Seed Masting Causes Fluctuations in Optimum Litter Size and Lag Load in a Seed Predator*

Andrew G. McAdam,1,† Stan Boutin,2 Ben Dantzer,3 and Jeffrey E. Lane4

1. Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada; 2. Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada; 3. Department of Psychology and Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109; 4. Department of Biological, University of Saskatchewan, Saskatoon, Saskatchewan, Canada

Submitted December 19, 2018; Accepted February 22, 2019; Electronically published August 20, 2019

Abstract: The episodic production of large seed crops by some perennial plants (masting) is known to increase seed escape by alternately starving and swamping seed predators. These pulses of resources might also act as an agent of selection on the life histories of seed predators, which could indirectly enhance seed escape by inducing an evolutionary load on seed predator populations. We measured natural selection on litter size of female North American red squirrels (Tamiasciurus hudsonicus) across 28 years and five white spruce (Picea glauca) masting events. Observed litter sizes were similar to optimum litter sizes during nonmast years but were well below optimum litter sizes during mast years. Mast events therefore caused selection for larger litters (β = 0.25) and a lag load (L = 0.25) on red squirrels during mast years. Reduced juvenile recruitment associated with this lag load increased the number of spruce cones escaping squirrel predation. Although offspring and parents often experienced opposite environments with respect to the mast, we found no effect of environmental mismatches across generations on either offspring survival or population growth. Instead, squirrels plastically increased litter sizes in anticipation of mast events, which partially, although not completely, reduced the lag load resulting from this change in food availability. These results therefore suggest that in addition to ecological and behavioral effects on seed predators, mast seed production can further enhance seed escape by inducing maladaptation in seed predators through fluctuations in optimal trait values.

Keywords: agent of selection, environmental variation, fluctuating selection, life history, natural selection, resource pulse.

* The Special Feature on Maladaptation is a product of a working group that convened in December 2015 and 2016 at McGill University’s Gault Preserve and of a symposium held at the 2018 meeting of the American Society of Naturalists in Asilomar, California, inspired by the working group.
† Corresponding author; email: amcadam@uoguelph.ca.

ORCIDs: McAdam, https://orcid.org/0000-0001-7323-2572; Boutin, https://orcid.org/0000-0001-6317-038X; Dantzer, https://orcid.org/0000-0002-3058-265X.

Am. Nat. 2019. Vol. 194, pp. 574–589. © 2019 by The University of Chicago. 0003-0147/2019/19404-5895$15.00. All rights reserved.
DOI: 10.1086/703743

When environments change, populations can find themselves removed from their adaptive peak, which results in a reduction in mean fitness and natural selection. As traits evolve toward the new adaptive peak, mean fitness in the population increases (Fisher 1930; Burt 1995). The magnitude of the initial decline in mean fitness and the rate of adaptation following a change in the environment are important components of a population’s ability to persist following an environmental change (Gomulkiewicz and Holt 1995). In the absence of extinction or absolute constraints on adaptation (Mezey and Houle 2005), the population will eventually reach a new equilibrium dictated by the new environment. That is, unless the environment changes again.

Variation in environmental conditions is present at all timescales (Bell 2010), so fluctuations in the magnitude and, more importantly, the direction of selection ought to be common (Bell 2010). While fluctuating selection can maintain genetic variance (Ellner and Hairston 1994), thereby facilitating adaptation over longer timescales, it can slow the process of local adaptation (Kawecki and Ebert 2004) and reduce mean fitness (Maynard Smith 1976a). Furthermore, large fluctuations in selection over short timescales can result in environmental mismatches across generations whereby high-fitness parents produce offspring with low fitness (Eshel and Hamilton 1984). In these instances, an evolutionary response to selection experienced by parents can cause environment-trait mismatches in offspring and a reduction in their fitness (i.e., maladaptation).

Evidence for the prevalence of fluctuating selection in nature has been equivocal (Kingsolver et al. 2012). Siepielski and Benkman (2008) suggested that selection is typically changeable in nature, but previous estimates of fluctuating selection likely overestimated the frequency of fluctuating selection because sampling error is often confounded with true fluctuations in selection (Morrissey and Hadfield 2012). Correctly accounting for sampling error suggested that evidence for fluctuating selection is limited (Kingsolver et al.
masting mixed effects models have been proposed as a more rigorous way to test for fluctuating selection within a single study (Morrissey and Hadfield 2012; Chevin et al. 2015), but these have not yet been widely implemented (but see Chevin et al. 2015; Bonnet and Postma 2018).

Some of the most compelling examples of fluctuating selection come from individual cases where the ecological causes of natural selection (agents of selection; Wade and Kalisz 1990) have been identified. For example, natural selection on the beak morphology of the medium ground finch (Geospiza fortis) is caused by changes in food availability associated with episodic drought and rainfall events (Grant and Grant 2002). Fluctuating selection on clutch size and egg size in side-blotched lizards (Uta stansburiana) is caused by changes in population density (Sinervo et al. 2000), and selection on the color and patterning of stick insects (Timema cristinae) is caused by climate and the frequency of each pattern morph, respectively (Nosil et al. 2018). Notwithstanding these important examples, the causes of natural selection in the wild are rarely known (MacColl 2011), but the magnitude and prevalence of environmental variation suggest that fluctuations in natural selection ought to be common in nature (Bell 2010).

