether females in fact have different patterns than males, as research on females did not distinguish between females who did or did not encounter a mast year (Descamps *et al.* 2006). All males sired more pups and recruits if they achieved a longer longevity, although the effect of longevity on total recruits was stronger when male did not encounter a mast year during their lifetime. Variable resources that influence reproductive success, such as white spruce cone masts that influence red squirrel reproduction (Boutin *et al.* 2006), are predicted to select for long-lived individuals with late primiparity (Schaffer 1974). Similar effects of pulsed resources on life history traits and reproductive success have been found in other species that exhibit anticipatory reproduction. Eastern chipmunks, for example, will produce more offspring during a mast year (Bergeron *et al.* 2011), and the timing of mast years determined the age at which individuals would have the opportunity to breed (Bergeron *et al.* 2011; Montiglio *et al.* 2014). Similarly, edible dormice also breed in anticipation of mast years (Lebl *et al.* 2010), they produce more juveniles during mast years, and they time their reproduction to coincide with mast years (Ruf *et* *al.* 2006). Edible dormice have lower survival following reproduction, suggesting that the most beneficial life history strategy is to skip reproduction until they encounter a mast year (Ruf *et al.* 2006). My research and these studies suggest that the optimal life history strategy for animals that exhibit anticipatory reproduction in response to resource pulse is to invest in longer lifespan in order to encounter a mast year. It is also beneficial to adjust their age at first reproduction in order to receive fitness benefits from encountering a mast year when encountered as a young animal.

Table 3.1. Model coefficients from model sets testing the effects of encountering a mast (Yearling Mast and Mast Year) or the age at which they encountered a mast (Mast Age) on age at first reproduction (AFR), longevity, total pups sired (Pups), and total recruits sired (Recruits). For each response variable, its coefficient is indicated by Coefficient. When analyzing age at first reproduction, whether a male encountered a mast as a yearling (Yearling Mast) was the predictor variable. For other models, males could have encountered mast years at any time in their life (Mast Year). In each model set, I controlled for the effects of study area by including it as a covariate. I controlled for longevity where indicated, except for model 2 (indicated by "-" where it was not included). Coefficients were from models ranked by AICc, including all models ≤6AICc from the top model. Where there were multiple top models, coefficients are the result of model averaging. Model numbers correspond to the full model sets presented in Appendix 2 (Table A2.3). Coefficients whose confidence intervals do not overlap zero are indicated in bold.

Response	Model	Predictor	Intercept	Coefficient	Longevity	Study Area
AFR	1	Yearling Mast	-0.25 ± 0.29	**-1.45 ± 0.76**	**1.60 ± 0.63**	-0.30 ± 0.59
Longevity	2	Mast Year	**0.99 ± 0.08**	**0.40 ± 0.17**	-	0.08 ± 0.16
Pups	3	Mast Year	**1.61 ± 0.06**	0.02 ± 0.09	**1.06 ± 0.11**	**-0.22 ± 0.11**
Recruits	4	Mast Year	0.03 ± 0.14	**0.71 ± 0.31**	**0.62 ± 0.24**	**-0.43 ± 0.25**
Pups	5	Mast Age	**1.75 ± 0.08**	**-0.27 ± 0.14**	**1.22 ± 0.16**	**-0.32 ± 0.14**
Recruits	6	Mast Age	**0.40 ± 0.15**	**-0.48 ± 0.30**	**0.97 ± 0.30**	**-0.59 ± 0.29**

Table 3.2. Model coefficients from top-ranked models testing the effects of encountering a mast year on life history trade-offs and the fitness consequences of life history traits. In each case, I tested an interaction (whose coefficient is indicated by Interaction) between whether a male had encountered a mast during his lifetime (Mast) and the predictor. I tested the following predictors, whose coefficients are indicated by Coefficient: age at first reproduction (AFR), longevity and total pups sired (Pups). The response variable included these variables as well as total recruits sired (Recruits). I included study area as a covariate in all models, and where indicated I included longevity. When the interaction coefficient was small with confidence intervals overlapping zero, I also analyzed models without the Mast or Interaction terms included (Models 2, 5, and 7). When analyzing the effects of total pups on total recruits (Model 9), I did not include an interaction term. “-“ indicates that the variable was not included in that model set. Coefficients were generated from the top-ranked models in the model sets whose numbers correspond to “Model” below, see Appendix 2 for full model sets (Table A2.4). Top models were any models ≤6 ΔAICc from the top model, ranked according to their AICc. Coefficients were the result of model averaging when there were multiple top models. Coefficients are indicated in bold when their confidence intervals do not overlap zero.

Response	Model	Predictor	Intercept	Coefficient	Mast	Longevity	Interaction	Study Area
Longevity	1	AFR	**0.98 ± 0.08**	**0.32 ± 0.16**	**0.37 ± 0.17**	-	-0.20 ± 0.40	0.09 ± 0.16
Pups	2	AFR	**1.62 ± 0.06**	-0.08 ± 0.11	0.08 ± 0.13	**1.05 ± 0.12**	**-0.46 ± 0.24**	**-0.21 ± 0.11**
Recruits	3	AFR	0.01 ± 0.14	**-0.50 ± 0.26**	**0.70 ± 0.31**	**0.71 ± 0.25**	-0.04 ± 0.34	**-0.45 ± 0.26**
Pups	4	Longevity	**1.63 ± 0.07**	**1.11 ± 0.14**	0.05 ± 0.13	-	-0.28 ± 0.42	**-0.21 ± 0.11**
Pups	5	Longevity	**1.61 ± 0.06**	**1.06 ± 0.10**	-	-	-	**-0.22 ± 0.11**
Recruits	6	Longevity	0.04 ± 0.14	**0.69 ± 0.32**	**0.69 ± 0.31**	-	-0.28 ± 0.75	**-0.42 ± 0.26**
Recruits	7	Longevity	0.08 ± 0.13	**0.84 ± 0.23**	-	-	-	**-0.40 ± 0.25**
Recruits	8	Pups	-0.05 ± 0.14	**1.09 ± 0.16**	-	0.00 ± 0.15	-	-0.14 ± 0.26

Figure 3.1. Raw data and model coefficients showing the effect of encountering a mast year as a yearling. The proportion of males whose age at first reproduction (AFR) was one or later depending on whether they encountered a mast year as a yearling is shown by graph A. The sample size for each group of squirrels is indicated by the number above each bar graph. Graph B demonstrates the model predictions and their 95% confidence intervals from top models that show the age that males began breeding depending on whether they encountered a mast year. All other variables used to generate predictions for graph B were set to the population mean (ie. 0).

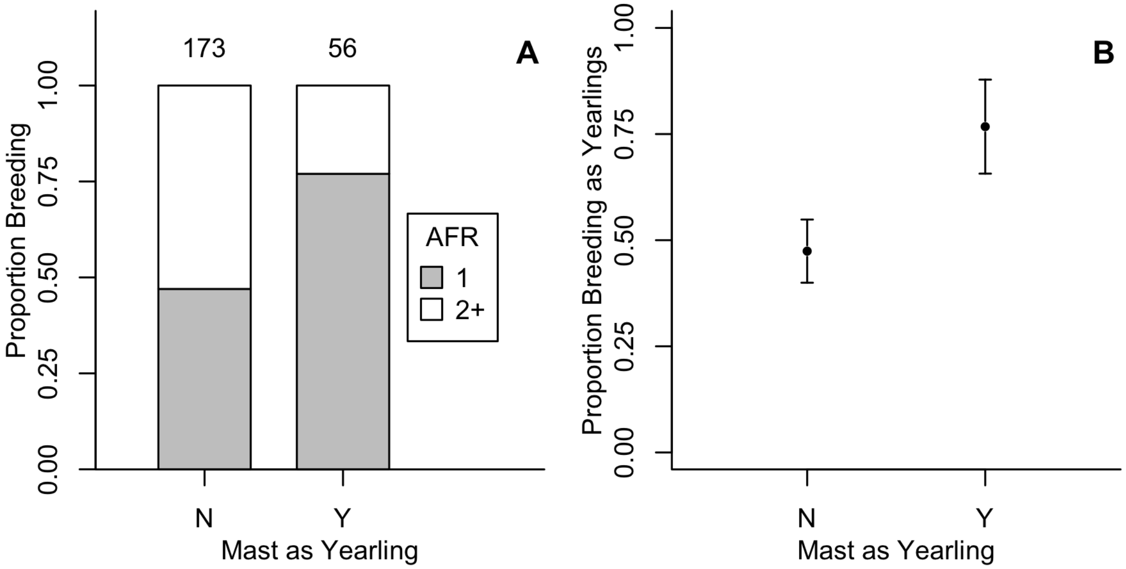


Figure 3.2. The mean ± standard error bars of the raw data (A) and model predictions with their 95% confidence intervals (B) showing the effects of encountering a mast year on the total number of recruits that males produced during their lifetime. Model predictions (Graph B) were generated from top models where all other variables were set to the population mean (ie. 0). The sample size for each group is included above the standard error bar in graph A.

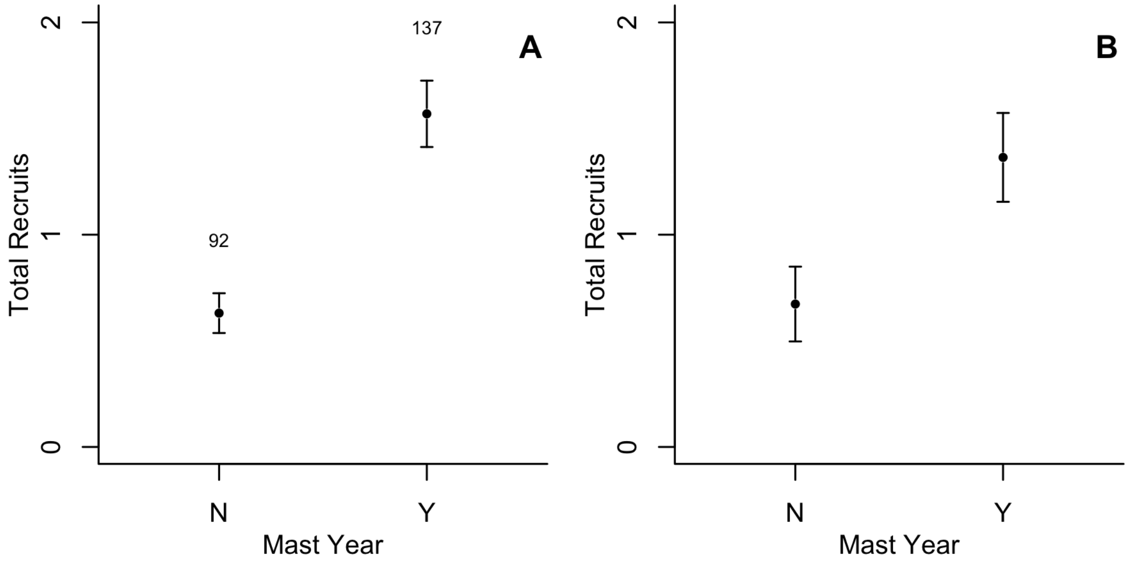


Figure 3.3. The relationship between age at first reproduction and longevity for males who did not (white dots) and who did (black dots) encounter a mast year during their lifetime. Graph A shows the mean ± standard error of the data and graph B model predictions with 95% confidence intervals. I generated model predictions from top-ranked models with other variables set to the population mean (ie. 0).

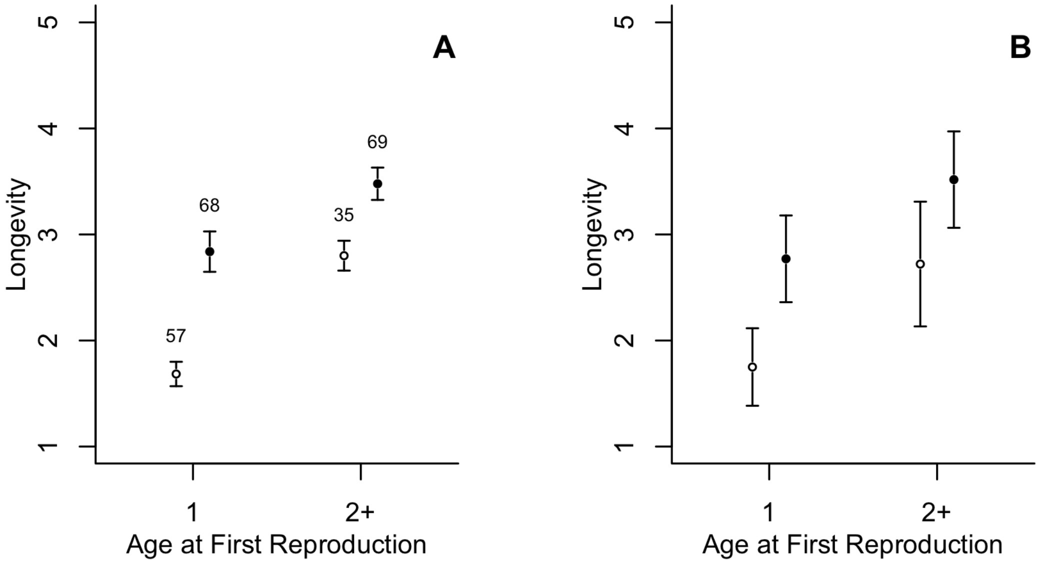


Figure 3.4. The mean ± standard error of the data (graph A) and model predictions with 95% confidence intervals (graph B) demonstrating the relationship between age at first reproduction and total pups sired for males who encountered a mast (black dots) or who did not encounter a mast (white dots) during their lifetime. Model predictions were generated from the top-ranked models and other variables were set to 0 (ie. the population mean). I controlled for longevity in the analysis (graph B) but not in graphing the original data (graph A).

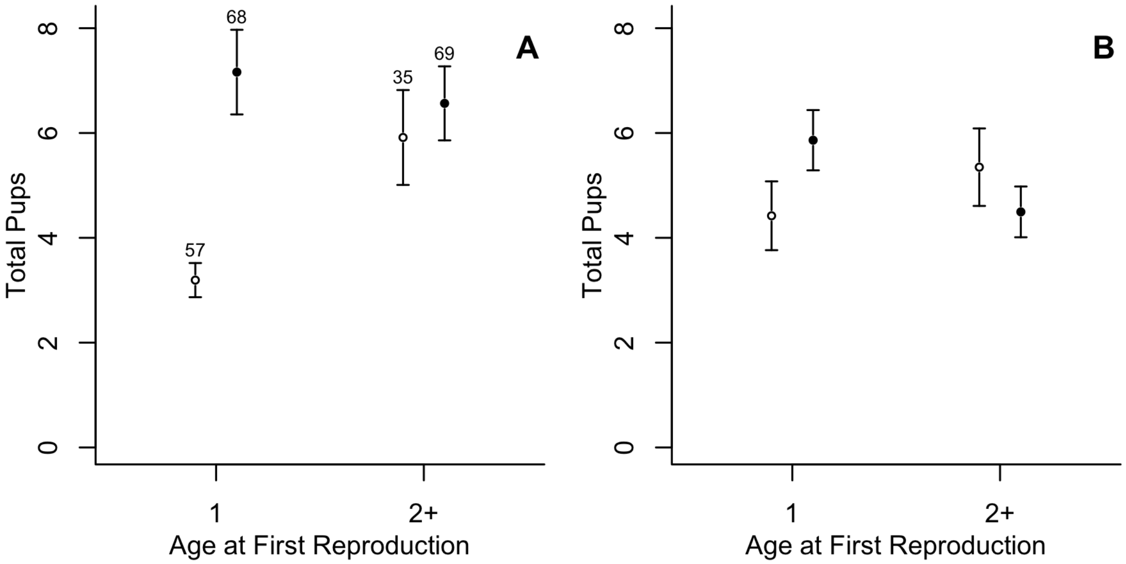
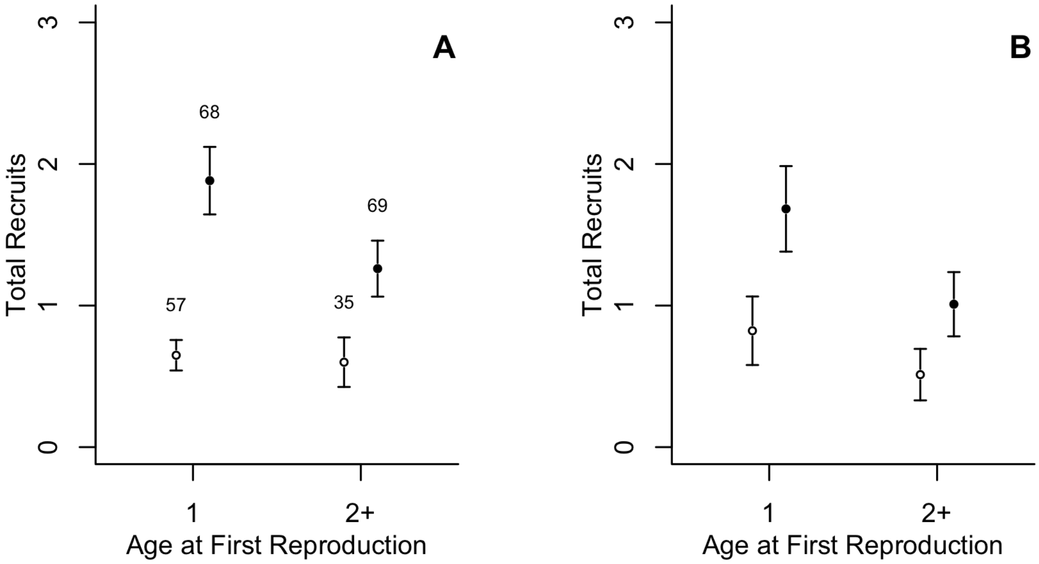


Figure 3.5. The relationship between age at first reproduction and total recruits in males who did encounter a mast year during their lifetime (black points) and those who did not (white points). The mean ± standard error of the data is presented in graph A and model predictions with 95% confidence intervals are presented in graph B. Other variables were sent to the population mean (ie. 0) to generate model predictions from the top-ranked models. I controlled for longevity in the model predictions (graph B) but not in graphing the original data (graph A).



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Chapter 4: Encountering a resource pulse influences mating behaviour and siring success in red squirrels

Introduction

Competition for access to mates is one of the main ways that sexual selection operates, and has produced a wide range of behavioural, morphological, and other adaptations that are used in intrasexual competition for mates (Clutton-Brock 2007). In species that lack paternal care, male mating success is most influenced by acquiring mating opportunities (Trivers 1972; Wade 1979). Ecological conditions may alter mate availability and reproductive investment by both sexes and thus alter sexual selection (Emlen & Oring 1977; Shuster & Wade 2003; Shuster 2009). As a result, the strength or direction of sexual selection may shift between or within populations (Chaine & Lyon 2008; Gosden & Svensson 2008; Weese *et al.* 2010) due to environmental or demographic factors that affect reproductive investment in either sex (Cockburn, Osmond & Double 2008; Gosden & Svensson 2008). Sexual selection is thus influenced by both mating opportunities and ecological factors that influence reproduction.

Males in many species influence mating opportunities by committing infanticide. Infanticide occurs in a wide range of animals and several adaptive explanations have been proposed (Hrdy 1979). Here I focus on the sexual selection hypothesis, which suggests that animals may commit infanticide when it results in competitive advantages in intrasexual competition (Hrdy 1979). There are two predictions from the sexual selection hypothesis (Hrdy 1979). First, offspring killed by infanticide are unlikely to be the adult's offspring and thus lower reproductive success of its competitors. Second, killing young leads to higher opportunities for the adult to breed, for example by ensuring that the female will go into oestrous sooner. With some exceptions (eg. Balme & Hunter 2013), infanticide providing sexually-selected benefits has predominantly been documented in social animals or where males can easily defend or monopolize females (eg. McLean 1983; Packer & Pusey 1983). Asocial or solitary animals are an interesting case as the lack of social structure may make it more challenging for a male to ensure paternity, and hence there could be lower paternity benefits of infanticide. In addition, the environmental influences on sexually-selected infanticide are not well-understood.

I tested for shifts in sexual selection and paternity in North American red squirrels who live in a pulsed resource system. Short, intense, and infrequent resource availability characterize pulsed resource systems (Yang *et al.* 2008). The main food for red squirrels during the breeding season is white spruce cones (Fletcher *et al.* 2013), and this tree species produces fluctuating amounts of cones annually with irregular mast years where they produce large amounts of cones (Lamontagne & Boutin 2007). Although some species respond to resource pulses by increasing reproduction after the pulse and using the resources as a food source (Yang *et al.* 2008), in other species females can anticipate the approach of a mast year and reproduce in order to time juvenile production to peak food availability (Boutin *et al.* 2006; Lebl *et al.* 2010; Bergeron *et al.* 2011; Montiglio *et al.* 2014). Thus, the resource pulse is simply a cue for reproductive investment not a source of energy for reproduction during a mast. Female red squirrels produce more pups, more litters, and more recruits during mast years (Boutin *et al.* 2006; Williams *et al.* 2014). Squirrels breed in late winter to spring but white spruce cones are only consumed beginning in July (Fletcher *et al.* 2013); thus this increased reproductive investment is anticipatory reproduction (Boutin *et al.* 2006). Although the effects of cones on males has not yet been studied, increased female reproduction will result in greater siring opportunities for males in mast years. Red squirrels are ideal for testing ecological impacts on sexual selection, as female red squirrels reproduce in response to fluctuations in white spruce cone production.

I investigated whether there is evidence that male mating behaviour, sexual selection, and paternity patterns differed in high resource (mast) years compared with low resource (non-mast) years. I first explore evidence for changes in female reproduction and pup recruitment depending on whether it is a mast year. I quantified these patterns in order to determine whether siring opportunities differed in mast years. One of the key differences between mast and non-mast years is that females are more likely to produce multiple litters in mast years (Boutin *et al.* 2006). So I also tested whether the occurrence of a mast year altered whether pups from first or subsequent litters recruited into the population. This would again provide evidence of whether siring opportunities changed between first and subsequent litters within mast years. I predicted that, similar to previous findings (Boutin *et al.* 2006; Williams *et al.* 2014), females would produce more pups in high resource years. Females produce multiple litters predominantly in high resource years (Boutin *et al.* 2006), which I will term first and late (ie. subsequent) litters. I thus predicted that females would produce more late litters in mast years and as a result a larger proportion of pup recruitment would originate from these litters. In contrast, in non-mast years I expected that few late litters would be produced and thus that pup recruitment from these litters would be low. Overall, I am thus predicting that there will be more siring opportunities in high resource years, and that these opportunities will be spread between first and subsequent litters.

Previous research has shown that male red squirrels who access large numbers of mates and travel large areas to access those mates also achieve the highest reproductive success (Lane *et al.* 2009). Red squirrels thus have a scramble competition mating system (Lane *et al.* 2009). However, I tested whether these patterns changed during mast years, given that I also expected that siring opportunities would change. I observed changes in mating behaviour in high resource years that suggested that mate guarding may occur, suggesting that males may change siring strategies in high resource years (unpublished data). Thus, I tested whether there was evidence that males changed their mating behaviour and siring patterns in mast years. I quantified both siring success by males, as well as paternity patterns within litters. And finally, I document evidence of infanticide by male red squirrels in mast years. To test whether this could be more prevalent in mast years, I compared litter loss between mast and non-mast years. I also tested whether infanticide resulted in a shorter period between litters, and thus could be a strategy by males to manipulate siring opportunities and increase their paternity success. I am thus testing whether there is evidence that masts influence siring opportunities, which in turn could alter male mating behaviour and infanticide.

Methods

Monitoring Survival, Female Reproduction, and Recruitment

Red squirrels were monitored as part of the Kluane Red Squirrel Project in two study areas in the Yukon (Humphries & Boutin 2000; McAdam *et al.* 2007; Lane *et al.* 2008). Survival of all individuals within each study area was determined by giving them unique coloured wires and alphanumeric tags in their ears, and then using regular trapping or behaviour observations. Red squirrels centre their territory on a food cache called a midden, and territory ownership was determined twice a year during two population censuses. Female reproductive status was assessed with trapping from March to August by measuring body mass to look for weight gain as well as by assessing nipples to look for evidence of lactation and fur wear from nursing pups.

Telemetry was used to locate nests shortly after parturition to count litter size and to take tissue samples for paternity analysis. Pups were then tagged at 25-days-old while still in the nest. Pups are weaned around 70 days of age, and litter loss prior to this age is evident as females' nipples become flaccid (McAdam *et al.* 2007). Thus, any litter that died prior to weaning was considered unsuccessful (McAdam *et al.* 2007). Females typically have one litter per season, but may re-nest following litter failure or produce multiple litters in high resource years (Boutin *et al.* 2006). I thus also determined whether it was a female's first, second, or third litter in that season. As third litters are rare, I categorized litters (herein called litter category) as either first litters or late litters (ie. second or third litters). I use trapping and behaviour observations the following spring to detect whether these pups recruited, as juveniles disperse over short distances within the study areas (Berteaux & Boutin 2000). Individuals were assigned a birth year based on when they were tagged in the nest or first trapped as a juvenile. If an individual was first trapped as an adult, they were assigned a birth year of the previous year. Based on their birth year, I calculated their age in years.

Paternity and Mating Behaviour

To assess paternity, ear tissue that was collected from pups in the nest, or juveniles and adults the first time they were trapped was used. DNeasy Tissue extraction kits (Qiagen) were used to extract DNA from these samples which were then amplified 16 microsatellite loci using PCR. Genotypes were assigned with GENEMAPPER software 3.5 (Applied Biosystems) and then paternity was assigned using CERVUS 2.0 with 95% confidence. Based on known maternal-offspring relationships from field data, estimated genotyping error was 2%. Sires were assigned to an average of 81% of pups between 2003-2014. More details of the genetic analyses are available elsewhere (Gunn *et al.* 2005; Lane *et al.* 2008; Haines et al. in prep.). I used paternity estimated from these genetic analyses as well as recruitment data from trapping to calculate the annual number of pups and number of recruits sired by each male. I also determined how many pups males sired in first or late litters, based on litter information collected in the field.

Home range area is a sexually-selected trait: males who have larger home ranges have higher mating success and sire more pups (Lane *et al.* 2009). When a female comes into oestrous, she mates with multiple males in a mating chase (Lane *et al.* 2008). Home range area was measured in 2003-2005, 2008, and 2013-2014. In 2003-2005 and 2008, females were radio-collared and followed on their day of oestrous, and more detailed description of the data collection during all mating chases can be found elsewhere (Lane *et al.* 2007, 2008, 2009; Taylor 2012). Identities and spatial locations of males in attendance were recorded. For some males in these years as well as in 2013-2014, radio-collared males were located regularly throughout the mating season, and their spatial location recorded each time. In all years, the spatial location of males who were observed or trapped as part of long-term monitoring was recorded. Home range area for each male was calculated with a 100% minimum convex polygon (Lane *et al.* 2009). In 2013-2014, values were calculated using the R version 3.1.2 (R Core Team 2014) and package adehabitatHR version 0.4.12 (Calenge 2006). In these years, males with 5 or less locations were excluded because of the requirements of the adehabitatHR package. This few locations means their home range estimation would not have been representative of their behaviour. Estimates of home range area are affected by the number of locations used in each calculation (Lane *et al.* 2009), so the number of locations was included as a covariate in all analyses of home range.

I used the pedigree to quantify siring patterns. Males who mate with more females have higher reproductive success (Lane *et al.* 2009) and females mate with multiple males (Lane *et al.* 2008). However, field observations suggested that patterns of paternity differed in high resource years (unpublished data). Thus, I used the pedigree to calculate the number of mates that males sired pups with. When males sired pups with the same female multiple times in a season (ie. because a female had multiple litters) I counted each litter separately as each would have required a separate mating chase. I also quantified how paternity was distributed within a litter, ie. whether a male dominated the paternity of pups in the litters that he sired. For each litter, I calculate the proportion of the litter that each male sired. I then calculated the average litter proportion (herein: litter proportion) within the litters sired in a year for each male. I also used the pedigree to quantify siring patterns in first and late litters in high resource years. To do so, I separated paternity from first and late litters. I calculated the maximum distance between males' middens and the females they sired pups with in first and late litters to quantify how far away males traveled to sire pups. I also quantified the number of mates males had in first and late litters only, as well as the average litter proportion that they sired in first and late litters only.

Male and female mating patterns can be very different, even within the same population (Jones *et al.* 2005). Thus, I also used the pedigree to calculate paternity of each litter to analyze it for each female. I determined the number of sires per litter. If the identity of pup's sire could not be determined (uncommon, and typically due to an unidentified male from outside the study area siring pups within the study area), I counted that as a separate sire. The number of sires in the litter does not describe how paternity is distributed in the litter. Thus, I also determined the proportion of the litter sired by each male, and calculated the weighted average proportion of the litter sired by all males (herein: weighted litter proportion). This was weighted by the number of pups each male sired as this would better reflect when paternity was skewed than the arithmetic mean.

Resource Availability

Red squirrels breed in spring, and then white spruce cones grow and mature in late summer and are consumed by red squirrels in the fall. In late summer, I assessed resource availability by counting the number of cones visible on one side of marked white spruce trees located systematically throughout the study areas (Lamontagne, Peters & Boutin 2005). The number of cones was log-transformed and then averaged for each study area and year. I used the number of cones produced to assess whether it was a mast or non-mast year, and determined that 2005, 2010, and 2014 were mast years.

Statistical Analyses

I used R Version 3.3.0 (R Core Team 2016) for all analyses. For each analysis I used a candidate model set ranked with AICc to test for the model of best fit, considering any models ≤ 6 ΔAICc from the top model to a top-ranked model as this generally will include 95% of the plausible models (Burnham & Anderson 2002; Richards 2005; Richards, Whittingham & Stephens 2011; Symonds & Moussalli 2011). I standardized models with a mean of 0 and standard deviation of 0.5 (Grueber *et al.* 2011) using the package arm and function standardize prior to ranking with AICc (Gelman & Su 2015). I used the model.avg function in the MuMIn package with the zero method of model averaging to generate model-averaging coefficients when there were more than one top-ranked model (Burnham & Anderson 2002; Grueber *et al.* 2011; Bartón 2016). I used model.sel and coeffTable in MuMIn to calculate coefficients. Random effects' intercepts but not slopes were allowed to vary. I used the lme4 function in R (Bates *et al.* 2015) when including random effects with glmer for Poisson-distributed and lmer for normally-distributed data. For the remaining models I used the glm and lm functions in R for Poisson and normal distributions, respectively. I used ReporteRs package version 0.7.2 (Gohel 2016) to export my results. Where I presented descriptive statistics, I have included the mean ± standard error, as well as the median in some cases.

To test whether female reproduction differed in high compared with low resource years, I included a categorical variable to indicate whether it was (1) or was not (0) a mast year as the independent variable. I then ran separate models with the annual number of recruits each female produced, the number of females who bred or attempted to breed (ie. whose pups died before they left the nest), the number of second litters, and the proportion of recruits that were born in first litters. This last analysis included only females who produced at least one pup in that season. I included quadratic age as a covariate when analyzing the number of recruits. When testing the number of breeding females or the number of first or second litters, I included the total number of females in the population as a covariate to control for possible differences in population density. Finally, I tested whether multiple paternity (number of sires) and the distribution of paternity among pups in the litter (weighted litter proportion) differed depending on resources or litter category. In separate models, I included number of sires or weighted litter proportion as the dependent variable, and resources or litter category as the independent variable. When analyzing resources, I first included all litters and then only first litters in order to confirm whether differences were due to females producing multiple litters in some years. To test litter category I only analyzed data in high resource years as multiple litters in low resource years are less common. I included litter size as a covariate. I also determined whether litter success or failure affected how quickly females re-nested in high resource years by including the number of days between the first and second litter as the dependent and litter success (Y/N) as the independent variable. I excluded third litters as they were rare, and I defined a litter as successful when pups survived to be weaned.

I analyzed whether male behaviour and siring patterns differed depending on resources or litter category by including home range area, number of mates, or litter proportion as the dependent variable and either resources or litter category as the independent variable. I included quadratic age as a covariate. I also tested whether there was a difference in maximum distance, average litter proportion, and number of mates between first and late litters, using only data from either first or late litters as the dependent variables and litter category as the independent variable, with quadratic age as a covariate.

I used Poisson distribution to analyze the number of recruits (for males and females), number of second litters, number of sires per litter, the number of mates that they sired, and maximum distance. I used a normal distribution for the number of breeding females, the number of first litters, the proportion of recruits that came from first litters, weighted litter proportion, interval between first and second litters, home range area, and litter proportion. Where there were multiple records per individual I included squirrel identity as a random effect. Where there were multiple measures per study area in a year, I concatenated study area and year and included that as a random effect. When there were only single records per year for each study year, I instead included study area as a covariate.

Results

Changes in Female Reproduction, Litter Paternity, and Litter Loss

Whether it was a mast year affected the number of recruits that females produced: females produced more recruits in mast years compared with non-mast years (mast years: 1.7±1.5, range 0-6; non-mast years: 0.6±0.9, range 0-5; Table 4.1). There was also a greater number of females in the population who produced recruits in mast years compared with non-mast years (proportion of females with recruits in mast years: 0.7±0.1, range 0.5-0.9; non-mast years: 0.4±0.1, range 0.05-0.6; Table 4.1). There were slightly more first litters produced in mast years compared with non-mast years (mast years: 33±16, range 15-61; non-mast years: 29±7, range 12-44; Table 4.1). There were also more late litters produced in mast years than in non-mast years (mast years: 18±8, range 8-30; non-mast years: 3 litters±2, range 0-9; Table 4.1). I restricted the data to females who produced at least one recruit. Among those females, whether it was a mast year influenced the proportion of their recruits that come from first compared with late litters. A lower proportion of their recruits came from first litters in mast years compared with non-mast years, with only about half of recruits coming from first litters in mast years (proportion of recruits from first litters in mast years: 0.5±0.5, range 0-1; non-mast years: 0.9±0.3, range 0-1; Table 4.1).

Among first litters whose fates (successful or not) were known, first litters were less successful in mast years compared with non-mast years (proportion of first litters successful in mast years: 0.56±0.15, range 0.38-0.71; proportion of first litters successful in non-mast years: 0.91±0.10, range 0.66-1.00; Table 4.1). Females whose first litter was not successful bred sooner following litter loss than females whose litter was successful (successful litters: 68±9 days, range 47-79; unsuccessful litters: 51±8, range 35-68; Table 4.1).

Changes in Siring Patterns and Mating Behaviour

I first focused on paternity within litters. When I consider the number of sires per litter across all years and all litters, mast year was in the top-ranked model and there were fewer sires per litter in mast years, but the difference between mast and non-mast years is marginal (mast years: 1.8±0.8, range 1-5; non-mast years: 1.9±0.8, range 1-5; Table 4.2). If I restrict the analysis to only first litters in all years, mast was again in the top-ranked models but again the difference was marginal and the coefficient was zero (mast years: 1.9±0.8, range 1-5, non-mast years: 2.1±0.8, range 1-5; Table 4.2). However, in mast years only, there were more sires per litter in first litters than late litters (first litters: median 2 sires, mean 2.1±0.8, range 1-5; late litters: median 1 sire, mean 1.4±0.5, range 1-3; Table 4.2). There was no effect of mast on the weighted mean proportion of litters sired by each male, ie. the distribution of siring within litters (mast years: 0.6±0.3, range 0.2-1; non-mast years 0.6±0.2, range 0.2-1; Table 4.2). This result was the same if only first litters were included in the analysis (mast years: 0.6±0.2, range 0.2-1; non-mast years: 0.6±0.2, range 0.2-1; Table 4.2). In mast years only, the weighted litter proportion was higher in late litters (first litter: median 0.5, mean 0.6±0.2, range 0.2-1; late litters: median 1.0, mean 0.8±0.2, range 0.2-1; Table 4.2). Paternity was thus skewed towards one of the sires and in many litters there was only a single sire.

There was an effect of whether it was a mast year on home range: males ranged farther in mast years compared with non-mast years (mast: 64,240±50,963m^2, range 31.5-229,800; non-mast years: 50,710±44,295m^2, range 0-192,900; Table 4.3). Whether it was a mast year also affected the number of mates that males had, with males mating with more females in mast years (mast years: 1.3±1.5, range 0-8; non-mast years: 0.8±1.1, range 0-6; Table 4.3). There was no effect of mast on the litter proportion that males sired (mast years: 0.3±0.3, range 0-1.0; non-mast years: 0.2±0.3, range 0-1.0; Table 4.3). During mast years, if I compare where males sired pups in first or late litters, pups were sired closer to their sire's midden in late litters compared with first litters (early litters: 189m±125, range 24-825; late litters: 165m±129, range 27-666; Table 4.3). Males had fewer mates in late litters compared with first litters (first litters: 1.8±1.2, range 1-8; late litters: 1.2±0.5, range 1-3; Table 4.3). There was also a difference between the proportion of the litter that males sired between first and late litters: males sired a higher proportion of late litters than first litters (early litters: 0.4±0.2, range 0.2-1; late litters: 0.7±0.3, range 0.2-1; Table 4.3).