Resource pulses (Yang et al. 2008) represent particularly dramatic changes in the environment that could have important consequences for natural selection on the life histories of species that consume these resources. In particular, some species of perennial plants produce large numbers of seeds during a brief period followed by several years in which seed production is low or absent (Kelly and Sork 2002). This phenomenon is referred to as masting, and it is considered to be a reproductive strategy designed to satiate seed predators and enhance seed escape (i.e., the number of seeds that escape predation and have the opportunity to germinate; Janzen 1971). Years of low seed production between mast events is expected to numerically depress populations of seed predators. The subsequent production of large amounts of seed in mast years is hypothesized to then satiate the ability of seed predators to harvest, store, and consume seed, thereby enhancing seed escape (Kelly and Sork 2002; for an empirical example, see Fletcher et al. 2010).

In addition to enhancing seed escape through the numerical depression of seed predators during years of low seed production and the satiation of seed predators during mast years (functional responses; Solomon 1949; Holling 1959), episodic mast seed production could also enhance seed escape by acting as an agent of selection on the life histories of seed predators. Fluctuations in natural selection on seed predators caused by masting might enhance the fitness of seed producers by inducing an evolutionary lag load on seed predators. Lag load refers to the difference between observed population mean fitness and the maximum fitness that would have been achieved had all individuals possessed optimum phenotypes (Maynard Smith 1976a), and it can be described as follows:

\[
L = \frac{W^* - W}{W}
\]

Here \(L\) represents the lag load, \(W^*\) represents the fitness of the best possible genotype or collection of phenotypes, and \(W\) represents the current mean fitness of the population. A lag load arises when there is a change in the environment and a population has not yet evolved the optimal phenotype for this new environment (Maynard Smith 1976a). When species interact negatively (e.g., predator and prey), one species can enhance its own fitness (i.e., reduce its load) by inducing an evolutionary load on another species with which it negatively interacts (Maynard Smith 1976b). If the episodic production of large seed crops induces a lag load on seed predators, this would represent an additional mechanism by which masting might enhance the fitness of seed producers through increased seed escape.

Life-history traits, such as brood size, represent possible targets of variable selection caused by seed masting because they are closely associated with fitness and are often resource dependent. Lack (1947) recognized that natural selection on brood size represents a balance between the fecundity benefits of producing more offspring and the survival costs to each offspring of being raised in a larger brood with fewer per capita resources (see also Smith and Fretwell 1974). Optimal brood sizes therefore represent a balance between these survival costs to offspring and the fecundity benefits of larger broods (Lack 1947). When resources are abundant, the per capita decline in offspring survival with increasing brood size should be lessened and optimal brood sizes are expected to increase (Lack 1947; see also Boyce and Perrins 1987). For example, Crossner (1977) found that the size of European starling (Sturnus vulgaris) chicks, which is frequently associated with survival, was negatively associated with clutch size, but this trade-off could be eliminated through ad lib. food supplementation. Fluctuations in seed production might therefore be expected to result in fluctuating optimum brood sizes in seed predators.

Environmentally induced fluctuations in the optimum brood size of seed predators could induce a lag load in seed predators (i.e., reduction in mean fitness) if realized brood sizes are unable to track changes in the optimum brood size. Fluctuations in optimum brood size could lead to the evolution of reduced overall brood size because of “bad-year effects” (Boyce and Perrins 1987) or the evolution of phenotypic plasticity in brood size (Leimar and McNamara 2015) if there are environmental cues that are predictive of a new optimum. However, if changes in optimum brood size exceed the ability of seed predators to track a changing
optimum through phenotypic plasticity, they might instead evolve brood sizes that match one optimum but perform poorly in the other environment (Levins 1968). Although the evolution of a reduced brood size with less variability in fitness or a brood size that is well suited to one environment but not another might maximize the fitness of seed predators over the long run (i.e., of most importance to the seed predators), these strategies might still incur a short-term load resulting from deviations from the currently most productive brood size (i.e., difference between trait values that maximizes geometric mean fitness vs. annual fitness), which could provide a fitness opportunity for seed producers. Furthermore, the repeated and intermittent nature of masting could induce negative temporal autocorrelation in the environment experienced by parents and offspring if the frequency of masting matches the generation time of seed predators. In this case, an evolutionary response to natural selection experienced in the parental generation might cause maladaptation in offspring that experience alternate environmental conditions (Eshel and Hamilton 1984). For example, the evolution of larger broods in response to positive selection under high-food conditions in the parental generation would reduce offspring fitness if they tend to experience low-food conditions with lower optimum brood sizes.

North American red squirrels (Tamiasciurus hudsonicus) in the Yukon, Canada, experience resource pulses in their primary food resource, seeds extracted from white spruce (Picea glauca) cones (Boutin et al. 2006, 2013; Fletcher et al. 2013). White spruce is a masting species that produces an annual cone crop ranging from a complete failure in some years to extremely large crops during mast years (LaMontagne and Boutin 2007; Krebs et al. 2012). Mast years usually occur every 2–6 years (Nienstaedt et al. 1990) and satiate the hoarding rate of red squirrels (Fletcher et al. 2010). In most cases juveniles settle in a previously occupied territory, but they can sometimes be given a territory by their mother (Price and Boutin 1993; Bertaux and Boutin 2000; Lane et al. 2015), and in some years cones are plentiful enough that they create a new territory. Squirrels that recruit into the adult population typically live only 3–4 years (McAdam et al. 2007), which is similar to the typical frequency of mast events. It is therefore possible, although rare, that a squirrel born during a mast year would survive long enough to experience a mast year as an adult.

Litter size in red squirrels is heritable ($h^2 = 0.15$) and was previously found to experience stabilizing selection around the population mean litter size (Réale et al. 2003). Previous observations and experimental manipulations of litter size in red squirrels have indicated that red squirrels are not physically or energetically prevented from producing larger litters, but larger litter sizes result in reduced offspring growth and survival (Humphries and Boutin 2000). Also, the experimental enlargement of litters had no effect on the survival of mothers (Humphries and Boutin 2000), indicating that selection on litter size acts primarily through the early survival of offspring. While the classic life-history trade-off between offspring size and number (Smith and Fretwell 1974) appears to be an important determinant of red squirrel litter sizes, there is reason to suspect that the relationships underlying the optimum litter size are not constant. Specifically, the observed trade-off between litter size and offspring growth rate can be eliminated through food supplementation (Dantzer et al. 2013). Second, while offspring growth is related to early-life survival, viability selection on offspring growth rates varies among years (McAdam and Boutin 2003), and these changes have been previously associated with changes in population density (Dantzer et al. 2013) and food availability (McAdam and Boutin 2003). It is therefore possible that temporal fluctuations in food abundance, resulting from mast seed production by white spruce trees, leads to fluctuations in optimum litter sizes in red squirrels.

Here we used a 29-year field study of red squirrels that spanned five mast events to first test whether the episodic production of spruce seed caused fluctuations in natural selection on litter size. Second, we quantified the reduction in fitness of red squirrels (lag load) resulting from fluctuations in the optimum litter size and used 7 years of data on spruce tree cone production and seed escape in our study areas to measure the consequences for spruce trees of the observed lag load in red squirrels. Third, we tracked the demography of squirrels to determine whether the observed frequency of mast events resulted in mismatches in environments between parents and offspring. Specifically, we determined whether females born during mast years typically bred during nonmast years and vice versa. If natural selection differed between mast and nonmast years and if mast environments were mismatched across generations, then an evolutionary response to the parental environment should result in a reduction of fitness in offspring experiencing the opposite environment. We therefore tested whether environmental mismatches between parents and offspring had measurable effects on the fitness of individual red squirrels or population growth rate.

**Material and Methods**

We studied the reproduction and survival of individually marked North American red squirrels (Tamiasciurus hudsonicus) between 1989 and 2017 in two study areas (designated SU [Sulphur] and KL [Kloo]) near Kluane Lake, Yukon, Canada (61°N, 138°W), on the traditional territory of the Champagne and Aishihik First Nations. In each ~40-ha area, we censused the entire population in May and August of each year with a yearly probability of detection that did not differ from 1.0 (Descamps et al. 2009). Regular livetrapping allowed us to determine when females...
gave birth. We located nest sites through behavioral observations and radiotelemetry to census and weigh offspring and assess litter size within days of birth and again at ~25 days of age to ear-tag nestlings and to calculate growth in body mass (McAdam et al. 2007).

We measured cone production by white spruce (Picea glauca) trees in each year for between 159 and 254 trees distributed systematically within our study areas (LaMontagne and Boutin 2007). We averaged these values across all trees within a year for each study area (following a ln[x + 1] transformation; see also Boutin et al. 2006) to quantify an index of the availability of food for red squirrels, but this cone index has been calibrated to the actual number of cones produced per tree (LaMontagne et al. 2005; Krebs et al. 2012). Mast years (1993, 1998, 2005, 2010, 2014) were evident by very large cone crops (LaMontagne and Boutin 2007). All data were deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.jf5flbh; McAdam et al. 2019).

We measured natural selection on litter size using annual reproductive success (ARS) as our fitness metric. ARS was defined as the number of offspring that recruited per year, where juveniles were defined to have recruited if they survived beyond 200 days of age. This measure of fitness mixes maternal fecundity with offspring viability (Thomson and Hadfield 2017) but can nevertheless result in appropriate measures of selection because litter size is a sex-limited trait and there does not appear to be a cost to adult longevity of producing larger litters (Humphries and Boutin 2000). Our study areas were large relative to the dispersal distance of red squirrels (Larsen and Boutin 1994; Berteaux and Boutin 2000; Cooper et al. 2017), and we have previously shown that our implicit assumption that disappearance of juveniles represents death is a valid one in this system (Kerr et al. 2007; McAdam et al. 2007). Squirrels will sometimes renest after a failed litter (Williams et al. 2014) or after a successful first litter during mast years (Boutin et al. 2006). Here we considered natural selection based only on those offspring born during first litters of the season, but our main results are not sensitive to the exclusion of subsequent litters.