Field Observations of Infanticide

I documented one case of infanticide and a likely case of infanticide in 2014, a mast year. A male (herein called sire 1) was observed killing a pup on 25-May-2014; I confirmed using genetics that he was not the sire of that pup nor any of the pup's siblings in that litter. A pup from this same litter was later found dead and partially eaten within 5m of the nest. The dam of this litter eventually suffered complete litter failure, though she bred again that season and sire 1 was the sole sire of her second litter. A different female (herein called dam 2) elsewhere in the study area was confirmed to be lactating with trapping and then located using telemetry in a nest the night of 25-April-2014. The following day a male (sire 2) was observed approaching the nest, during the day the nest was found to be empty, and that evening sire 2 was observed caching a dead, partially eaten pup. Using genetics, I determined that sire 2 was not the sire of the pup but that its mother was dam 2. I later used trapping to confirm that dam 2 was no longer lactating (had lost her litter). Although dam 2 eventually produced a second litter, sire 2 did not sire any of her pups. Other cases of possible infanticide were observed as well. Pups in several litters in 2014 were found with bruising and puncture wounds either dead or alive, sometimes along with uninjured siblings in the same nest.

Discussion

I have demonstrated substantial changes in female reproduction between mast and non-mast years. Similar to what has been shown in previous research (Boutin *et al.* 2006; Williams *et* *al.* 2014), females produced more recruits in mast years compared with non-mast years. In addition, a larger proportion of the females in the population successfully produced recruits during mast years. Previous research has shown that females are more likely to produce multiple litters in mast years (Boutin *et al.* 2006), and my results support this. In mast years there were marginally more first litters and substantially more second litters than in non-mast years. As a result, late litters produced on average half of the recruits in the population during mast years, compared with a low proportion of recruits from second litters in non-mast years. My results thus suggest that siring opportunities and the potential fitness benefits from pursuing those opportunities shift substantially between mast and non-mast years.

I have shown that male mating behaviour and siring success changes between mast and non-mast years, as well as between first and late litters in a mast year. Overall, males in mast years had larger home ranges and more mates, though there were no differences in litter proportion. In mast years, paternity patterns were also different between first and late litters. Males sired pups closer to their territory, they sired pups with fewer females, and they sired a higher proportion of the litter in late litters compared with first litters. Similarly, within litters there were fewer sires per litter in late litters and the paternity is more skewed towards a single male. The median values (see Results) indicated that most first litters have multiple sires with paternity distributed among them, whereas late litters are typically sired by a single male. Other studies have demonstrated that fluctuations in sexual selection occur between or within populations (Chaine & Lyon 2008; Cockburn *et al.* 2008; Gosden & Svensson 2008; Weese *et al.* 2010). The causes of these fluctuations are not always clear, but may result from changes in demographics or environmental conditions that influence reproductive investment (Cockburn *et al.* 2008; Gosden & Svensson 2008). Here, I have shown evidence that sexual selection on male red squirrels may fluctuate according to the occurrence of a resource pulse. Thus, sexual selection changes according to fluctuations in mating opportunities. In particular, I have demonstrated that the key difference between mast and non-mast years is that paternity patterns change between first and late litters. By analyzing female reproductive data, I demonstrated that in mast years there are many females who produce recruits and that recruits originate from both first and late litters. By analyzing male mating behaviour, I have demonstrated that there is a shift from accessing many females over a large area during non-mast years and first litters, to single-sired litters in a nearby territory in late litters in mast years. Field observations from 2014 (a mast year) suggest that this shift in paternity may be accompanied by mate-guarding of oestrous females (unpublished data). The red squirrel mating system may thus change from a scramble competition mating system in low resource years and first litters to a female defence system in late litters during mast years. In traits that are strongly connected with fitness, it is puzzling that variation is maintained in many wild populations. One potential explanation is that fluctuating environments result in traits having positive effects on fitness in some years, but negative effects on fitness in other years, resulting in multiple phenotypes being maintained within the population (Ellner & Hairston 1994). I have shown that there are differences in male behaviour and siring patterns between mast and non-mast years, as well as between first and late litters. This provides support that a fluctuating environment could maintain variation in sexually-selected traits in red squirrels.

I documented infanticide by male red squirrels during a mast year. Infanticide occurs in a wide range of animals (Hrdy 1979) including in rodents, such as Smith's bush squirrel (*Paraxerus cepapi*, de Villiers 1986), Arctic ground squirrels (*Spermophilus parryii*, McLean 1983), and alpine marmots (*Marmota marmota*, Hackländer & Arnold 1999). This was the first time this was documented in red squirrels. When infanticide is a sexually-selected behaviour, there are two predictions that arise (Hrdy 1979). First is that committing infanticide is unlikely to lower the reproductive success of the individual committing infanticide as it is unlikely to be their offspring, and thus it lowers the reproductive success of their competitors. Second, infanticide increases breeding opportunities, typically because the female will breed sooner following infanticide than following a successful litter. My results support both of these predictions. The two males that I observed or suspected committing infanticide were not the pups' sires, though these are small sample sizes. However, of 169 records of males who sired pups in first and/or late litters in mast years, 119 (70%) only sired pups in first or late litters. Males would not be at risk of killing their own offspring if they did not sire pups in first litters. Males would benefit from committing infanticide as females re-nest sooner following litter failure than when they have a successful litter. I also demonstrated that first litters are less likely to be successful in mast years compared with non-mast years. Although I am not suggesting that every litter loss is the result of infanticide, this difference suggests that infanticide was more common in mast years than in non-mast years. This may occur because females produce more late litters in mast years, and thus there are siring opportunities of subsequent litters. My paternity analyses also demonstrate that late litters are more likely to be single-sired litters. Thus, males could benefit from infanticide by dominating siring of the subsequent litter. Given that a higher proportion of the females in the population produce recruits in mast compared with non-mast years, dominating paternity in any particular litter would be a reasonable strategy in mast years. In non-mast years it could be difficult to predict whether a particular female would have a successful litter, and thus it would be a better strategy to spread success among many females. I have demonstrated that female reproductive success is influenced by white spruce tree masts, and that this in turn alters reproductive strategies by male red squirrels.

Table 4.1. Model sets used to determine whether the predictor (Predictor with coefficient listed under Predictor Coefficient) mast year (Mast) resulted in differences in the following response variables (Response): number of recruits that females produced (Recruits), the number of females in the population who bred (# Females), the number of first litters (# 1st Litters), the number of second litters (# Late Litters), the proportion of recruits that originated from first litters (Prop. 1st Litters), and the number of successful litters (# Successful Litters). I also tested whether the interval between first and second litters (Litter Interval) depended on litter success (Success). Where relevant, I included the following covariates: age (Age), the number of females in the population (Tot. Females), the total number of litters (Total Litters), or study area (Study Area). The covariate coefficient was indicated as Covariate Coefficient when I included a linear effect, and as both Covariate Coefficient and Covariate Coefficient^2 when I included a quadratic. I included study area-year and squirrel id as random effects in model sets 1 and 5, and study area-year as a random effect in model set 7. For models with random effects, the null model includes only random effects, whereas models without random effects did not include any variables. Coefficients were generated from model-averaging coefficients from the top-ranked models, which included models ≤6 ΔAICc of the top model. Model selection tables are given in Appendix 3 (Table A3.1), with model set numbers matching the model set number (Model) listed here.

Model	Response	Predictor	Subset	Intercept	Predictor Coefficient	Covariate	Covariate Coefficient	Covariate Covariate^2	Study Area
1	Recruits	Mast	All	**-0.33 ± 0.23**	**1.15 ± 0.51**	Age	0.07 ± 0.23	**-0.32 ± 0.31**	-
2	# Females	Mast	All	**12.67 ± 1.30**	**11.25 ± 3.01**	Tot. Females	**7.03 ± 2.85**	-	-
3	# 1st Litters	Mast	All	**29.88 ± 1.94**	4.74 ± 5.51	Tot. Females	**16.32 ± 4.29**	-	-1.81 ± 4.19
4	# Late Litters	Mast	All	**1.54 ± 0.21**	**1.78 ± 0.32**	Tot. Females	**0.39 ± 0.26**	-	-0.14 ± 0.34
5	Prop. 1st Litter	Mast	All	**0.75 ± 0.07**	**-0.42 ± 0.16**	-	-	-	-

Model	Response	Predictor	Subset	Intercept	Predictor Coefficient	Covariate	Covariate Coefficient	Covariate Covariate^2	Study Area
6	# Successful Litters	Mast	1st Litters	**22.58 ± 1.47**	**-10.00 ± 3.43**	Total Litters	**9.76 ± 3.38**	-	-2.00 ± 3.48
7	Litter Int.	Success	Mast	**55.84 ± 3.70**	**19.26 ± 4.35**	-	-	-	-

Table 4.2. Model sets used to determine whether the siring patterns within litters were different depending on two predictors (listed as Predictor with the coefficient indicated by Predictor Coefficient): 1) whether or not it was a mast year (Mast) or 2) whether it was a first or late litter (Litter #). Siring patterns were quantified as either the number of sires in the litter (# Sires) or the proportion of the litter sired by each sire weighted by the number of pups sired by each sire (Litter Prop.); this was the response variable (Response). Litter size was included as a covariate in all models. Data were subset prior to analysis, including all data (All), all years but first litters only (1st), or mast years only but all litters (Mast). I included study area-year and squirrel id as random effects in all model sets. The null model includes only random effects. Model-averaged coefficients were generated from the top-ranked models, which included any models ≤6 ΔAICc of the top model ranked according to AICc. Model set numbers (Model) match model selection tables presented in Appendix 3 (Table A3.2).

Model	Response	Predictor	Subset	Intercept	Predictor Coefficient	Litter Size
1	# Sires	Mast	All	**0.63 ± 0.06**	-0.04 ± 0.12	**0.22 ± 0.12**
2	# Sires	Mast	1st	**0.69 ± 0.06**	0.00 ± 0.07	**0.35 ± 0.13**
3	# Sires	Litter #	Mast	**0.59 ± 0.10**	**-0.50 ± 0.23**	**0.26 ± 0.21**
4	Litter Prop.	Mast	All	**0.62 ± 0.02**	X	X
5	Litter Prop.	Mast	1st	**0.58 ± 0.03**	X	**-0.08 ± 0.04**
6	Litter Prop.	Litter #	Mast	**0.64 ± 0.06**	**0.26 ± 0.06**	-0.02 ± 0.07

Table 4.3. Model sets used to test whether male mating behaviour or paternity differed depending on whether it was a mast year, as well as depending on whether he was successful in a first or later litter. In each model, the predictor (Predictor) was thus either whether or not it was a mast year (Mast) as well as whether or not it was a first or later litter (Litter Number); the coefficient for the predictor was indicated by Coefficient. When analyzing whether it was a mast year, I quantified home range area using behaviour (Home Range) and number of mates (No. Mates) or proportion of the litter sired (Litter Proportion). When analyzing whether litter number affected paternity patterns, I compared the maximum distance between male and female territories where males sired pups (Distance), the number of mates (No. Mates) and the proportion of the litter that they sired (Litter Proportion). I included quadratic age (Age and Age^2) as covariates in all models. As the number of times a male was located during behaviour observations would have influenced the home range area, I included the number of behaviour observations (No. Locations) as a covariate in that model. Study area-year and squirrel id were included as random effects in all model sets. Only random effects were included in the null model. Model-averaged coefficients from any models ≤6 ΔAICc of the top model ranked according to AICc were used to calculate these model coefficients. Full model sets ranked according to AICc are presented Appendix 3, with model set numbers (Model) matching those in Table A3.3.

Model	Response	Predictor	Intercept	Coefficient	Age	Age^2	No. Locations
1	Home Range	Mast	**6.26 ± 1.55**	0.67 ± 2.69	0.06 ± 1.13	**-2.06 ± 1.84**	**3.76 ± 1.11**
2	No. Mates	Mast	-0.07 ± 0.14	**0.34 ± 0.28**	**1.10 ± 0.21**	**-1.21 ± 0.30**	-
3	Litter Proportion	Mast	**0.30 ± 0.03**	0.01 ± 0.05	**0.21 ± 0.05**	**-0.22 ± 0.05**	-
4	Distance	Litter Number	**5.00 ± 0.17**	**-0.23 ± 0.03**	**-0.21 ± 0.16**	0.05 ± 0.12	-
5	No. Mates	Litter Number	**1.54 ± 0.26**	**-0.53 ± 0.27**	**0.35 ± 0.32**	**-0.10 ± 0.55**	-
6	Litter Proportion	Litter Number	**0.53 ± 0.07**	**0.27 ± 0.07**	0.02 ± 0.07	-0.07 ± 0.12	-

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Chapter 5: Sex-specific effects of cached food on reproductive timing and fitness in red squirrels

Introduction

Reproductive investment, such as lactation or mating behaviour, is energetically demanding (Lane *et al.* 2010; Fletcher *et al.* 2012). It is thus intuitive to expect that resource availability would influence reproductive success. And, indeed, natural variation in food availability or experimental food supplementation may result in advancements in breeding timing, larger broods or litter sizes, and overall higher reproductive success (Boutin 1990; Pelletier & McNeil 2003; Derbyshire, Strickland & Norris 2015; Kaiser *et al.* 2015). However, the intuitive influence of food on fitness is not universally detected. Several studies have found no effect of food availability on reproduction under natural and experimental conditions (Boutin 1990; Dawson & Bortolotti 2000; Sim *et al.* 2015; Crates *et al.* 2016), or even a reduction in reproductive success as a result of experimental food addition (Harrison *et al.* 2010). These studies demonstrate that the link between food and fitness may not be straightforward. Additionally, animals may be capital or income breeders: capital breeders use previously stored food to fuel reproduction, whereas income breeders use resources acquired during reproduction as energy (Jonsson 1997). Capital breeders are thus less sensitive to immediate changes in resource availability, as they are depending on resources acquired prior to reproduction. Thus, this may affect whether a connection between reproductive success and resources is detected.

Sex-specific selection can result in different life history patterns between the sexes (Wedell *et al.* 2006), and thus their responses to resource availability. Males are predicted to invest in offspring quantity due to their higher potential reproductive rate and reduced role in parental care in many species, particularly in polygamous mating systems (Bateman 1948; Trivers 1972; Clutton-Brock 2007). Their reproductive success is thus increased by achieving more mating opportunities (Bateman 1948; Trivers 1972; Clutton-Brock 2007). Females are predicted to invest in offspring quality, and they are therefore more likely to compete for access to resources for successful reproduction rather than for access to mates (Bateman 1948; Clutton-Brock 2007, 2009). Sexually-selected traits, such as weapons or ornamentation, have evolved to increase success in intra-sexual competition for mates (Darwin 1871). Traits that increase success in intra-sexual or inter-sexual competition are thought to have this function as they are condition-dependent: only high-quality males may achieve and maintain sexually-selected traits (Andersson 1982). Thus, males may be sensitive to resource availability like females if resources affect their condition and sexually-selected traits, and thus their mating opportunities.

I am studying the connection between resource availability and reproduction in North American red squirrels (*Tamiasciurus hudsonicus*). Red squirrels store food in a central cache within their territory, which they defend against conspecifics. This makes them ideal for studying the effects of resources on reproduction as individual-level resource availability can be assessed. White spruce cones are their main food source particularly during winter and spring (Fletcher *et al.* 2013). White spruce trees produce fluctuating amounts of cones, and irregularly produce exceptionally large crops called mast years. Red squirrel reproduction is linked with white spruce cone production, with females producing more pups in years with higher cone production (Boutin *et al.* 2006). Females also breed earlier in the year following a high resource year (Williams *et al.* 2014), and advancements in breeding likely result in competitive advantages for juveniles competing for territories (Larsen *et al.* 1997). Squirrels reproduce in spring but cones are available the following autumn, so increases in reproductive success in a high-resource year represent anticipatory reproduction in anticipation of the higher recruitment of juveniles in these years (Boutin *et al.* 2006; Williams *et al.* 2014). In this species and other tree squirrels, studies on the link between individual-level resources and fitness components have found mixed results. Cached cones increase overwinter juvenile survival, and juveniles that do not obtain a midden prior to winter will likely not survive to the following spring (Larsen & Boutin 1994; LaMontagne *et al.* 2013). Female North American red squirrels with experimentally manipulated hoards did not have increased reproductive success, though they advanced their breeding dates in one year of the study (Larsen *et al.* 1997). In contrast, Eurasian red squirrels who spent more time recovering cached seeds had higher annual survival, longevity, and lifetime reproductive success (Wauters, Suhonen & Dhondt 1995). However, this study did not make a distinction between foraging behaviour and resource consumption, and thus did not demonstrate a direct link between resource availability and reproduction. Thus, the connection between population-level food availability and reproduction has been well-studied, but the link between individual-level resources and reproduction is not yet clear.

I first explored general patterns of hoard sizes to determine whether there were any sex-specific differences in individual-level resource availability. I also tested whether there was evidence for individual consistency in the amount of resources that they had cached. I also tested whether having large amounts of resources leads to increased annual reproductive success and advanced breeding phenology in males and females, as well as increased mating behaviour in males. Although it is likely that resources could affect survival, as I was studying mature animals many of them had high survival rates and I was unable to test this. Finally, I examined whether having more cached cones increased lifetime reproductive success or longevity in both males and females.

Methods

Measuring Reproductive Success and Longevity

As part of the Kluane Red Squirrel Project in the Yukon, Canada, male and female red squirrels were regularly monitored in two study areas (Kloo and Sulphur) from March to August each year for almost 30 years. More details about the field methodology can be found elsewhere (McAdam *et al.* 2007). Each individual received alphanumeric ear tags with coloured wires threaded through them, enabling individual identification through trapping and behaviour observations throughout their lives. Behaviour observations and trapping were used to detect survival from March to August each year. Trapping was used to monitor female reproductive status. Although females may produce multiple litters within a season (Boutin *et al.* 2006), I only included data from the first litter in each season. Data on cached cones (see below) was limited to a subset of years for which reproductive data was available and the sample size of second or third litters within that time frame was limited. Trapping dates, body mass, and evidence of lactation were used to estimate parturition date for each litter, which I then converted to Julian dates. Telemetry was used to locate nests, then pups were weighed at birth and again at 25 days old. I calculated growth rate for each pup, and then average growth rate for each litter so that only one measure per litter was included in the analysis. Pups were also tagged at 25 days, and as they disperse over short distances (Larsen & Boutin 1994; Berteaux & Boutin 2000) their recruitment into the population by the following breeding season was monitored.

To monitor male reproduction, tissue samples were collected when the pups were in the nest or as juveniles the first time they were trapped. Ear tissue was also collected from all adults. From these samples, DNA was extracted using Qiagen DNeasy Tissue extraction kits and amplified 16 microsatellite loci using PCR. GENEMAPPER software 3.5 (Applied Biosystems) was used to assign loci, and then CERVUS 2.0 was used to assign paternity with 95% confidence. Maternity was assigned based on field data when the nest was located, and genotyping error from these known mother-offspring pairs was 2%. Sires were assigned to 81% of pups on average (SE: ±0.02) between 2003-2014 (Haines et al. in prep.). More detailed descriptions of genetic paternity assignment have previously been reported (Gunn *et al.* 2005; Lane *et al.* 2008; Haines et al. in prep). Using these genetic analyses and recruitment data from population monitoring, I calculated annual reproductive success for each male both as the total number of pups sired and the total number of recruits. I included pups sired in both first and second litters. I used parturition dates for each litter estimated from monitoring females to determine the earliest date that males sired pups within a season. I used the actual parturition dates in analyses rather than estimates of the mating dates, but as the mating dates are simply parturition dates minus gestation time the pattern would remain the same regardless.