**Fluctuating Selection**

We assessed hypotheses about temporal changes in natural selection on litter size by comparing the fit of seven a priori models using the Akaike information criterion (AIC; Burnham and Anderson 2002). Following Chevin et al. (2015), all models were based on generalized linear mixed models of ARS based on a Poisson error distribution (log link function) fitted with maximum likelihood using the lme4 package (Bates et al. 2015) with a bobyqa optimizer. This log link means that selection gradients can be directly extracted from the parameters of this model (sensu Lande and Arnold 1983; see also Chevin et al. 2015; Bonnet and Postma 2018).

Model 1 assumed that all natural selection was constant. This model included litter size as well as a quadratic term for litter size to measure directional and stabilizing selection on litter size, respectively. This model also included parturition date and the average growth rate of offspring as two additional maternal traits. All traits were standardized (mean = 0, SD = 1) within each year–study area combination prior to analysis. Whether the year was a mast year and the study area (SU vs. KL) were also included as fixed effects. The mother’s identity and year were included as random effects to account for differences in ARS among squirrels and among years. All subsequent models were based on this basic model structure. Model 2 allowed directional selection on litter size to differ between mast and nonmast years by including an interaction between litter size and whether it was a mast year. Model 3 similarly allowed both directional and stabilizing selection to differ between mast and nonmast years. We tested for annual variation in natural selection instead of (models 4, 5) and in addition to (models 6, 7) differences in selection between mast and nonmast years by fitting random interactions between linear and quadratic effects of litter size and year (i.e., random regression mixed models; see Chevin et al. 2015). Model 4 tested for annual variation in directional selection. Model 5 tested for annual variation in both directional and stabilizing selection. Model 6 was similar to model 4 but also included a fixed interaction between litter size and mast year. Model 7 was similar to model 6 but also allowed quadratic selection to vary among years.

We visualized the relationship between litter size and ARS in mast and nonmast years by fitting separate generalized linear mixed models (Poisson error distribution, log link) for mast and nonmast years that included raw litter size, litter size$^2$, and study area as fixed effects. Squirrel identity and year were fitted as random effects as described above ($n=1,541$, litters, 714 squirrels, 28 years). This approach was therefore conceptually similar to model 3 (described above). Results based on raw litter sizes and excluding other maternal traits were consistent with the analysis of standardized traits (described above), but such results were more useful for visualizing and describing the Gaussian fitness functions in raw units.

This set of models treated litter size, pup growth rates, and parturition date as three independent traits, whereas the negative association between litter size and growth might be better represented by a causal negative effect of litter size on offspring growth rates. However, assuming a causal effect of litter size on fitness and considering effects of growth on fitness only marginal to the effects of litter size by fitting the residuals of the growth–litter size relationship (calculated separately for each year) instead of raw growth rates did not change the conclusions, so we did not consider this issue further.

We also estimated directional and quadratic selection gradients (following Lande and Arnold 1983) separately
for mast and nonmast environments. In this analysis, relative fitness was calculated for each squirrel based on the mean ARS for each year–study area combination separately, and traits were standardized within year–study area combinations as described above. Values are reported ±1 SE, which were calculated using a delete-one jackknife procedure.

### Calculation of Lag Load

We calculated the lag load experienced by red squirrel populations associated with how well observed mean litter sizes matched optimum litter sizes in mast and nonmast years separately. Our generalized linear mixed effects model of ARS based on raw litter sizes (described above) provided all the necessary parameters to describe separate Gaussian fitness functions for litter size in mast and nonmast years (following Chevin et al. 2015), including the location of the optimum litter size, \( \bar{\theta} \), calculated as \(-\beta_m / 2\sigma^2\) (see also Phillips and Arnold 1989). Following Gomulkiewicz and Houle (2009), we calculated the maximum mean ARS, \( \bar{F} \), which would have been achieved had the population mean litter size been equal to \( \bar{\theta} \), as

\[
\bar{F} = F(\bar{\omega}^2 / \bar{v}^2)^{1/2},
\]

where \( F \) is the maximum of the Gaussian fitness function, \( \bar{\omega} \) is the width of the fitness function (standard deviation of fitness), and \( \bar{v} \) is the sum of \( \bar{\omega}^2 \) and the phenotypic variance, \( \sigma^2 \). Following Gomulkiewicz and Houle (2009), we then calculated \( \bar{ARS}(\bar{z}) \), the expected mean ARS based on the observed mean litter size, \( \bar{\bar{z}} \), as

\[
\bar{ARS}(\bar{z}) = \bar{F} \left[ 1 - \frac{(\bar{z} - \bar{\theta})^2}{2\bar{\omega}^2} \right],
\]

where variables are defined as above. Finally, we calculated the lag load (Maynard Smith 1976a) as described previously, where the fitness of the best possible genotype was replaced by \( \bar{F} \) and the observed mean fitness was \( \bar{ARS}(\bar{z}) \). We also calculated the difference between the maximum expected number of recruits based on \( \bar{F} \times N_{\text{breeding female}} \) and the observed number of recruits in each year to determine how many more offspring could have been recruited had the population mean litter size matched the optimum litter size.

### Effects of Squirrel Recruitment on Cone Escape

In addition to measuring spruce cone production within our study areas, between 2007 and 2013 we also measured the number of cones that remained on each spruce tree at the end of the cone-harvesting season by squirrels, which successfully opened to release seed (553 total observations from 163 trees). While there are more seeds per cone and larger seeds during mast years than nonmast years (Deasley 2014), the number of cones escaping squirrel predation provides a reasonable annual measure of seed escape (see also Archibald et al. 2012). Note that no cones were produced by any of these trees in 2011, so there were no data on cone escape from 2011. We fitted a power law model to assess the effects of cone production (\( \ln(x) \) transformed) and the local density of red squirrels on the number of cones escaping squirrel predation (\( \ln(x + 1) \) transformed) using a general linear mixed model. We measured the local density of squirrels surrounding each tree as the number of squirrels owning a territory within 56.4 m of each cone count tree (i.e., a 1-ha area around each tree) based on our autumn population census. In addition to the local density of squirrels, we also fitted the study area (SU or KL) as a fixed effect and whether it was a mast year. We fitted an interaction between mast year and the local density of squirrels and an interaction between mast year and ln(cone production). We fitted the identity of each tree (\( n = 163 \)) and year (\( n = 6 \)) as random effects.

### Evidence of Environmental Mismatches across Generations

We used our semiannual complete enumeration of the population in spring to track the proportion of the population in each year that was born during mast conditions. We tagged most squirrels in the study area within their natal nest, so their birth year was known with certainty. Immigrants to the population (~35% of residents) were defined to be yearlings or, rarely, 2 years of age based on their size and reproductive status at the time they were first captured.

We have previously estimated the heritability of litter size and parturition date as 0.15 and 0.16, respectively (Réal et al. 2003). We predicted the difference in litter size that we expected to see between offspring born in mast and nonmast cohorts using \( (\beta_{\text{mast}} - \beta_{\text{nonmast}}) \times h^2 \times \sigma \times 0.5 \). The final term, 0.5, is applied because selection on litter size is assumed to be zero through male ARS. Differences among birth cohorts do not persist beyond one generation of selection because breeding occurs between as well as within cohorts. This calculation ignores selection on genetically correlated traits (Lande 1979) and possible genotype-environment interactions and assumes that selection acts proportionally on the genetic basis to traits and not disproportionately on environmental deviations (Rausher 1992), but it provides an estimate of the magnitude of difference between mast and nonmast cohorts that might result from one generation of selection.

We assessed whether litter sizes differed between mothers recruited during mast years versus those that recruited during nonmast years while also testing whether females adjusted litter sizes to match upcoming mast conditions. We did this by fitting a general linear mixed effects model where litter size was modeled by whether the female was born during a mast year or a nonmast year and whether
the cone crop later that summer was going to be a mast or nonmast crop. We also included study area and the female’s age (as linear and quadratic terms) as fixed effects. We included each female’s birth year, the current year, and the identity of the squirrel as random effects. We fitted the models using the lme4 package in R and assessed the significance of the fixed effects using the Satterthwaite approximation. This analysis of litter size was based on 1,462 litters from 673 dams in 28 cohorts over 28 years.

**Effects of Mismatch on Offspring Survival and Population Growth**

We looked for evidence of temporal maladaptation caused by masting events using both juvenile survival and population growth rate. We tested for effects on juvenile survival by fitting a generalized linear mixed model (binomial error distribution, logit link function) of the survival of individual offspring using the lme4 package (Bates et al. 2015). This model included whether the year in which they were born was a mast year and whether the year in which their mother was born was a mast year. Importantly, we also included an interaction between these two fixed effects to test for evidence of temporal maladaptation. This interaction tested whether the effects of a mast event on juvenile recruitment depended on whether the juvenile’s mother also recruited in a mast year. Adaptation to mast conditions would be represented by an interaction in which the positive effects of a mast event on offspring recruitment were stronger for females that themselves recruited during a mast year (mothers and offspring environments matched). This model also included the sex of the offspring and the study area as fixed effects and litter identity and year as random effects.

Similarly, we assessed the effects of environmental mismatch on population growth. Population growth rate was measured separately for each of the two study areas as the finite annual rate of population growth (λ) from year t to year t+1. We assessed the effects of spring population size and whether it was a mast year on population growth rates using a general linear mixed model between 1994 and 2017 (n = 23 years of population growth data). We also tested whether the proportion of squirrels in the population that recruited during a mast year affected population growth rate and tested for an interaction between this term and whether it was a mast year. This model also included a nominal fixed effect for the two study areas and a random year effect.