Squirrels were assigned a birth year when they were tagged in the nest or trapped as a juvenile. When they were first trapped as an adult, for example because they recruited too late in fall to be detected by trapping and behaviour observations, they were assigned a birth year of the previous year as has been done previously (Lane *et al.* 2009). I used birth year to estimate their age in years. I used the last year that they were detected to determine longevity for males and females as detection probability was high in these populations (close to 1; Descamps *et al.* 2009). I calculated female lifetime reproductive success as 1) total number of pups and 2) total number of recruits that they produced from first litters during their lifetime. For males, I calculated 1) the total number of pups that they sired from all litters and 2) the total number of recruits that they sired from all litters within their lifetime.

Red squirrels have a scramble competition mating system and males have higher success when they travel further to access females (Lane *et al.* 2009); thus, home range area during the breeding season is a sexually-selected trait. Male mating behaviour was measured by locating males regularly during the 2013-2014 breeding seasons using telemetry (see Haines et al. in prep. for more details). They were located at least daily but usually several times a day, and each time their spatial location was recorded. Male locations were also recorded each time they were trapped or observed during regular monitoring activities. I used the R version 3.1.2 (R Core Team 2014) and package adehabitatHR version 0.4.12 (Calenge 2006) to calculate home range size with 100% minimum convex polygons following Lane et al. (2009).

Individual-Level Resource Availability

White spruce cones mature in the late summer and squirrels begin caching them in the fall. I assessed individual-level cone availability in the fall from 2007-2015. Red squirrels cached cones in larder hoards called middens, which were characterized by large amounts of debris from consumed cones (called cone bracts) as well as cones cached within the layer of cone bracts or within tunnels in the ground. Midden use was traditional and squirrels cached cones in the same location on a territory even when ownership changed. Rarely, a new midden was established and as these lacked the accumulated cone bracts the midden boundaries were delineated only by locating the cached cones. Cached cones were counted within 30cm x 30cm quadrats on the midden, within 10cm of the surface in the cone bracts or within 30cm of the surface in tunnels. I also measured length and width of the midden. Prior to 2011, 16 quadrats that were sampled; in 2011 and later, 8 quadrats were sampled. I calculated the average number of cones per quadrat and multiplied it by the number of quadrats that would fit on the midden to take this methodological variation into account (see Appendix 4 for the equation). This calculation included both the amount of cones cached and the area of the midden in which the cones were cached and is thus an estimate of the total number of cached cones in each midden. Because of the distribution of this data, I ln-transformed this count. I used the estimation of cached cones in the fall as an index of resource availability the following spring. Cached cones cannot be assessed during spring as snow cover typically persists through most of the breeding season, obscuring the boundaries of the midden as well as covering cached cones except where squirrels dug tunnels to access their cache. I calculated repeatability measures and age-related changes in cached cones in the breeding seasons 2008-2015. Female reproductive data was collected from 1988-2016, but male reproductive data was collected from 2003-2014; thus, I restricted my analysis of reproduction and cones to the breeding seasons 2008-2014.

I also estimated lifetime number of cones cached. Because cached cones were repeatable between years for each individual (see Results), I included all squirrels for whom I had at least one measure of cached cones. I calculated average standardized, ln-transformed number of cached cones as a measure of lifetime cones (see below for explanation of calculations of standardized values). As I didn't assess cones in all years, I counted the number of years that cones were assessed within each individual's lifetime and divided that number by their longevity to estimate the proportion of their lifespan I assessed cones.

White spruce cone production is variable, but can be distinguished as mast (high cone production) years or non-mast (low to moderate cone production) years (Lamontagne & Boutin 2007). Mast years influence female and male reproduction (Boutin *et al.* 2006; Descamps *et al.* 2008; Williams *et al.* 2014; Haines et al. in prep.), as well as the availability of cones for caching. Thus, I also assessed population-level food availability in order to control for its potential effects on lifetime reproductive success and lifetime cached resources. I first assessed cone production by counting cones in the top 3 metres of marked trees each year (Lamontagne, Peters & Boutin 2005), which I used to classify mast years. Mast years occurred in 2005, 2010, and 2014 (Williams *et al.* 2014 and this study). I then determined whether males encountered a mast year during their adult life, coded as males who encountered mast years (1) and males who did not (0).

Statistical Analyses

I used R Version 3.3.0 (R Core Team 2016) for all analyses. I created a candidate model set for each analysis and used AICc ranking to test for the model of best fit (Burnham & Anderson 2002). I used the function standardize from the R package arm (Gelman & Su 2015) to standardize models with a mean of 0 and standard deviation of 0.5 (Grueber *et al.* 2011) prior to ranking with AICc. I considered a model to be the top-ranked model if it was ≤6 AICc different from the other candidate models (Burnham & Anderson 2002). When there were more than one top-ranked model, I used the model.avg function in the MuMIn package with the zero method of model averaging to generate model-averaged coefficients (Burnham & Anderson 2002; Grueber *et al.* 2011; Bartón 2016). I calculated coefficients using model.sel and coeffTable in MuMIn and presented the relevant coefficients with 95% confidence intervals from top-ranked models. I used the mode.sel and coeffTable functions in the MuMIn package to generate these tables. When I included a random effect, I allowed the intercept but not the slope to vary. For random effects, I used the lme4 function in R (Bates *et al.* 2015) with glmer for Poisson-distributed and lmer for normally-distributed data. When random effects were not included, I used the glm and lm functions in R for poisson and normal distributions, respectively. I graphed model predictions from the top-ranked model, or the model-averaged coefficients in the case of multiple top-ranked models, using the predict function with all variables that were not of interest set to the population mean (ie. set to zero). I exported statistical output and figures using the ReporteRs package version 0.7.2 (Gohel 2016). For many datasets I detected outliers using diagnostic plots, which I then excluded prior to completing statistical analyses. I reported model sets ranked by AICc (see Appendix 4), and coefficients from top-ranked were presented in Results. Where descriptive statistics were presented, I included the mean ± standard deviation in order to show the variability in the data. In presenting data to compliment statistical models, I presented the mean ± standard error.

White spruce cone production fluctuates annually, resulting in fluctuating amounts of cones available for caching each year. So I included study area and year concatenated together as a random effect in analyses of annual measures. To account for multiple measures per individual when analyzing annual measured, I included squirrel identity as a random effect in those models. I then included ln-transformed cones as the dependent variable and sex as the independent variable to determine if there were sex differences in caching. There were sex differences in the number of cones cached (see Results), so I separated males and females in all further analyses. To further account for yearly differences, I calculated standardized cones: ln-transformed cached cones – average for that study area and year, keeping male and female data separate. I then analyzed the repeatability of the number of cached cones using the rpt.remlLMM function of the package rptR (Nakagawa & Schielzeth 2010; Schielzeth & Nakagawa 2013).

I first tested whether there were age-related changes in cones cached, including cached cones as the dependent variable with quadratic age as the independent variable. To test whether there was support for a linear effect, I also included age as a linear effect in the model set. I then tested whether breeding season timing influenced the relationship between cached cones and mating behaviour, breeding phenology, and reproductive success. Both males and females have age-related variation in reproduction, so I included quadratic age as covariates in all models. I ran a separate set of candidate models for each of the following dependent variables for males with standardized cones as the independent variable: number of pups, number of recruits, home range area, and earliest siring date. Because home range size could be influenced by the number of times a male was located during the breeding season, I included the number of spatial locations that were used to calculate home range area as a covariate in these models. For females, I included standardized cones as the independent variable and ran a separate set of candidate models for each of the following dependent variables: litter size, growth rate, parturition date, and number of recruits. For variables with a normal distribution (home range, siring date, parturition dates, growth rates, and litter size). I calculated the standardized value (actual value – average for that study area and year) to account for annual and study area variation. For variables with a Poisson distribution (number of pups sired, number of recruits), I instead used the actual number. I only had home range data for two years on one study area, so I excluded study area from these models and included year as a covariate rather than a random effect.

I also assessed whether there was evidence that cached cones affected lifetime reproductive success and longevity. I included average cones cached as the independent variable, with total pups, total recruits, and longevity as dependent variables in separate model sets. I included the proportion of their lifetime that I assessed cached cones as a covariate to account for how complete was my assessment of lifetime cones. I also included longevity as a covariate as well as whether they encountered a mast year as an adult, as these variables may influence lifetime reproductive success. The proportion of their lifetime that I counted cones and longevity were highly correlated, and thus could only be included in competing models within the same model set but not within the same models. I included study area as a covariate, and no random effects were included as these are lifetime measures and thus there was only one measure per squirrel.

Results

Based on average cones counted in quadrats combined with midden area, I estimated that red squirrels had an average of 19,790 cones (±912, range 0-146,500) cached in their middens. Estimates of cones cached indicated that males had more cones cached than females (males: 26,740±1,429, range 0-146,500; females: 13,660±1,049, range 0-122,200). The data was ln-transformed for all further analyses. I statistically tested for sex differences in the ln-transformed cached cones, which also showed that males had more cones cached than females (Table 5.1). Thus, I also separated males and females in further analyses, including when I standardized cached cones by the study area-year average. Individuals cached repeatable amounts of cones, with a repeatability of 0.48 for females and 0.37 for males. There was a quadratic effect of age on cached cones in both males and females (Table 5.1): there was an early-life increase and a late-life decrease in the amount of cones cached. However, this quadratic relationship was more pronounced in males than in females, with males taking many years to reach their peak amount of cached cones (Figure 5.1).

Effects of Resources on Reproduction and Longevity

Males with more cached cones sired more pups and recruits (Table 5.1, Table A4.1, Figure 5.2). Males who had more cached resources had smaller home range areas (Table 5.1, Table A4.1, Figure 5.3). Males with more cached cones also bred earlier in the season than males with fewer cones (Table 5.1, Table A4.1, Figure 5.3). There was no effect of average cones cached on total pups sired in their lifetime, but there was a positive effect of average cones cached on the total number of recruits that males sired (Table 5.2, Table A4.2, Figure 5.4). There was also a positive relationship between average cached cones during their lifetime and their longevity (Table 5.2, Table A4.2).

In females, there was a negative relationship between parturition date and cached cones: females with more cached cones also bred earlier in the season (Table 5.1, Table A4.1, Figure 5.5). There was no relationship between the number of cones cached and female litter size, pup growth rate, or the number of recruits (Table 5.1, Table A4.1). There was no effect of average cached cones in their lifetime on total pups and total recruits produced (Table 5.2, Table A4.2). There was a negative relationship between longevity and average cones females cached during their lifetime, as females who had higher amounts of cached cones also lived shorter lives (Table 5.2, Table A4.2).

Discussion

My analysis revealed that there were sex differences in the amount of cones cached: males had more cones than females. I also found that there were sex differences in how strongly fitness components were connected with resource availability. Males with large amounts of cached resources sired more pups and recruits as well as began breeding earlier. Females who had more cones also bred earlier, but otherwise their reproduction was not affected by the amount of cached cones. Having more cached cones was associated with higher lifetime reproductive success in males, but there was no link between cached cones and lifetime reproductive success in females. These differences could be caused by differences in the timing of peak reproductive investment between males and females. Mating season occurred earlier than pups were born, so male energy needs peaked earlier than it did for females. During winter and early spring, red squirrels feed almost exclusively on cached cones (Fletcher *et al.* 2013). However, as spring green-up occurred and fresh foods become available, red squirrels began eating other foods in addition to cached cones (Fletcher *et al.* 2013). Parturition dates vary annually and thus peak reproduction does not occur at the same time each year. However, as males breed earlier than females, male reproduction is more likely to coincide with the time period when they are relying exclusively on cached cones. Females, on the other hand, bred later and thus their peak energy needs were more likely to overlap with spring green-up when foods other than cached cones were available (Fletcher *et al.* 2013). Male reproduction was also more likely to overlap with cold winter conditions, potentially resulting in them requiring more energy to maintain their reproductive investment. Thus, the difference in the timing of male and female reproduction could have selected for a stronger connection between male reproduction and cached cones.

Previous work on red squirrels showed that home range area was a sexually-selected trait: males who traveled farther during the breeding season accessed more mates and achieved higher reproductive success (Lane *et al.* 2009). I have shown that cones influenced home range area but that the relationship was negative, with males who had more cones traveling shorter distances. This seems contradictory, as males who have more cached cones also have higher reproductive success. Red squirrel reproduction is influenced by white spruce cone production, with females exhibiting anticipatory reproduction and increasing reproductive effort in years with high cone availability (Boutin *et al.* 2006). Of particular importance are years of high cone production called mast years. Mast years influence life history traits and fitness of male red squirrels, and alters mating opportunities with effects on the mating system (Haines *et al. in prep.*). In particular, home range area may be less important for achieving reproductive success during mast years (Haines *et al. in prep.*). As this data was collected during mast and non-mast years, it is possible that the conflicting relationships between cones and reproductive success or home range area are a consequence of fluctuations in the relationship between reproductive success and home range area during these years.

As cached cones are linked with reproductive success in males, this suggests that the amount of cones that a male has cached is a sexually-selected trait. Sexual selection can result in sexual dimorphism in body size due to sex-specific differences in optimal body size (Darwin 1871). Sexual size dimorphism is most pronounced in polygynous mating systems, and in some species sexual dimorphism is particularly pronounced in polygynous mating systems where few males dominate the mating opportunities and thus there is high competition for mates (Weckerly 1998). There is little difference in body size between male and female red squirrels (Descamps *et al.* 2008), though males can be up to 5-10% larger than females (Boutin & Larsen 1993). To date there has therefore been little evidence of sexual dimorphism in this population. However, this research suggests that red squirrels are capital breeders, and thus show sexual dimorphism in their food stores. Capital breeders use stored energy to fuel reproduction, whereas income breeders use energy acquired during reproduction (Jonsson 1997). Red squirrels cache cones during the autumn (Fletcher *et al.* 2010; Archibald *et al.* 2013), and which they then feed on during the breeding season (Archibald *et al.* 2013; Fletcher *et al.* 2013). Thus, their food cache functions like body fat reserves in capital breeders, but they store cones in their midden rather than on their body. The link between reproduction and cones, particularly in males, further supports that they are capital breeders that depend on food stores external to their body. Thus, red squirrels show sexual dimorphism, but in their food caches rather than in body size. In some sexually-dimorphic species, males may take multiple years to achieve their maximum body size (Weckerly 1998), which may explain the observations of sex differences in how cached cones changed with age. Males take several years to reach the age at which they have peak cached cones, whereas females reach their peak at a young age; this may therefore occur due to cached cones being a sexually-selected trait.

Without experimental food manipulations it is unclear whether cached cones are a sexually selected trait because they provide energy to the male or because they serve as a signal of male quality to females. Mating chases tend to be centred on the female’s midden and thus would not provide females with opportunities to assess male cached cones (Lane *et al.* 2008), so it is most likely that large amounts of cached cones would provide fuel for the energetic cost of accessing females (Lane *et al.* 2010). Males who breed earlier with the female on her day of oestrous have a higher chance of siring her pups (Taylor 2012), so it is possible that cached cones may also provide energy for males to achieve dominance over other males similar to body mass in some income breeders (eg. Pelletier & Festa-Bianchet 2006). However, field observations suggest that some females may occasionally pilfer male cones during the breeding season (unpublished data), so I cannot completely exclude the possibility that cached cones could be a signal of male quality to be used in female mate choice. If cached cones do function in female mate choice or in allowing males to achieve dominance in the copulation order, it is possible that there is a negative relationship between home range area and cones because some males use different reproductive tactics other than traveling large areas; this is evident during mast years (Haines *et al. in prep*.).

Previous research has shown that individuals have consistent foraging behaviour (van Overveld & Matthysen 2010), and now I have shown that individuals cache repeatable amounts of resources between years. Red squirrels typically have the same territory throughout life, as adults rarely disperse. Thus, consistent differences in hoard size could arise from differences in territory quality. However, if this were the case then it is surprising that adults do not disperse in order to gain access to higher resource availability. Additionally, territory quality is not consistent between years in this population (LaMontagne *et al.* 2013), suggesting that this does not fully explain repeatable differences in cached resources. The consistency in caching that I found is comparable to the repeatability of personality traits found in other studies (eg. Réale *et al.* 2000; Dingemanse *et al.* 2002; Boon, Réale & Boutin 2007). Personality in great tits influences foraging behaviour and responses to changes in food availability (van Overveld & Matthysen 2010). In muroid rodents, superficial explorers and early-breeders also had faster metabolic rates (Careau *et al.* 2009). These studies suggest that individuals have consistent differences in personality, metabolism, and foraging behaviour. Personality may also influence dispersal (Cote *et al.* 2010) and thus is not necessarily independent of territory effects on resource acquisition. My results suggest that squirrels may have a consistent caching strategy or consistent foraging behaviour. Differences in sex-specific selection may result in antagonistic selection on traits due to differences in life history optima between males and females, which may maintain genetic variation in a trait within a population (Wedell *et al.* 2006). Given that the fitness consequences of caching differ between the sexes and that individuals show consistent differences in caching, it is possible that sexual conflict could maintain variation in caching behaviour in this population.

Table 5.1. Standardized coefficients (±95% confidence intervals) of the top-ranked models exploring whether cones showed sex- and age-related variation, as well as whether cones affected reproductive success, mating behaviour, and breeding phenology. In each case, the response variable is indicated by Response, and the model structure by the remaining columns. I first explored whether there was a difference between males and females in the number of cones they cached (indicated by sex: a positive value indicates that males have more cones than females); in this case, cones was quantified as the actual number of cones, ie. prior to standardizing the value. For all other references to cones in the table, data were standardized by year and study area with male and female data separate. Data for each sex was analyzed separately (indicated by the Sex column). I then explored whether cones were affected by quadratic age (indicated by Age^2 and Age). Finally, I explored whether cones influenced each of several response variables: the number of pups sired (No. Pups), the number of recruits sired or produced (No. Recruits), home range area (Home Range), the earliest date that a male sired a pup (Earliest Date), parturition date of first litters (Parturition Date), litter size of first litters (Litter Size), and average growth rate of the pups in first litters (Growth Rate). Quadratic age was included as a covariate in models analyzing reproduction, mating behaviour, and breeding phenology. As the home range area is affected by the number of times a male was located during the breeding season, the number of observations (No. Locations) was included as a covariate in that model. Where a variable was included in the model set but was not in the top-ranked models, this is indicated by “X”; “-“ indicates that the variable was not included in that model. To account for multiple measures per individual I included Squirrel ID as a random effect, and I accounted for annual- and study site-specific variation by including Study Area-Year as a random effect. Coefficients whose confidence intervals did not overlap zero are indicated in bold. The model number for each model set (Model) corresponds to the model sets in Appendix4 (Table A4.1).

Model	Response	Sex	Intercept	Cones	Age	Age^2	No. Locations
1	Cones (Actual)	**1.02 ± 0.15**	**8.75 ± 0.21**	-	-	-	-
2	Cones	Male	**0.36 ± 0.11**	-	**0.82 ± 0.12**	**-0.61 ± 0.19**	-
3	Cones	Female	**0.31 ± 0.14**	-	-0.09 ± 0.19	**-0.37 ± 0.33**	-
4	No. Pups	Male	**0.83 ± 0.15**	**0.28 ± 0.20**	**0.28 ± 0.17**	**-0.56 ± 0.20**	-

Model	Response	Sex	Intercept	Cones	Age	Age^2	No. Locations
5	No. Recruits	Male	**-0.78 ± 0.29**	0.15 ± 0.26	0.01 ± 0.21	-0.38 ± 0.46	-
6	Home Range	Male	**3.14 ± 2.73**	-0.33 ± 0.58	**-0.86 ± 0.65**	**-0.46 ± 1.07**	**6.58 ± 0.64**
7	Earliest Date	Male	**-15.52 ± 3.95**	-2.70 ± 3.59	**-7.16 ± 3.94**	**-4.66 ± 4.38**	-
8	Litter Size	Female	0.01 ± 0.07	X	0.01 ± 0.05	-0.01 ± 0.07	-
9	Growth Rate	Female	-0.03 ± 0.04	X	X	X	-
10	Parturition Date	Female	**-16.89 ± 3.77**	**-5.22 ± 2.06**	**-16.93 ± 2.40**	**16.81 ± 2.63**	-
11	No. Recruits	Female	**-0.22 ± 0.19**	0.00 ± 0.04	-0.01 ± 0.07	0.00 ± 0.08	-

Table 5.2. Standardized coefficients (±95% confidence intervals) from top-ranked models testing whether there was a relationship between lifetime reproductive success (LRS Pups for total pups or LRS Recruits for total recruits) or longevity and average cones cached throughout their lifetime (Cones). Males and females were analyzed separately, indicated by the Sex column. As cones were not measured in all years, I controlled for the proportion of a squirrel's lifetime that cones were measured (Proportion). I also controlled for study area, longevity, and whether it was a mast year; these variables could also affect lifetime reproductive success and/or longevity. When a variable was not in the top-ranked models, this was indicated by "X". If the variable was not included in that analysis, this was indicated by "-". When confidence intervals did not overlap zero, I indicated this in bold. Full model sets with AICc comparisons are included in Appendix 4 (Table A4.2), with the number for each model set indicated by Model.

Model	Response	Sex	Intercept	Cones	Study Area	Proportion	Longevity	Mast Year
1	LRS Pups	Male	**1.68 ± 0.05**	X	**-0.46 ± 0.09**	X	**1.17 ± 0.10**	**0.24 ± 0.13**
2	LRS Recruits	Male	-0.09 ± 0.12	**0.90 ± 0.22**	**-0.35 ± 0.21**	**-0.28 ± 0.25**	X	**1.09 ± 0.25**
3	Longevity	Male	**1.08 ± 0.06**	**0.14 ± 0.13**	0.11 ± 0.12	**-0.56 ± 0.15**	-	**0.25 ± 0.16**
4	LRS Pups	Female	**1.69 ± 0.04**	X	-0.03 ± 0.08	X	**0.91 ± 0.07**	0.01 ± 0.05
5	LRS Recruits	Female	0.00 ± 0.10	X	-0.07 ± 0.19	X	**0.82 ± 0.18**	**0.37 ± 0.29**
8	Longevity	Female	**0.95 ± 0.06**	-0.05 ± 0.12	-0.06 ± 0.13	**-0.54 ± 0.15**	-	**0.32 ± 0.15**

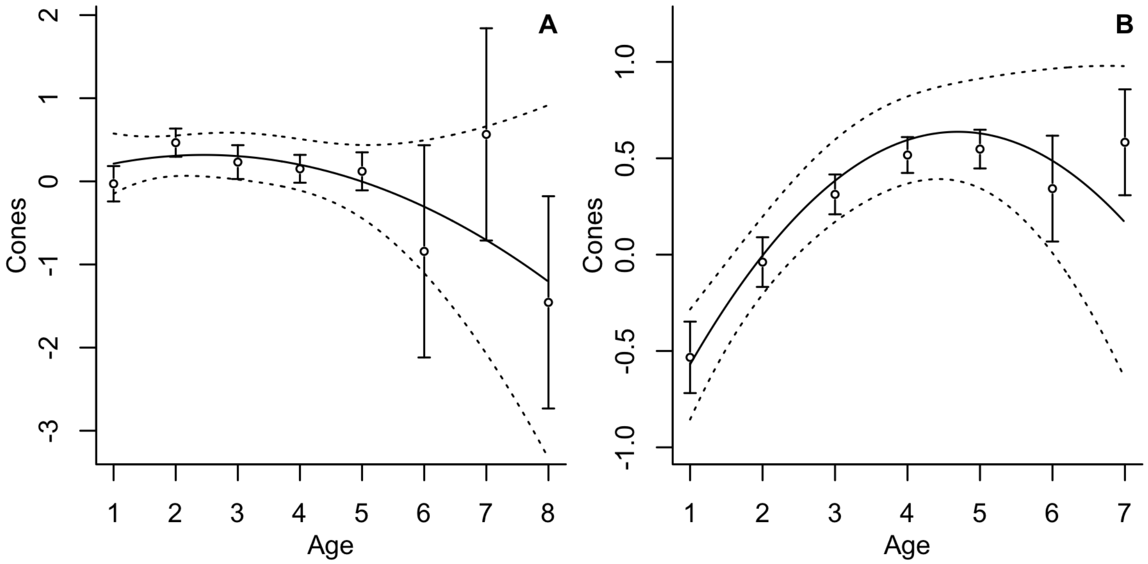

Figure 5.1. Mean (± standard error) amount of log-transformed cones for each age class for females (A) and males (B), as well as the model predictions (±95% confidence intervals) for top-ranked models testing the relationship between age and cached cones. The random effects were set to 0.

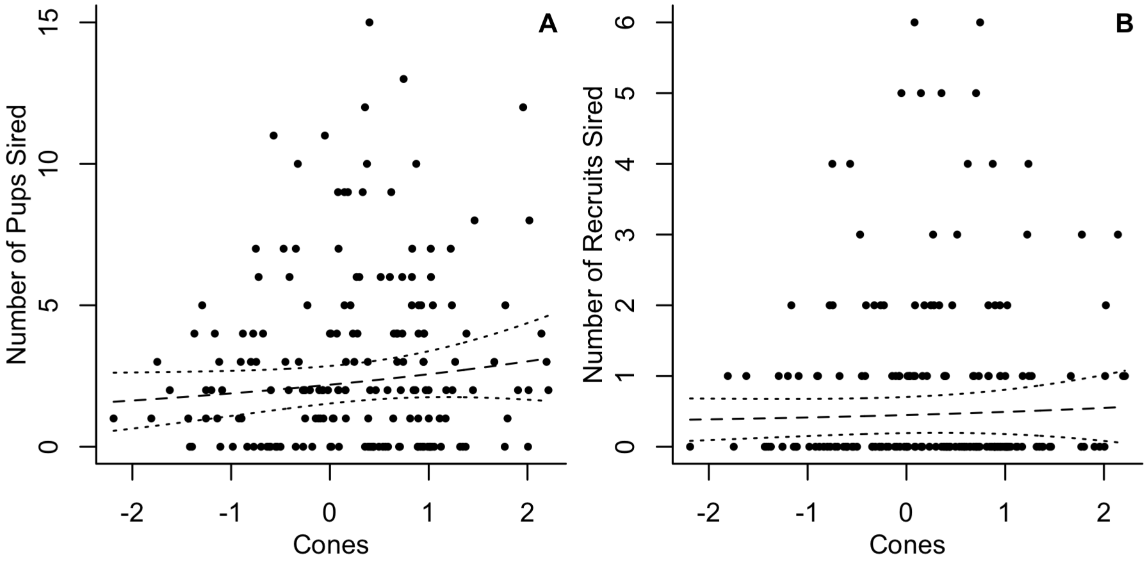

Figure 5.2. Relationship between the number of pups (A) or the number of recruits (B) that males sired and the amount of log-transformed cones they had cached in their middens (indicated by points). Lines represent model predictions (±95% confidence intervals) from the top-ranked models. All covariates and random effects were set to the population mean (ie. 0).

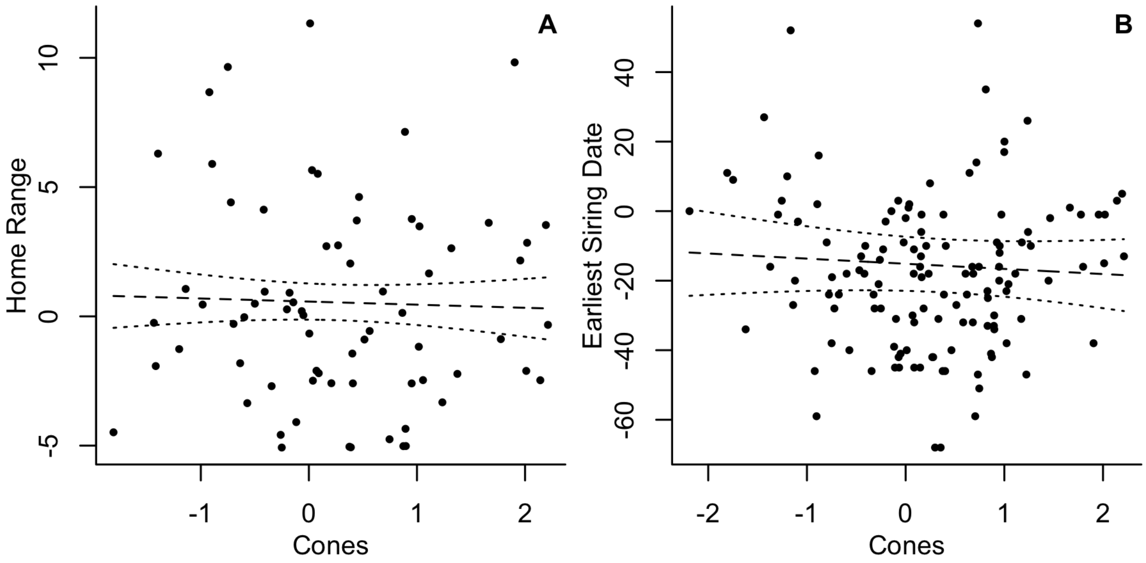

Figure 5.3. Relationship between log-transformed cones males had cached in their midden and home range area (A) or earliest siring date (B). Points indicate the data, while the lines represent predictions from top-ranked models (±95% confidence intervals). All covariates and random effects were set to 0 (ie. the mean).

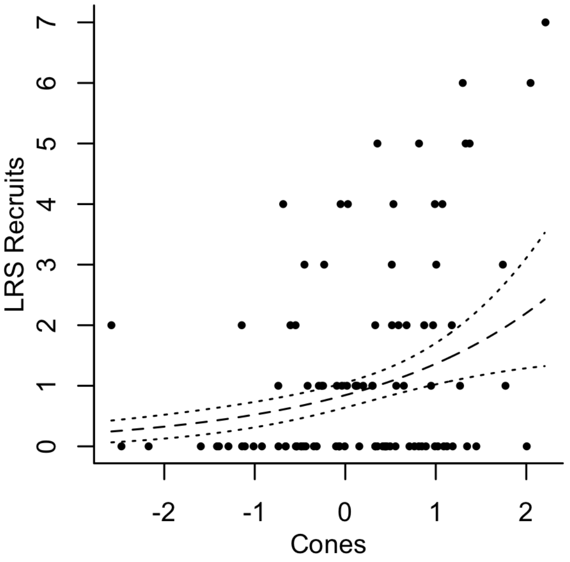

Figure 5.4. The relationship between the total number of recruits males sired and the average cones they cached throughout their lifetime. Black points represent the data, with lines representing the predictions (±95% confidence intervals) from the top-ranked model. All covariates were set to the mean (ie. 0).

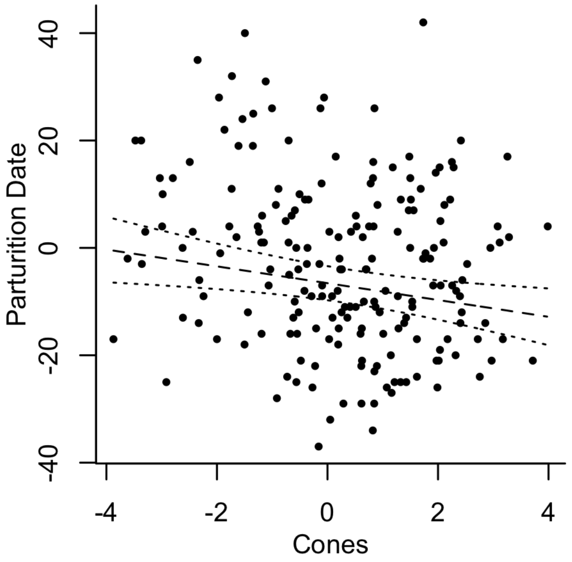

Figure 5.5. The relationship between parturition date of first litters for females and log-transformed cones they had cached in their middens. The points demonstrate the raw data, while the lines represent predictions (±95% confidence intervals) from the top-ranked models. Other variables were set to the population mean (ie. 0).

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Chapter 6: Conclusion

I used a long-term dataset collected in the Yukon to study the effects of reproductive trade-offs and resources on red squirrels. I first tested whether there was evidence for a trade-off between early-life reproduction and senescent decline later in life. I then tested for the influence of the encountering a mast year on life history trade-offs. I also tested whether the occurrence of a mast year affects sexually-selected traits. And finally, I tested for a link between individual-level food availability and reproduction. These analyses have revealed evidence of both intrinsic and extrinsic influences on red squirrel reproduction and behaviour.

Evolutionary theory predicts that there are trade-offs between different functions such as growth, maturation, reproduction, and survival (Stearns 1989). Investment in current reproduction can thus lead to costs to future reproduction, resulting in senescent decline late in life (Monaghan *et al.* 2008; Wilson, Charmantier & Hadfield 2008). These trade-offs may also constrain life history traits to certain trait combinations (Stearns 1989). This has been tested in many species, and this empirical research has demonstrated that animals may rank along a fast-slow continuum (Gaillard *et al.* 1989; Bielby *et al.* 2007): fast animals have early primiparity, high fecundity, and short lifespans while slow animals have the opposite traits. Fast animals may also experience faster senescence (Jones *et al.* 2008). These life history traits may also be linked to physiology and behaviour (Ricklefs & Wikelski 2002; Réale *et al.* 2010), now called the pace-of-life syndrome (Réale *et al.* 2010). My research has demonstrated that male red squirrels fit many of these predictions. I demonstrated that males who sire pups early in life also have shorter longevity, supporting that they may rank along a fast-slow life history continuum. Male red squirrel reproductive success and one sexually-selected trait senescence in older age classes, although the rate of senescence was not affected by age at first reproduction. I demonstrated that males who encountered a mast year achieve higher lifetime reproductive success if they bred at a younger age, but males who do not encounter a mast year achieved higher success by delaying breeding. Thus, in addition to finding support for predictions of life history patterns, my research has suggested that these life history patterns have different fitness consequences depending on the environmental conditions they encountered.

Pulsed resource systems are characterized by infrequent, short, and intense resource availability (Yang *et al.* 2008), often called masts. In some systems animals that experience these pulses respond to increased food availability by increasing their reproductive success in subsequent years (Yang *et al.* 2008). However, some species, including red squirrels, increase their reproductive investment in anticipation, rather than in response, to a mast year (Boutin *et al.* 2006; Lebl *et al.* 2010; Bergeron *et al.* 2011; Montiglio *et al.* 2014). These high resource years not only influence fitness in these species, but also alter life history traits (Boutin *et al.* 2006). The ability to quantify these pulses makes them ideal systems to study the influence of resources on life history and reproduction. In my study populations in the Yukon, white spruce cones are their primary food source, particularly during winter and the breeding season (Fletcher *et al.* 2013). White spruce cone production is highly variable, but are characterized in particular by irregularly-occurring mast years (Lamontagne & Boutin 2007). Previous research has demonstrated that female red squirrels have higher reproductive success, higher juvenile recruitment, and are more likely to have an earlier primiparity when they encounter a mast year (Boutin *et al.* 2006; Williams *et al.* 2014). Females also adjust their breeding timing according to white spruce cone production: they breed later during a mast year but earlier following a mast year (Williams *et al.* 2014). However, the effects of white spruce cones on male reproduction were not previously examined. In addition, red squirrels cache white spruce cones in hoards called middens, and this individual-level resource availability affects overwinter survival (LaMontagne *et al.* 2013). The influence of individual-level resource availability on reproductive success has not been tested in either males or females. It is important to note that the effect of population-level and individual-level resources are due to different mechanisms. Population-level cones are not available until autumn even though squirrels breed in the previous spring, so it represents anticipatory reproduction in the absence of additional food resources (Boutin *et al.* 2006). In contrast, having higher individual-level food resources would provide squirrels with more energy for reproduction. My research has shown that mast years affect male success and life history, and that individual-level resources influence both sexes. Males who encounter a mast year at some point during their lives have longer longevity. As previously demonstrated for female red squirrels (Boutin *et al.* 2006), males who encounter a mast year as a yearling were more likely to breed that year, suggesting that males also exhibit anticipatory reproduction in anticipation of a mast year. Encountering a mast year has substantial fitness consequences, as these males achieve higher lifetime reproductive success than males who do not encounter a mast year during their lifetime. Individual-level resources also influenced reproduction in both sexes. Males with large amounts of cached resources sired more pups and recruits as well as began breeding earlier in the breeding season. Females who had more cones also bred earlier, although there was no effect of cached resources on any other measure of female reproductive success. Thus, my research demonstrates that mast years and individual-level resource availability affects male reproductive success, breeding phenology, and life history traits.