**Results**

Across the 29 years of this study, there were five mast events by white spruce (Picea glauca): 1993, 1998, 2005, 2010, and 2014 (fig. 1A). During mast years, hundreds to thousands of cones were produced per tree, whereas in nonmast years there were few to no cones produced (fig. 1A). Discrete population growth rates of red squirrels (λ) were typically less than 1 during nonmast years (mean ± SE based on n years = 0.90 ± 0.04, n = 23 years) but averaged 2.03 (SE = 0.18, n = 5 years) during resource-rich mast years (fig. 1B). We also found evidence that λ was negatively affected by the size of the squirrel population, and this density dependence was significantly greater during mast years (spring number × mast interaction; table 1). Mast events and spring population numbers together explained 81% of the variation in the population growth rates of squirrels.

**Mast-Induced Selection on Litter Size**

During this 29-year period, we tracked the ARS, litter size, parturition date, and offspring growth rates of 714 female red squirrels across 1,541 reproductive events. AIC model comparison indicated that the model with the highest degree of support allowed directional selection on litter size to differ between mast and nonmast years (table A1; tables A1, A2 are available online). The model in which both directional and stabilizing selection on litter size differed between mast and nonmast years also had substantial support (ΔAIC = 1.7). Models of consistent directional selection on litter size (ΔAIC = 4.0) and all other models that did not allow natural selection on litter size to differ between mast and nonmast years had considerably less support (ΔAIC ≥ 4.9). There did not appear to be annual fluctuations in natural selection on litter size beyond the differences between mast and nonmast years. Models that allowed natural selection on litter size to differ between mast and nonmast years and to also vary among years had less support (ΔAIC ≥ 3.1) than the models that considered only differences in selection between mast and nonmast years.

In the best model of female ARS, there was no directional effect of litter size on ARS during nonmast years (b = 0.05 ± 0.05, z = 1.1, P = .25), but there was a significant interaction between litter size and whether it was a mast year (b = 0.26 ± 0.08, z = 3.3, P = .001). This positive interaction indicates that the strength of directional selection on litter size was significantly more positive during mast years than nonmast years (table 2). Mast years also had much higher ARS on average (b = 0.92 ± 0.28, z = 3.3, P = .001) and there was a significant negative quadratic effect of litter size (b = −0.08 ± 0.03, z = −2.9, P = .003), indicating stabilizing selection on litter size.

This Poisson generalized linear model provided all of the necessary parameters to describe separate Gaussian fitness functions for litter size in mast and nonmast years (Chevin et al. 2015). From our data, the optimum litter size differed substantially between mast (θmast = 5.2 offspring)
and nonmast (θ_{nonmast} = 3.4 offspring) years, and the maximum of the fitness function also differed substantially between mast (W_{max,mast} = 1.91 recruits) and nonmast (W_{max,nonmast} = 0.47 recruits; fig. 2A) years. The magnitude of stabilizing selection (1/(σ^2 + σ'_l^2)) was equal to 0.16. In nonmast years, the mean observed litter size (3.0 offspring; fig. 2B) was close to the optimum (3.4 offspring), resulting in weak directional selection based on this Gaussian fitness function (selection gradient β_{nonmast} = 0.07, standardized selection gradient β'_{nonmast} = 0.08). The mean litter size during mast years (3.3 offspring) was greater than that during nonmast years (fig. 2B) but still substantially below θ_{mast}, resulting in positive directional selection on litter size (β_{mast} = 0.30, β'_{mast} = 0.34).

Estimates of directional and quadratic selection gradients (sensu Lande and Arnold 1983) in mast and nonmast years were consistent with interpretations from the Gaussian fitness functions. There was weak directional selection favoring larger litter sizes during nonmast years (β' = 0.11 ± 0.05) but stronger directional selection for larger litters during mast years (β' = 0.25 ± 0.07). There was significant stabilizing selection on litter size during nonmast years (γ' = −0.22 ± 0.06). In mast years, stabilizing selection was only slightly weaker but not significantly different from zero (γ' = −0.18 ± 0.10). This analysis also revealed significant directional selection favoring earlier parturition dates (β' = −0.14 ± 0.05) and faster-growing offspring (β' = 0.28 ± 0.08) during nonmast years and selection for later...
parturition dates during mast years ($\beta' = 0.17 \pm 0.07$). There was no directional selection on offspring growth during mast years ($\beta' = 0.12 \pm 0.10$).

### Lag Load Resulting from a Changing Optimum Litter Size

For nonmast years, the expected fitness based on the observed distribution of litter sizes (0.43 offspring) was close to the maximum expected fitness (0.44 offspring), indicating very little lag load (0.02) during nonmast years. In contrast, the expected fitness based on the observed distribution of litter sizes in mast years (1.34 offspring) was well below the expected maximum fitness (1.77 offspring), resulting in a substantial lag load (0.25). If we assume a constant lag load in mast years but multiply this per capita load across the population of breeding females, which varied in size among the five mast years, we can calculate that the lag load resulted in ~32 fewer recruited offspring in the population than would have been recruited per mast year had litter sizes in the population been larger (range = 8–80 offspring, mean = 32.4, $n = 5$ mast years).