Changing environmental conditions can create fluctuating selection on the fitness consequences of traits (Dingemanse *et al.* 2004; Kasumovic *et al.* 2008; Montiglio *et al.* 2014; Taylor *et al.* 2014). This is one proposal for how diversity in genetic variation is maintained in a population, even when there are negative fitness consequences for having those traits in some years (Ellner & Hairston 1994; Roff & Fairbairn 2007). Alternatively, variation in traits may occur because of differences in selection on males and females (Roff & Fairbairn 2007). I found support for both of these theories. Red squirrels experience widely fluctuating conditions because of variation in white spruce cone availability. I demonstrated that the occurrence of mast years affects life history traits and male mating behaviour, as well as the fitness consequences of these traits. Interestingly, this applies whether I considered mast years and success or behaviour annually, or whether I simply consider whether they encountered a mast year at some point in their lives. For example, encountering a mast year altered the link between age at first reproduction and longevity. The best life history strategy depends on whether they encounter a mast year. Males achieve the highest lifetime reproductive success if they had an earlier age at first reproduction when they encounter a mast year during their lifetime, but achieve the highest lifetime reproductive success if they begin breeding later in life when they do not encounter a mast year. The male behaviours that resulted in high annual success changed depending on the occurrence of a mast. Males who had larger home ranges to access mating opportunities had higher reproductive success in non-mast years, but low success in mast years. I also show evidence that males may commit infanticide in high resource years. Fluctuations in sexual selection have been reported in other species (Chaine & Lyon 2008; Cockburn, Osmond & Double 2008; Gosden & Svensson 2008; Weese *et al.* 2010) and I have shown that changes in paternity patterns occur due to occurrence of mast years, likely as a result of the effects on mating opportunities. I also demonstrated a sex-specific link between cached resources and reproductive success. Cached resources had an effect on male reproductive success, but only influenced the timing of reproductive success in females. Males also achieved higher lifetime reproductive success when they had more cached cones, but it did not affect female lifetime reproductive success. Thus, I demonstrated that fluctuations in resources altered life history traits and fitness, and there were sex-specific effects of resources on reproductive success.

Sexual selection and sexual conflict can cause different patterns of reproductive trade-offs, ageing, and life history traits in males and females (Bonduriansky *et al.* 2008). Males are thought to adopt higher wear-and-tear strategies than females, resulting in shorter lifespans and faster senescence (Promislow 2003; Clutton-Brock & Isvaran 2007; Bonduriansky *et al.* 2008). My research on life history traits shows that males and females show similar patterns, as in both sexes individuals who bred earlier also had shorter longevities. My results supported this, as males senesced earlier in life than females whether I considered reproductive success or survival (Descamps *et al.* 2008; this thesis). Thus, my research has shown evidence that males may adopt a higher wear-and-tear strategy than females. Thus, my research has revealed sex-specific patterns of reproductive success, senescence, and life history traits.

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Appendix 1

Table A1.1. Annual success rate of assigning sires to pups in the population on each study area. The total number of pups tagged in the nest and trapped as juveniles were combined to calculate the total number of pups produced in the study areas (No. Pups). The number of pups whose sires were identified was also shown (No. Sired), which was used to calculate the success rate of identifying sires of the pups in the population.

Study Area	Year	No. Pups	No. Sired	Success Rate
KL	2003	79	40	0.5
KL	2004	64	41	0.6
KL	2005	140	88	0.6
KL	2006	110	76	0.7
KL	2007	104	78	0.8
KL	2008	112	94	0.8
KL	2009	84	78	0.9
KL	2010	147	126	0.9
KL	2011	146	121	0.8
KL	2012	150	134	0.9
KL	2013	110	97	0.9
KL	2014	287	258	0.9
SU	2003	70	65	0.9
SU	2004	65	49	0.8
SU	2005	109	77	0.7
SU	2006	90	75	0.8
SU	2007	89	79	0.9
SU	2008	67	59	0.9
SU	2009	46	35	0.8
SU	2010	118	85	0.7
SU	2011	69	65	0.9
SU	2012	79	75	0.9
SU	2013	88	82	0.9
SU	2014	176	156	0.9

Table A1.2. Sample size of all age classes detected in my populations. Each record represents a measure of annual number of pups sired when a male was alive. All males in this study sired at least one pup in their lifetimes, but their annual reproductive success was included even if they were unsuccessful in that year. There are 628 annual records of 229 males.

Age	Sample Size
1	229
2	175
3	119
4	71
5	25
6	8
7	1
Total	628

Table A1.3. Descriptive statistics of siring success, life history traits, and behavior for males included in this study.

Variable	Mean	Std. Deviation	Min.	Max.
Longevity	2.7	1.4	1	7
Annual Pups Sired	2.1	2.6	0	17
Annual Recruits Sired	0.5	1.0	0	7
Lifetime Pups Sired	5.8	5.6	1	30
Lifetime Recruits Sired	1.2	1.8	0	12
Age at First Reproduction	1.5	0.6	1	4
Age at Last Reproduction	2.4	1.3	1	7
Reproductive Lifespan	1.9	1.1	1	5
Longevity After Siring Pups	0.3	0.6	0	3
Age First Sired Recruits	1.9	1.0	1	6
Age Last Sired Recruits	2.3	1.2	1	6
Reproductive Lifespan for Recruits	1.5	0.9	1	5
Longevity After Siring Recruits	0.7	1.0	0	4
Age at Peak Reproduction	1.9	1.0	1	5
Home Range Area (ha)	5.2	4.6	0	20.5

Table A1.4. Model sets used to assess whether annual pups sired, annual recruits sired, home range, and survival change with age. The first model in each model set was the top-ranked model and models were arranged sequentially in order of increasing AICc, indicated by ΔAICc. Models ≤6 ΔAICc of the top-ranked model were indicated in bold and were used to calculate coefficients in Table 2.1. To test whether age-related changes were linear or quadratic, age was included as a quadratic (indicated by Age^2 and Age) or a linear (indicated by Age only) term. AFR and ALR represent age at first and last reproduction. To account for multiple measures per individual, squirrel ID was included as a random effect in all models. Study area-year was included as a random effect to account for study area and year variation. Home range area was affected by the number of spatial locations (Loc.) recorded for each male, so this was included as a covariate in model set three. The null model included random effects only. Sample size varied for each model set, and so I indicated both the number of individuals and the number of records. Pseudo R^2 was calculated for each model (see Methods for details).

Model Set	# Indiv.	# Records	Dependent	Model Structure	df	ΔAICc	weight	R^2
1	229	628	# Pups	**Age + Age^2 + AFR + ALR**	**7**	**0.00**	**0.51**	**0.16**
				Age + Age^2 + AFR	**6**	**0.12**	**0.48**	**0.18**
				Age + Age^2	5	9.54	0.00	0.16
				Age + Age^2 + ALR	6	11.52	0.00	0.15
				Age + AFR + ALR	6	86.69	0.00	0.07
				Age + AFR	5	88.04	0.00	0.07
				Age	4	92.21	0.00	0.06
				Age + ALR	5	93.49	0.00	0.06
				AFR + ALR	5	104.61	0.00	0.06
				ALR	4	112.26	0.00	0.05
				AFR	4	116.24	0.00	0.04
				Null	3	117.83	0.00	0.03
2	125	380	# Recruits	**Age + Age^2 + AFR**	**6**	**0.00**	**0.59**	**0.26**
				Age + Age^2 + AFR + ALR	**7**	**0.77**	**0.40**	**0.25**
				Age + Age^2 + ALR	6	8.21	0.01	0.21
				Age + Age^2	5	10.62	0.00	0.21
				AFR	4	12.63	0.00	0.17
				AFR + ALR	5	12.74	0.00	0.16

Model Set	# Indiv.	# Records	Dependent	Model Structure	df	ΔAICc	weight	R^2
				Age + AFR	5	14.44	0.00	0.16
				Age + AFR + ALR	6	14.80	0.00	0.16
				ALR	4	16.65	0.00	0.15
				Age + ALR	5	18.70	0.00	0.15
				Null	3	19.93	0.00	0.15
				Age	4	21.05	0.00	0.15
3	72	91	Home Range	**Age + Age^2 + Loc.**	**7**	**0.00**	**0.23**	**0.11**
				Age + Age^2 + ALR + Loc.	**8**	**0.28**	**0.20**	**0.12**
				Age + Age^2 + ALR + Loc.	**8**	**0.65**	**0.17**	**0.12**
				Age + Age^2 + AFR + ALR + Loc.	**9**	**1.04**	**0.14**	**0.12**
				AFR + Loc.	**6**	**3.31**	**0.04**	**0.09**
				Loc.	**5**	**3.50**	**0.04**	**0.08**
				ALR + Loc.	**6**	**3.99**	**0.03**	**0.08**
				AFR + ALR + Loc.	**7**	**4.07**	**0.03**	**0.09**
				Age + AFR + Loc.	**7**	**4.28**	**0.03**	**0.09**
				Age + Loc.	**6**	**4.40**	**0.03**	**0.08**
				Age + ALR + Loc.	**7**	**4.50**	**0.02**	**0.08**
				Age + AFR + ALR + Loc.	**8**	**4.66**	**0.02**	**0.09**
				Null	4	9.84	0.00	0.00
4	229	628	Survival	**Age + AFR**	**5**	**0.00**	**0.71**	**0.51**
				Age + Age^2 + AFR	**6**	**1.81**	**0.29**	**0.51**
				Age	4	20.51	0.00	0.31
				Age + Age^2	5	22.22	0.00	0.31
				AFR	4	46.98	0.00	0.32
				Null	3	59.06	0.00	0.29
5	229	507	# Pups	**Age + Age^2 + AFR + ALR**	**7**	**0.00**	**0.45**	**0.19**
				Age + AFR + ALR	**6**	**0.18**	**0.41**	**0.19**
				Age + Age^2 + ALR	**6**	**2.73**	**0.11**	**0.20**
				Age + ALR	**5**	**5.34**	**0.03**	**0.20**
				Age + Age^2 + AFR	6	19.25	0.00	0.21
				Age + AFR	5	20.26	0.00	0.21
				AFR + ALR	5	23.00	0.00	0.18
				Age + Age^2	5	27.98	0.00	0.21
				Age	4	33.81	0.00	0.20
				Null	3	37.92	0.00	0.17

Model Set	# Indiv.	# Records	Dependent	Model Structure	df	ΔAICc	weight	R^2
6	125	272	# Recruits	**Age + AFR + ALR**	**6**	**0.00**	**0.37**	**0.33**
				Age + ALR	**5**	**0.38**	**0.30**	**0.34**
				Age + Age^2 + ALR	**6**	**1.85**	**0.15**	**0.35**
				Age + Age^2 + AFR + ALR	**7**	**2.02**	**0.13**	**0.33**
				Age + AFR	**5**	**5.45**	**0.02**	**0.32**
				Age	4	7.31	0.01	0.33
				Age + Age^2 + AFR	6	7.37	0.01	0.33
				Age + Age^2	5	8.26	0.01	0.34
				Null	3	35.46	0.00	0.24
				ALR	4	37.16	0.00	0.24
				AFR	4	37.29	0.00	0.24
				AFR + ALR	5	39.15	0.00	0.24
7	68	80	Home Range	**Age + Age^2 + AFR + ALR + Loc.**	**9**	**0.00**	**0.18**	**0.11**
				Age + Age^2 + AFR + Loc.	**8**	**0.09**	**0.18**	**0.11**
				Age + Age^2 + ALR + Loc.	**8**	**0.12**	**0.17**	**0.12**
				Age + Age^2 + Loc.	**7**	**0.54**	**0.14**	**0.10**
				Age + AFR + ALR + Loc.	**8**	**2.13**	**0.06**	**0.10**
				AFR + Loc.	**6**	**2.19**	**0.06**	**0.09**
				Age + AFR + Loc.	**7**	**2.38**	**0.06**	**0.09**
				AFR + ALR + Loc.	**7**	**2.86**	**0.04**	**0.08**
				Age + ALR + Loc.	**7**	**3.55**	**0.03**	**0.07**
				Loc.	**5**	**3.78**	**0.03**	**0.06**
				ALR + Loc.	**6**	**4.08**	**0.02**	**0.06**
				Age + Loc.	**6**	**4.48**	**0.02**	**0.06**
				Null	4	7.96	0.00	0.00
8	229	507	Survival	**Age + Age^2**	**5**	**0.00**	**0.69**	**0.25**
				Age + Age^2 + AFR	**6**	**2.03**	**0.25**	**0.25**
				Age	**4**	**5.60**	**0.04**	**0.23**
				Age + AFR	5	6.77	0.02	0.24
				Null	3	12.99	0.00	0.24
				AFR	4	14.98	0.00	0.24

Table A1.5. Model sets used to test whether the rate of senescence was affected by age at first reproduction (AFR) and lifetime pups sired (LRS). I included annual number of pups sired as the dependent variable, including the data from peak reproduction to death in order to analyze senescence rate. I included an interaction between Years Since Peak Reproduction (Years) and AFR (Years:AFR) or LRS (Years:LRS) to test whether they influence senescence rate. Age was standardized so that peak reproduction occurred at age 0. Models were arranged sequentially with increasing AICc, with ΔAICc from the top-ranked model indicated. The models ≤6 ΔAICc of the top-ranked model are indicated in bold and were used to calculate coefficients in Table 2.2. As there were multiple measures per individual, squirrel ID was included as a random effect. To account for variation in annual and study area values, study area-year was included as a random effect. The null model included random effects only. I indicated both the number of squirrels and the total sample size of annual measures for each model set. I also indicated the pseudo R^2 for each model (see Methods for details).

Model Set	# Indiv.	Sample Size	Model Structure	df	ΔAICc	weight	R^2
1	117	306	**Years + AFR + ALR**	**6**	**0.00**	**0.45**	**0.56**
			Years + ALR	**5**	**0.45**	**0.36**	**0.57**
			Years:AFR + Years + AFR + ALR	**7**	**1.62**	**0.20**	**0.57**
			Years	4	47.00	0.00	0.59
			Years + AFR	5	48.38	0.00	0.59
			Years:AFR + Years + AFR	6	49.88	0.00	0.59
			ALR	4	166.44	0.00	0.29
			Null	3	203.27	0.00	0.22
2	117	306	**Years:LRS + Years + LRS + ALR**	**7**	**0.00**	**0.48**	**0.66**
			Years:LRS + Years + LRS + AFR + ALR	**8**	**1.17**	**0.27**	**0.66**
			Years:LRS + Years + LRS + AFR	**7**	**1.87**	**0.19**	**0.65**
			Years:LRS + Years + LRS	**6**	**3.88**	**0.07**	**0.65**
			Years + LRS + ALR	6	16.62	0.00	0.59
			Years + LRS + AFR + ALR	6	17.09	0.00	0.59
			Years + LRS + AFR	7	17.59	0.00	0.59
			Years + LRS	5	18.67	0.00	0.58
			Years + AFR + ALR	6	147.30	0.00	0.56
			Years + ALR	5	151.96	0.00	0.57
			Years	4	198.51	0.00	0.59
			Years + AFR	5	200.34	0.00	0.59
			Null	3	354.78	0.00	0.22

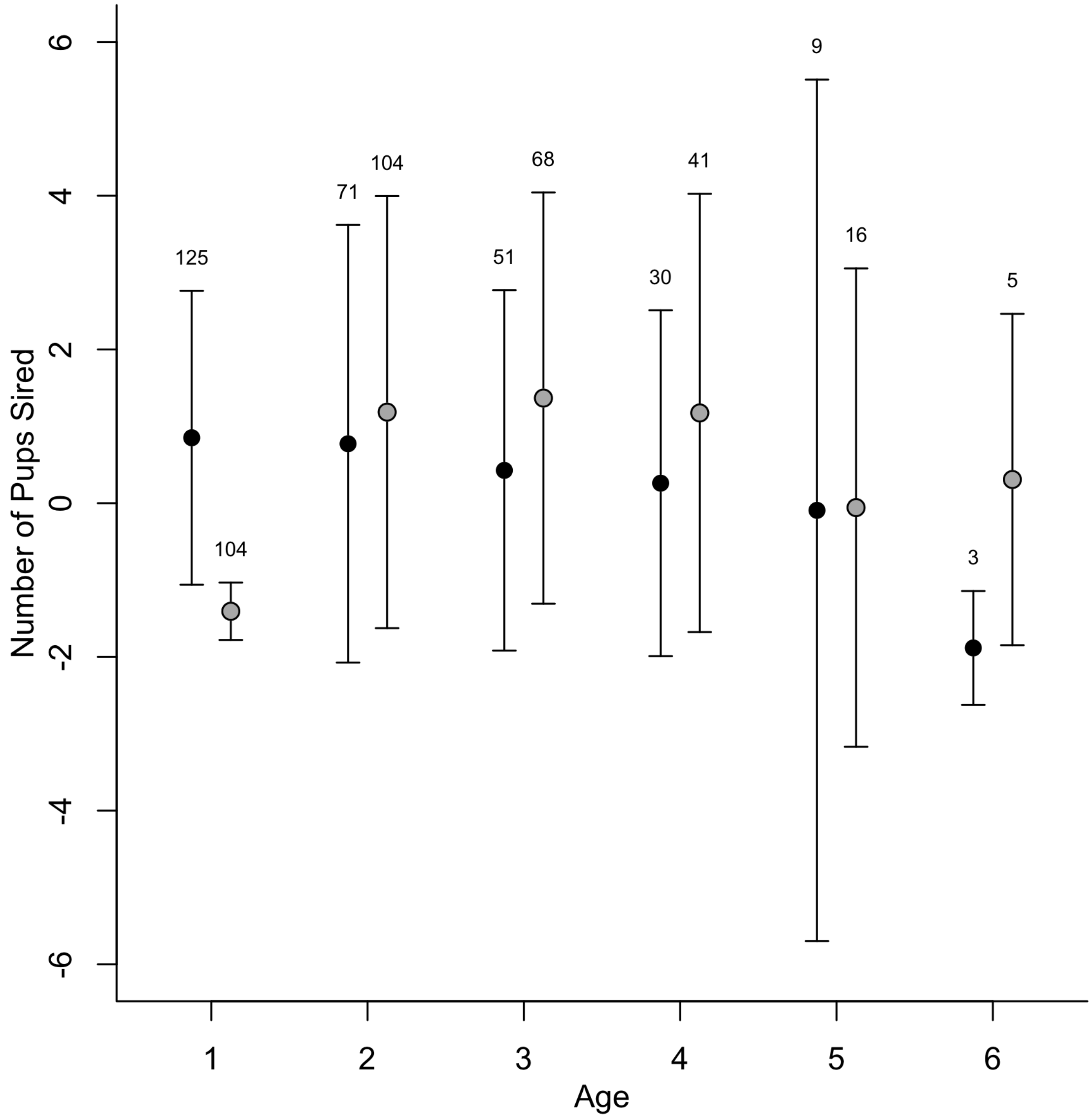

Figure A1.1. Standardized annual number of pups sired (± standard deviation) at different ages of males who began breeding at one year (black dots) or two or more years (grey dots). Sample size for each is indicated.

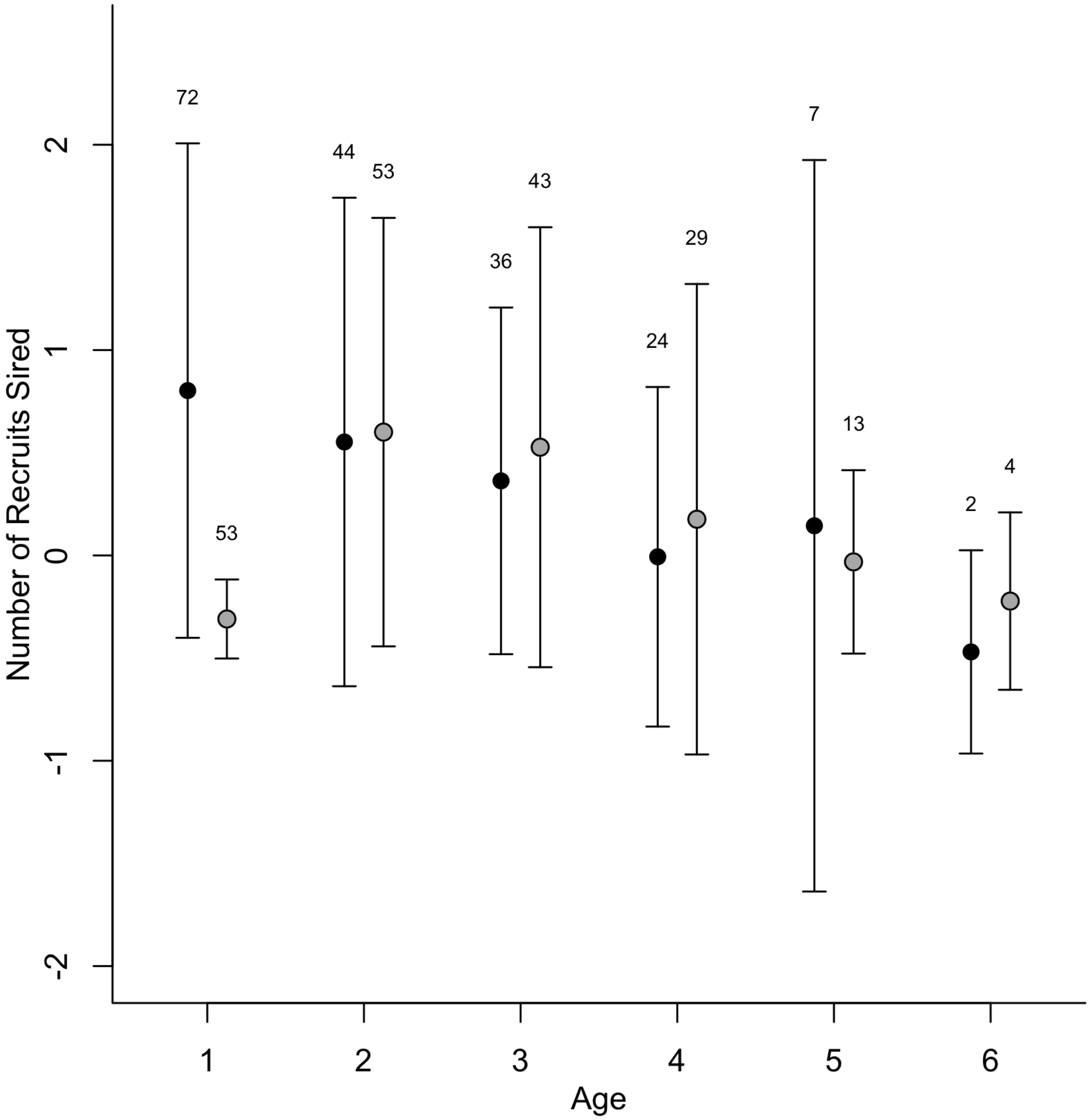

Figure A1.2. Standardized annual number of recruits (± standard deviation) at different ages of males who began breeding at one year (black dots) and two or more years (grey dots). I indicated the sample size for each.

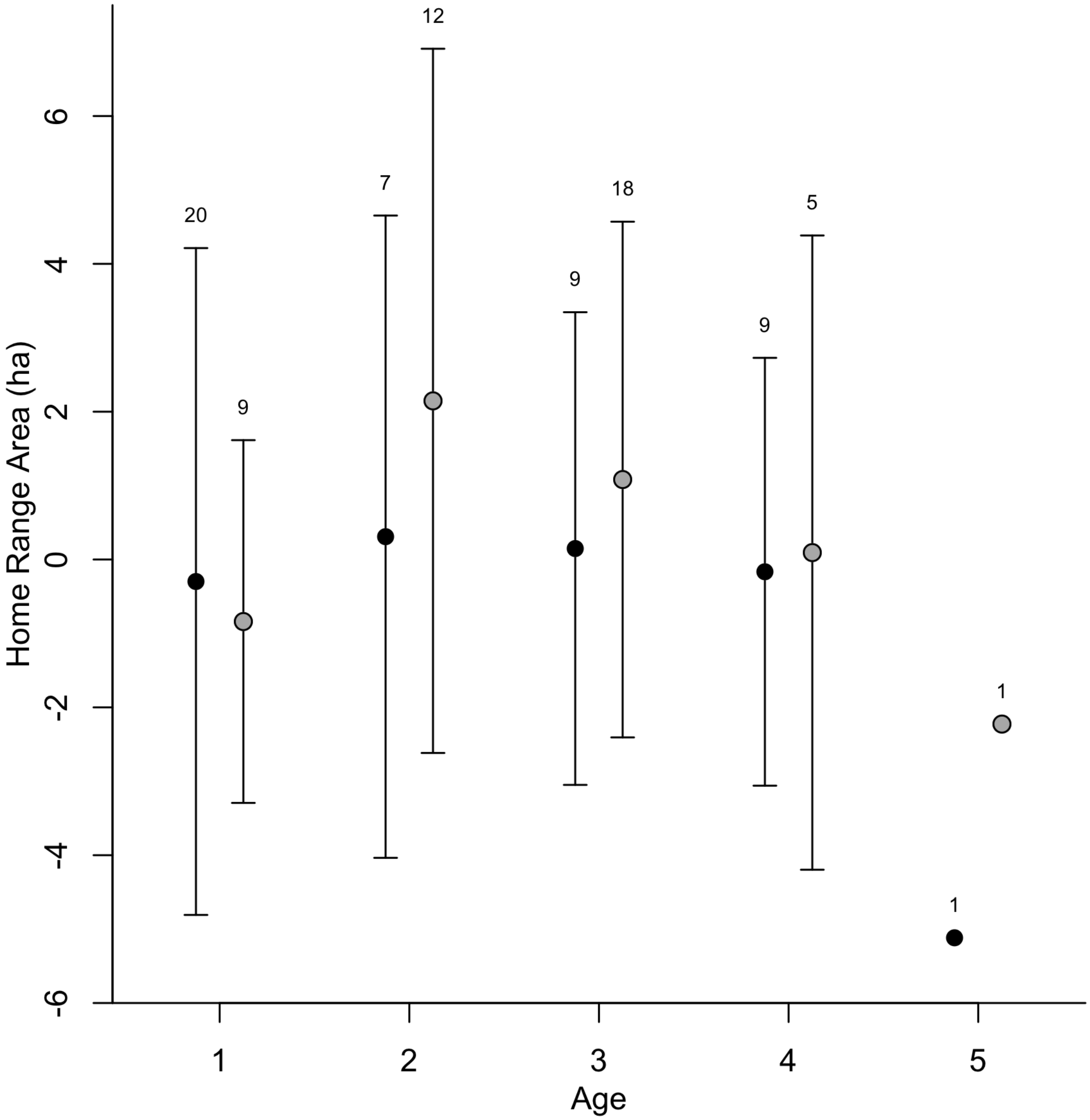

Figure A1.3. Standardized annual home range area (± standard deviation) at different ages of males who began breeding at one year (black dots) and two or more years (grey dots). Sample size for each was indicated.

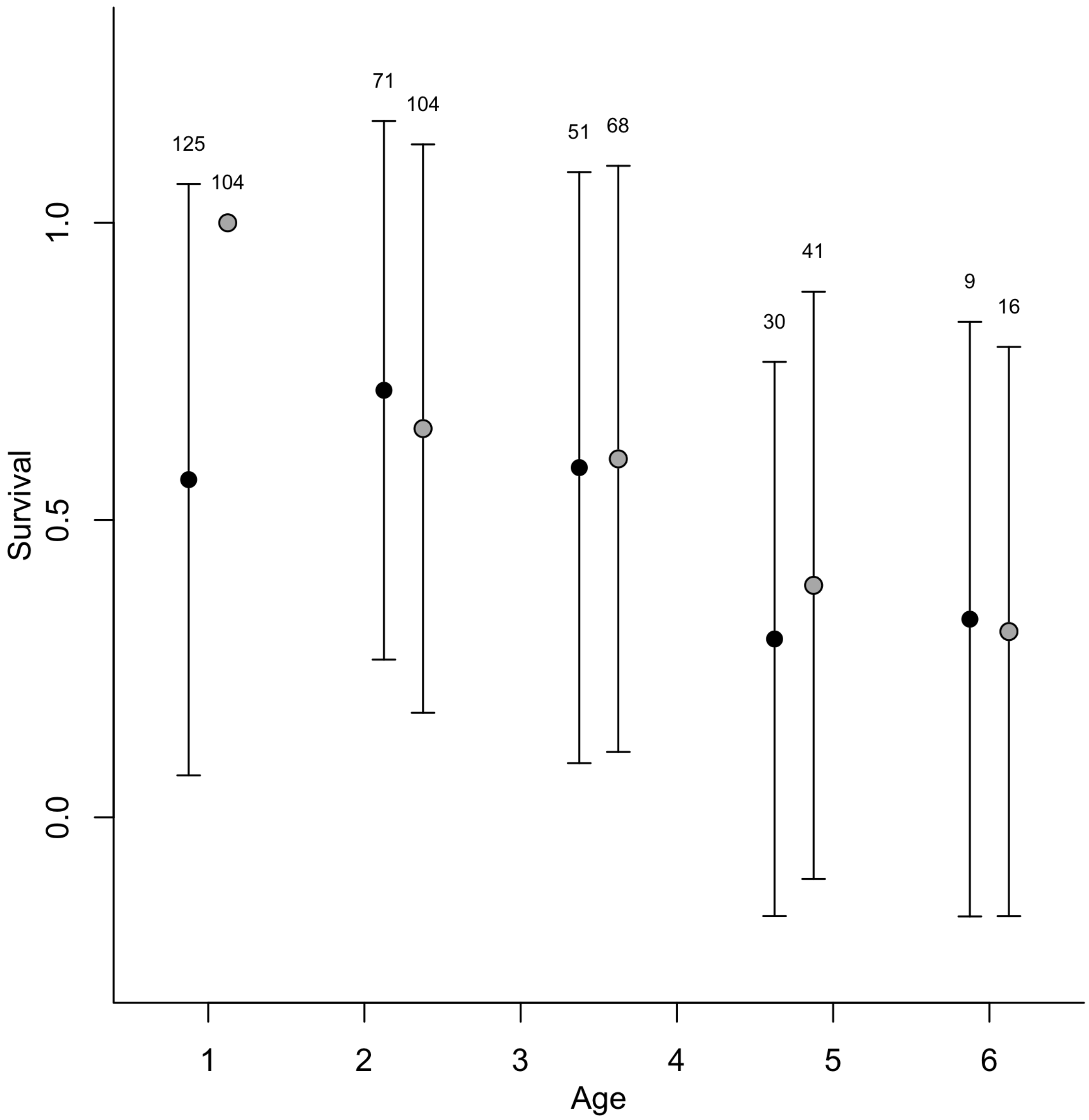

Figure A1.4. Survival (± standard deviation) at different ages of males who began breeding at one year (black dots) and two or more years (grey dots). Sample size for each was indicated.

Appendix 2

Table A2.1. The sample size for each age at first reproduction.

Age at first reproduction	No. Individuals
1	125
2	89
3	13
4	2

Table A2.2. The sample size for each longevity.

Longevity	No. Individuals
1	54
2	56
3	48
4	46
5	17
6	7
7	1

Table A2.3. Model sets used to assess whether age at first reproduction (AFR; quantified as whether or not males bred as a yearling) was affected by whether or not males encountered a mast year as a yearling (Yearling Mast), as well as whether encountering a mast year at some point in their life (Mast) affected longevity, total pups sired (LRS Pups), and total recruits sired (LRS Recruits). The first model in each model set is the top-ranked model, and models are arranged sequentially in order of increasing AICc; the change in AICc from the top model is indicated by ΔAICc. I also included the model weight (weight), degrees of freedom (df), and sample size (# individuals) for each model. The top-ranked model and models ≤6 AICc from the top-ranked model are indicated in bold. The coefficients from the top-ranked model, or model-averaged coefficient in the case of multiple top-ranked models, are presented in Table 3.1. Study area (Grid) was included as a covariate in all models, with the exception of null models.

Model Set	# Individuals	Dependent	Model Structure	df	ΔAICc	weight
1	229	AFR	**Yearling Mast + Long + Grid**	**4**	**0.00**	**1.00**
			Long + Grid	3	13.88	0.00
			Null	1	37.85	0.00
			Grid	2	39.65	0.00
2	229	Longevity	**Mast Year + Grid**	**3**	**0.00**	**1.00**
			Null	1	19.82	0.00
			Grid	2	19.92	0.00
3	229	LRS Pups	**Long + Grid**	**3**	**0.00**	**0.68**
			Mast + Long + Grid	**4**	**1.50**	**0.32**
			Null	1	392.09	0.00
			Grid	2	392.87	0.00
4	229	LRS Recruits	**Mast + Long + Grid**	**4**	**0.00**	**1.00**
			Long + Grid	3	19.78	0.00
			Grid	2	67.53	0.00
			Null	1	70.36	0.00
5	129	LRS Pups	**Mast Age + Longevity + Grid**	**4**	**0.00**	**1.00**
			Longevity + Grid	3	11.82	0.00
			Mast Age + Grid	3	220.12	0.00
			Grid	2	245.41	0.00

			Null	1	250.16	0.00
6	129	LRS Recruits	**Mast Age + Longevity + Grid**	**4**	**0.00**	**0.98**
			Longevity + Grid	3	8.06	0.02
			Grid	2	33.20	0.00
			Mast Age + Grid	3	35.25	0.00
			Null	1	43.10	0.00

Table A2.4. Model sets used to assess whether a trade-off between age at first reproduction (AFR) and longevity was affected by whether they encountered a mast year at some point during their lifetime (Mast). I also tested whether the effect of age at first reproduction or longevity (Long) on total pups sired (LRS Pups) or total recruits sired (LRS Recruits) depended on whether they encountered a mast year at some point during their lifetime. I included an interaction between these variables and mast year (indicated by :Mast). When the interaction was not in the top-ranked model set, or where the effect of the interaction was small, I also tested the relationship between AFR, Longevity, and LRS Pups and the other life history traits and fitness measures. Models are arranged sequentially from the top-ranked model in each model set in order of increasing AICc, I indicated the change in AICc from the top-ranked model (ΔAICc) as well as the degrees of freedom (df), model weight (weight), and sample size (# individuals) for each model. Models ≤6 AICc of the top-ranked model are indicated in bold; these were considered the top-ranked models. Study area (Grid) was included as a covariate in all models except for the null model. Coefficients from top models were presented in Table 3.2, and in the case of multiple top models the coefficients were averaged across all top models.

Model Set	# Individuals	Dependent	Model Structure	df	ΔAICc	weight
1	229	Longevity	**AFR + Mast + AFR:Mast + Grid**	**5**	**0.00**	**0.64**
			AFR + Mast + Grid	**4**	**1.19**	**0.36**
			Mast + Grid	3	13.16	0.00
			AFR + Grid	3	16.60	0.00
			Null	1	32.98	0.00
			Grid	2	33.09	0.00
2	229	LRS Pups	**AFR + Mast + AFR:Mast + Longevity + Grid**	**6**	**0.00**	**0.99**
			AFR + Longevity + Grid	4	10.25	0.01
			AFR + Mast + Longevity + Grid	5	11.91	0.00
			Longevity + Grid	3	14.36	0.00
			Mast + Longevity + Grid	4	15.86	0.00
			AFR + Mast + AFR:Mast + Grid	5	305.45	0.00
			AFR + Mast + Grid	4	336.47	0.00
			Mast + Grid	3	338.69	0.00
			AFR + Grid	3	399.87	0.00

Model Set	# Individuals	Dependent	Model Structure	df	ΔAICc	weight
			Null	1	406.45	0.00
			Grid	2	407.23	0.00
3	229	LRS Recruits	**AFR + Mast + Longevity + Grid**	**5**	**0.00**	**0.72**
			AFR + Mast + AFR:Mast + Longevity + Grid	**6**	**1.92**	**0.28**
			Mast + Longevity + Grid	4	14.18	0.00
			AFR + Longevity + Grid	4	19.03	0.00
			AFR + Mast + Grid	4	30.81	0.00
			AFR + Mast + AFR:Mast + Grid	5	32.02	0.00
			Mast + Grid	3	36.60	0.00
			AFR + Grid	3	79.68	0.00
			Null	2	81.71	0.00
4	229	LRS Pups	**Longevity + Mast + Longevity:Mast + Grid**	**5**	**0.00**	**0.74**
			Longevity + Grid	**3**	**2.83**	**0.18**
			Longevity + Mast + Grid	**4**	**4.32**	**0.08**
			Mast + Grid	3	327.16	0.00
			Null	1	394.91	0.00
			Grid	2	395.70	0.00
5	229	LRS Pups	**Longevity + Grid**	**3**	**0.00**	**1.00**
			Null	1	392.09	0.00
			Grid	2	392.87	0.00
6	229	LRS Recruits	**Longevity + Mast + Longevity:Mast + Grid**	**5**	**0.00**	**0.51**
			Longevity + Mast + Grid	**4**	**0.06**	**0.49**
			Longevity + Grid	3	19.84	0.00
			Mast + Grid	3	22.47	0.00
			Grid	2	67.59	0.00
			Null	1	70.42	0.00
7	229	LRS Recruits	**Longevity + Grid**	**3**	**0.00**	**1.00**
			Grid	2	47.75	0.00
			Null	1	50.58	0.00
8	229	LRS Recruits	**LRS Pups + Grid**	**3**	**0.00**	**0.74**
			LRS Pups + Longevity + Grid	**4**	**2.07**	**0.26**
			Longevity + Grid	3	113.26	0.00

Model Set	# Individuals	Dependent	Model Structure	df	ΔAICc	weight
			Grid	2	161.01	0.00
			Null	1	163.84	0.00

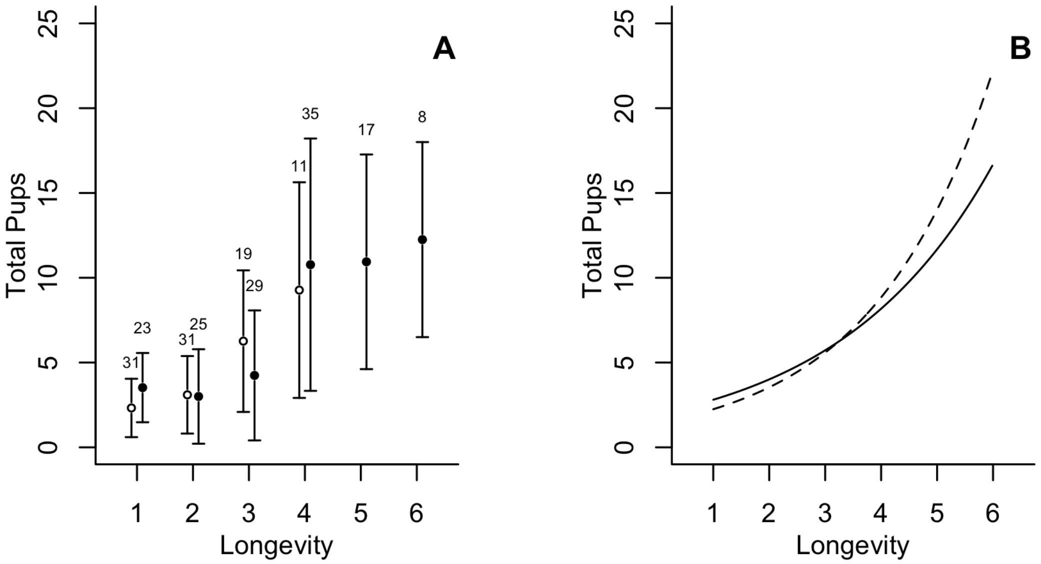

Figure A2.1. The mean ± standard error of the relationship between longevity and total pups sired (graph A), with model predictions of the top-ranked models analyzing this relationship (graph B). Data and model predictions were presented separately for males who did not encounter a mast year (white dots and dotted line) and those who did encounter a mast year (black dots and solid line) during their lifetime. All other variables were set to 0 (ie. the population mean).