### Effects of Squirrel Lag Load on Cone Escape

Young of the year can make up a substantial proportion of the entire population of squirrels during autumn, when spruce cones are ripe and harvested by squirrels (range = 4%–43%, mean = 22%; fig. 3). Juvenile recruitment below what would have been supported by the environment had litter sizes been larger therefore has the potential to have measurable effects on the number of spruce cones escaping squirrel predation because it will reduce the number of squirrels clipping and hoarding spruce cones in the autumn.

The number of spruce cones escaping seed predation by red squirrels (log transformed) increased with the number of cones produced (log transformed), but in a hypoallo-

### Table 1: Effects of white spruce mast events, spring population size, and their interaction on the discrete population growth rates of two nearby populations of red squirrels

| Variable | Estimate ± SE | t     | df | P   |
|----------|---------------|-------|----|-----|
| Intercept | .91 ± .04     | 20.7  | 46.78 | <.0001 |
| Mast (yes) | .93 ± .10  | 9.5   | 25.83 | <.0001 |
| Population size | −.003 ± .001 | −2.2  | 33.14 | 0.03 |
| Grid (SU) | .01 ± .05    | 26.63 | .87  |     |
| Mast (yes) × population size | −.01 ± .004 | −2.5  | 31.37 | 0.02 |

Note: Spring population size was mean-centered prior to analysis. Differences between the two study areas is denoted by “grid (SU),” which represents the contrast between the SU study area and the KL study area (reference level). The fitted model was a general linear mixed effects model that included year as a random effect. Random effects: among-year variance $= 0.007$, residual variance $= 0.040$.

### Table 2: Effects of litter size, parturition date, and offspring growth rate on the annual reproductive success of female red squirrels in mast and nonmast years

| Variable | Estimate ± SE | z     | P   |
|----------|---------------|-------|-----|
| Intercept | −2.22 ± .49   | −4.5  | <.001 |
| Study area (SU) | −.03 ± .08 | −.4   | .71  |
| Mast (yes) | .06 ± .50    | .11   | .91  |
| Parturition date | −.07 ± .04 | −1.7  | .10  |
| Growth rate | .26 ± .10    | 2.6   | .01  |
| Litter size | .62 ± .26    | 2.4   | .02  |
| Litter size$^c$ | −.08 ± .04 | −1.9  | .06  |
| Litter size × mast (yes) | .28 ± .12 | 2.4   | .02  |

Note: Parturition date was standardized to a mean of zero and unit variance prior to analysis. For nominal fixed effects, the level corresponding to the parameter is specified. The fitted model was a generalized linear mixed effects model with a Poisson error distribution and a log link function. This model was based on 975 litters by 563 squirrels in 28 years. Residual deviance $= 1.923$, residual df $= 965$. Random effects: among-squirrel variance $= 0.00$, among-year variance $= 0.36$. 

Masting Causes Lag Load in Seed Predator
Figure 2: In resource-rich mast years, the litter size that maximizes the annual reproductive success (ARS) of female red squirrels was much larger (5.2 offspring) than the optimum litter size during nonmast years (3.4 offspring; A). The plotted lines (mast = dotted; nonmast = solid) represent predicted values from a generalized linear model of ARS based on raw litter sizes. Red squirrels plasticly increase litter sizes during mast years (B). The mean litter size during the spring of mast years (3.3 offspring; blue) was larger than the mean litter size during nonmast years (3.0 offspring; red). Despite differences in natural selection between mast and nonmast years, we found no difference between the litter sizes of females born during mast (blue) and nonmast (red) years (C).
the number of spruce cones per tree that escaped squirrel predation \((913 - 828) / 828\).

**Mismatches in Selection across Generations**

Although not cyclic, the episodic production of spruce mast seed and the corresponding shift in the optimum litter size of red squirrels occurs every 4–7 years (fig. 1A). The observed interval between mast years and the demography of red squirrels was such that there was often a mismatch between the mast seed environment in which squirrels recruited into the population and the seed crop that they experienced as adults. High juvenile recruitment during mast years meant that in years following a mast event most of the population was composed of squirrels that recruited during mast conditions (fig. 4A). However, few squirrels that recruited during mast years were still alive at the time of the next mast event. At this point, almost all of the population was composed of squirrels that recruited during nonmast years (fig. 4A). This was particularly true for four of the five mast events, but the short interval between the 2010 and 2014 mast events meant that there were still many squirrels from the 2010 cohort that were still alive during the mast event of 2014 (fig. 4A).

The mismatch between the mast conditions under which some juveniles recruited into the population and the mast conditions they experienced as breeding adults (fig. 4B) might result in mismatches in selection across environments. For example, offspring born during mast years, in which there is a large optimum litter size (5.2 offspring), bred almost entirely during nonmast years, in which the optimum litter size is much lower (3.4 offspring; fig. 4B). Although we did not predict differences in the direction of selection on parturition date between mast and nonmast years, these opposite patterns of selection that we documented meant that offspring born during years in which later breeding was favored reproduced as adults mostly during years in which earlier breeding is favored. Given this mismatch in selection across generations, an evolutionary response to the maternal environment should reduce rather than improve individual fitness (individual maladaptation), and populations composed primarily of mismatched individuals ought to exhibit reduced population growth rate (population maladaptation).