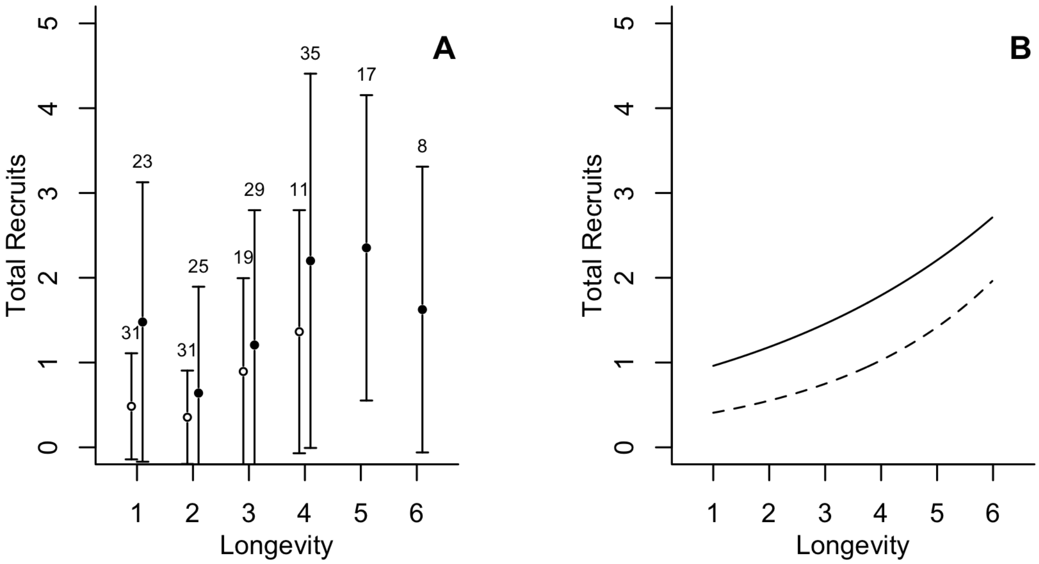

Figure A2.2. The relationship between total recruits and longevity, demonstrated as A) the mean ± standard error of the data and B) model predictions of the top-ranked models, with other variables set to the population mean (i.e. 0). Data and model predictions were shown for males who encountered a mast (black dots and solid line) or who did not encounter a mast (white dots and dotted line) during their lifetime.

Appendix 3

Table A3.1. Models exploring whether masting (Mast) affected female reproduction and litter paternity. Each model set had separate response variables (Response) for each model set was: number of recruits that females produced (Recruits), the number of females in the population who bred (No. Females), the number of first litters (No. 1st Litters), the number of second litters (No. Late Litters), the proportion of recruits that originated from first litters (Prop. 1st Litters), and the number of successful litters (# Successful Litters). I also tested whether the interval between first and second litters (Litter Interval) depended on litter success (Success). Where relevant, I included the following covariates: quadratic age (Age and Age^2), the number of females in the population (Tot. Females), the total number of litters (Total Litters), or study area (Grid). Model sets 1 and 5 included study area-year and squirrel id as random effects, and model set 7 included study area-year as a random effect. The null model includes only random effects for models with random effects, whereas no variables were included for the models without random effects. Models were ranked according to AICc, and the degrees of freedom (df), ΔAICc, and model weight (weight) for each model were indicated. Models ≤6 ΔAICc of the top model are indicated in bold, and were used to calculate model coefficients to the corresponding models in Table 4.1. For some analyses, all data was included (Subset = All), only first litters were included in other analyses (Subset = 1st Litters), and finally all litters in mast years were included in other analyses (Subset = Mast). Sample size is indicated (# Records) as well as the number of individuals included in this analysis (# Individuals) where annual measures were used.

Model	# Individuals	# Records	Response	Subset	Model Structure	df	ΔAICc	weight
1	328	654	Recruits	All	**Mast + Age + Age^2**	**5**	**0.00**	**1.00**
					Age + Age^2	4	20.04	0.00
					Null	2	28.78	0.00
2	-	24	No. Females	All	**Mast + Grid + Tot. Females**	**5**	**0.00**	**1.00**
					Grid + Tot. Females	4	28.00	0.00
					Null	2	33.57	0.00
3	-	24	No. 1st Litters	All	**Mast + Grid + Tot. Females**	**5**	**0.00**	**0.86**
					Grid + Tot. Females	**4**	**3.70**	**0.14**
					Grid	3	30.00	0.00

Model	# Individuals	# Records	Response	Subset	Model Structure	df	ΔAICc	weight
					Null	2	31.73	0.00
4	-	24	No. Late Litters	All	**Mast + Grid + Tot. Females**	**4**	**0.00**	**1.00**
					Grid + Tot. Females	3	121.67	0.00
					Grid	2	127.77	0.00
					Null	1	129.52	0.00
5	206	304	Prop. 1st Litters	All	**Mast**	**5**	**0.00**	**1.00**
					Null	4	13.44	0.00
6	-	24	# Successful Litters	1st Litters	**Mast + Grid + Total Litters**	**5**	**0.00**	**1.00**
					Grid + Total Litters	4	20.04	0.00
					Null	2	28.78	0.00
7	-	70	Litter Interval	Mast	**Litter Success**	**4**	**0.00**	**1.00**
					Null	3	51.73	0.00

Table A3.2. Model sets exploring whether the number of sires per litter (Response = No. Sires) or the weighted average proportion of the litter (Response = Prop. Litter) either whether it was a mast year (Mast) or the litter number. Litter size was included as a covariate in all models. Analyses were done with different data subsets, indicated by Subset; some analyses included all data (All), some included all years but first litters only (1st Litters), or mast years only but all litters (Mast). Study area-year and squirrel id were included as random effects in all models. The null model includes only random effects. Models in bold are top-ranked models that were ≤6 ΔAICc of the top model and were used to generate model coefficients which correspond to the model set numbers (Model) in Table 4.2. Also indicated are the degrees of freedom (df), ΔAICc from the top model, and model weight (weight) for each model set. The number of individuals used (# Individuals) as well as the sample size (# Records) were indicated for each model set.

Model	# Individuals	# Records	Dependent	Subset	Model Structure	df	ΔAICc	weight
1	290	607	No. Sires	All	**Litter Size**	**4**	**0.00**	**0.51**
					Mast + Litter Size	**5**	**0.08**	**0.49**
					Null	3	10.20	0.00
2	271	490	No. Sires	1st Litters	**Litter Size**	**4**	**0.00**	**0.73**
					Mast + Litter Size	**5**	**2.00**	**0.27**
					Null	3	27.32	0.00
3	162	213	No. Sires	Mast	**Litter Number + Litter Size**	**5**	**0.00**	**1.00**
					Litter Size	3	17.62	0.00
					Null	4	17.86	0.00
4	290	607	Prop. Litter	All	**Null**	**4**	**0.00**	**0.98**
					Litter Size	5	7.88	0.02
					Mast + Litter Size	6	13.56	0.00
5	271	490	Prop. Litter	1st Litter	**Litter Size**	**5**	**0.00**	**0.92**
					Null	4	6.11	0.04
					Mast + Litter Size	6	6.39	0.04
6	162	213	Prop. Litter	Mast	**Litter Number + Litter Size**	**6**	**0.00**	**1.00**
					Null	4	39.08	0.00
					Litter Size	5	44.89	0.00

Table A3.3. Model sets testing whether male mating behaviour or paternity differed depending on whether it was a mast year (Mast) or whether it was first or later litter (Litter No.). Each model set had one of several response variables: home range area using behaviour (Area), distance between male and female territories (Distance), number of mates (No. Mates), or proportion of the litter sired (Litter Proportion). Quadratic age (Age + Age^2) was included in all models, and the number of behaviour observations (Loc.) was included when analyzing home range as the number of times a male was located during behaviour observations influences that measurement. Study area-year and squirrel id were included as random effects in all model sets, including the null models. The degrees of freedom (df), change in AICc from the top-ranked model (ΔAICc), and model weight (weight), number of individuals measured (# Individuals), and the sample size (# Records) were indicated for each model. Models ≤6 ΔAICc of the top model were indicated in bold; the model-averaged coefficients from these models were presented in Table 4.3.

Model	# Individuals	# Records	Dependent	Model Structure	df	ΔAICc	weight
1	185	259	Area	**Mast + Age + Age^2 + Loc.**	**8**	**0.00**	**0.63**
				Age + Age^2 + Loc.	**7**	**1.06**	**0.37**
				Null	4	45.05	0.00
2	485	1050	No. Mates	**Mast + Age + Age^2**	**6**	**0.00**	**0.93**
				Age + Age^2	**5**	**5.33**	**0.07**
				Null	3	114.93	0.00
3	485	1050	Prop. Litter	**Age + Age2**	**6**	**0.00**	**0.80**
				Mast + Age + Age^2	**7**	**2.80**	**0.20**
				Null	4	69.01	0.00
4	146	198	Distance	**Litter No. + Age + Age^2**	**6**	**0.00**	**1.00**
				Age + Age^2	5	237.44	0.00
				Null	3	237.45	0.00
5	165	219	No. Mates	**Litter No. + Age + Age^2**	**7**	**0.00**	**0.98**
				Age + Age^2	6	9.39	0.01
				Null	4	9.70	0.01
6	146	198	Prop. Litter	**Litter No. + Age + Age^2**	**7**	**0.00**	**1.00**
				Null	4	37.77	0.00
				Age + Age^2	6	47.88	0.00

Appendix 4

Cached Cone Index Calculation

I calculated cone index as follows:

$$\text{Avg. Cones Per Quadrat} = \frac{\text{Total Cones in all Quadrats}}{\text{Number of Quadrats}}$$

$$\text{No. Quadrats Per Midden} = \frac{\text{Elliptical Midden Area}}{\text{Quadrat Area}}$$

$$\text{Cached Cone Index} = \ln\big((\text{Avg. Cones per Quadrat}) * (\text{No. Quadrats Per Midden})\big)$$

Table A4.1. Fixed effects in model sets used to assess if cones cached in middens (Cones) vary by sex and age. For males, I also assessed whether number of pups sired (No. Pups), number of recruits sired (No. Recruits), home range area (Home Range), or earliest siring date (Date) were affected by cached cones. For females, I tested whether cached cones influenced litter size of first litters each season (Litter Size), average growth rate in their first litter (Growth Rate), parturition date of their earliest litter (Part. Date) or the number of recruits from first litters (No. Recruits). The first model in each model set is the top-ranked model, and models are arranged sequentially in order of increasing AICc. I have indicated the change in AICc (ΔAICc) from the top-ranked model, as well as the model weight (weight), degrees of freedom for each model (df), the number of individuals used in that analysis, and the number of annual measures (sample size) used in that analysis. Models ≤6 AICc of the top-ranked model were indicated in bold; these were considered the top-ranked models and the coefficients are presented in Results (Table 5.1). I controlled for quadratic age in each model analyzing annual reproductive success, reproductive timing, and behaviour. Study area-year and squirrel identification were included as random effects in all models. The null model in all cases included only random effects. Where data were subset into male and female data, it is by the column Sex.

Model Set	Sex	# Individuals	Sample Size	Dependent	Model Structure	df	ΔAICc	weight
1	All	346	576	Cones	**Sex**	**5**	**0.00**	**1.00**
					Null	4	37.63	0.00
2	Males	172	267	Cones	**Age^2 + Age**	**6**	**0.00**	**0.95**
					Age	5	6.09	0.05
					Null	4	36.44	0.00
3	Females	171	302	Cones	**Age^2 + Age**	**6**	**0.00**	**0.65**
					Null	**4**	**2.15**	**0.22**
					Age	**5**	**3.13**	**0.13**
4	Males	121	183	No. Pups	**Age^2 + Age + Cones**	**6**	**0.00**	**0.80**
					Age^2 + Age	**5**	**2.80**	**0.20**
					Null	3	10.85	0.00
5	Males	121	183	No. Recruits	**Null**	**3**	**0.00**	**0.42**
					Age^2 + Age + Cones	**6**	**0.38**	**0.35**
					Age^2 + Age	**5**	**1.18**	**0.23**
6	Males	51	71	Home Range	**Age^2 + Age + No. Locs**	**8**	**0.00**	**0.39**
					Age^2 + Age + Cones + No. Locs	**9**	**0.39**	**0.32**
					No. Locs	**6**	**0.61**	**0.29**

Model Set	Sex	# Individuals	Sample Size	Dependent	Model Structure	df	ΔAICc	weight
					Null	3	72.72	0.00
7	Males	91	129	Date	**Age^2 + Age + Cones**	**7**	**0.00**	**0.82**
					Age^2 + Age	**6**	**2.99**	**0.18**
					Null	4	14.48	0.00
8	Females	114	185	Litter Size	**Null**	**4**	**0.00**	**0.91**
					Age^2 + Age	**6**	**4.83**	**0.08**
					Age^2 + Age + Cones	7	8.99	0.01
9	Females	81	118	Growth Rate	**Null**	**4**	**0.00**	**0.95**
					Age^2 + Age	6	6.13	0.04
					Age^2 + Age + Cones	7	11.69	0.00
10	Females	119	194	Part. Date	**Age^2 + Age + Cones**	**7**	**0.00**	**0.98**
					Age^2 + Age	6	7.71	0.02
					Null	4	65.75	0.00
11	Females	116	184	No. Recruits	**Null**	**3**	**0.00**	**0.52**
					Age^2 + Age	**5**	**0.84**	**0.34**
					Age^2 + Age + Cones	**6**	**2.71**	**0.14**

Table A4.2. Fixed effects in model sets used to assess if average cones cached in middens throughout their lives (Cones) affect lifetime reproductive success, quantified either as pups (LRS Pups) or recruits (LRS Recruits), and longevity. Cones were not counted for all years for these squirrels, so I also included the proportion of their lifetime that I assessed cached cones (Proportion). In some models I also controlled for longevity and whether squirrels encountered a mast year at some point during their lives (Mast). As longevity and proportion of their lifetime that I assessed cones were highly correlated, these variables were included in the same model sets but not the same models. I included study area (Grid) as a covariate in all models. The first model in each model set is the top-ranked model, and models are arranged sequentially in order of increasing AICc. I have indicated the change in AICc from the top-ranked model (ΔAICc), the degrees of freedom for each model (df), the model weight (weight) as well as the number of squirrels (# Individuals) used in each analysis. The top-ranked model and models within ≤6 AICc of the top-ranked model are indicated in bold; these were considered the top-ranked models and their coefficients are presented in Results (Table 5.2). Data were subset into male and female data where indicated by the column Sex.

Model Set	Sex	# Individuals	Dependent	Model Structure	df	ΔAICc	weight
1	Males	101	LRS Pups	**Grid + Longevity + Mast**	**4**	**0.00**	**0.90**
				Grid + Longevity	**3**	**4.30**	**0.10**
				Cones + Proportion + Grid + Mast	5	93.95	0.00
				Cones + Proportion + Grid	4	148.72	0.00
				Grid + Mast	3	165.06	0.00
				Null	1	238.82	0.00
				Grid	2	240.21	0.00
2	Males	99	LRS Recruits	**Cones + Proportion + Grid + Mast**	**5**	**0.00**	**0.99**
				Grid + Longevity + Mast	4	10.02	0.01
				Grid + Longevity	3	20.10	0.00
				Cones + Proportion + Grid	4	20.95	0.00
				Grid + Mast	3	23.26	0.00
				Grid	2	50.49	0.00
				Null	1	50.71	0.00
3	Males	101	Longevity	**Cones + Proportion + Grid + Mast**	**5**	**0.00**	**0.85**
				Cones + Proportion + Grid	**4**	**3.40**	**0.15**
				Grid + Mast	3	18.48	0.00
				Grid	2	26.71	0.00

				Null	1	27.29	0.00
4	Females	110	LRS Pups	**Grid + Longevity**	**3**	**0.00**	**0.73**
				Grid + Longevity + Mast	**4**	**1.99**	**0.27**
				Cones + Proportion + Grid + Mast	5	93.06	0.00
				Cones + Proportion + Grid	4	116.37	0.00
				Grid + Mast	3	128.08	0.00
				Null	1	162.45	0.00
				Grid	2	164.47	0.00
5	Females	111	LRS Recruits	**Grid + Longevity + Mast**	**4**	**0.00**	**0.76**
				Grid + Longevity	**3**	**2.35**	**0.24**
				Grid + Mast	3	17.63	0.00
				Cones + Proportion + Grid + Mast	5	20.32	0.00
				Null	1	34.12	0.00
				Grid	2	36.13	0.00
				Cones + Proportion + Grid	4	36.45	0.00
6	Females	107	Longevity	**Cones + Proportion + Grid + Longevity + Mast**	**5**	**0.00**	**0.94**
				Cones + Proportion + Grid + Longevity	**4**	**5.55**	**0.06**
				Grid + Longevity + Mast	3	10.08	0.01
				Null	1	17.57	0.00
				Grid + Longevity	2	19.45	0.00