Based on the observed differences in natural selection on litter size between mast and nonmast cohorts, we would expect to see only a very small difference between the mean litter size of females born in mast and nonmast years of +0.01 offspring on the basis of an evolutionary response to one generation of selection. The difference in selection on parturition date between mast and nonmast years was larger, but the expected difference between mast and nonmast cohorts in parturition date due to one generation of selection was +0.61 days. We found no evidence that females born in mast and nonmast cohorts differed in either their litter size \(b_{\text{birth, mast}} = 0.06 \pm 0.08, t_{\text{df}} = 0.7, P = .49;\) table 3; fig. 2C) or their parturition date \(b_{\text{birth, mast}} = \)
Females plastically increased their litter sizes during years in which mast seed crop would be available in the autumn (year, mast, $t_{18,4} = 0.41 \pm 0.13$, $P = .006$; table 3; fig. 2B). In contrast, females born during nonmast years reproduced more frequently in nonmast conditions than in mast conditions (B). The prevalence of females breeding under conditions that matched their birth conditions are shown in gray, whereas mismatched breeding conditions are shown in red."

---

Given the high degree of plasticity in these traits and the lack of difference between mast and nonmast cohorts, it is not surprising that we found no interaction between the environment experienced by offspring and the environment experienced by their mother on offspring survival. Offspring survival was much higher in mast years than in nonmast years (table 5), but we found no effect of the environment experienced by mothers during recruitment on the survival of her offspring and no significant interaction between the maternal and offspring mast environments (table 5).

We also found no evidence that population growth rate was affected by the composition of the population or an interaction between current mast conditions and the proportion of the population that recruited during mast years (table 6). When these terms were added to the model predicting population growth rate shown in table 1, the effects
Masting Causes Lag Load in Seed Predator

Table 3: Effects of a mast event in the current year, birth cohort (mast vs. nonmast), and maternal age on litter size in red squirrels

| Variable | Estimate ± SE | t | df | P  |
|----------|---------------|---|----|----|
| Intercept | 2.56 ± .11    | 23.7 | 166.4 | <.0001 |
| Mast (yes) | .41 ± .13    | 3.1 | 18.4 | .006 |
| Birth cohort (mast) | .06 ± .08 | .7 | 9.1 | .49 |
| Age | .29 ± .06 | 5.2 | 1,231.9 | <.0001 |
| Age² | -.04 ± .01 | -.49 | 1,218.1 | <.0001 |
| Grid (SU) | -.06 ± .05 | -.11 | 610.3 | .26 |

Note: Maternal age (years) was fitted as both a linear and quadratic term to account for a nonlinear effect of age on litter size. Differences between the two study areas is denoted by "grid (SU)," which represents the contrast between the SU study area and the KL study area (reference level). The fitted model was a general linear mixed effects model that included year, birth year, and squirrel identity as random effects. Degrees of freedom (df) were estimated based on a Satterthwaite approximation using lmerTest. The model was based on 1,462 observations from 673 squirrels from 28 birth years, breeding in 28 years. Random effects: among-squirrel variance ≈ 3.7, residual variance ≈ 5.4.

Table 4: Effects of a mast event in the current year, birth cohort (mast vs. nonmast), and maternal age on parturition date (day of the year) in red squirrels

| Variable | Estimate ± SE | t | df | P  |
|----------|---------------|---|----|----|
| Intercept | 140.5 ± 4.5 | 31.5 | 34.7 | <.0001 |
| Mast (yes) | 14.2 ± 9.8 | 1.5 | 25.8 | .16 |
| Birth cohort (mast) | -1.4 ± 1.6 | -.9 | 9.9 | .39 |
| Age | -15.1 ± 1.0 | -15.1 | 1,182.6 | <.0001 |
| Age² | 1.8 ± .1 | 12.2 | 1,226.7 | <.0001 |
| Grid (SU) | 3.7 ± .9 | 4.3 | 573.1 | <.0001 |

Note: Maternal age (years) was fitted as both a linear and a quadratic term to account for a nonlinear effect of age on parturition date. Differences between the two study areas is denoted by "grid (SU)," which represents the contrast between the SU study area and the KL study area (reference level). The fitted model was a general linear mixed effects model that included year, birth year, and squirrel identity as random effects. Degrees of freedom (df) were estimated based on a Satterthwaite approximation using lmerTest. The model was based on 1,480 observations from 676 squirrels from 28 birth years, breeding in 28 years. Random effects: among-squirrel variance ≈ 31.4, among-birth-year variance ≈ 6.1, among-year variance ≈ 387.2, residual variance ≈ 175.0.

Discussion

The predator satiation hypothesis proposes that the intermittent production of large amounts of seeds through mast ing has evolved as a mechanism to alternately starve and swamp seed predators (Janzen 1971; Silvertown 1980). This hypothesis is based on numerical declines in seed predator abundance between mast events and the saturation of the functional response (Solomon 1949; Holling 1959) of seed predators during mast events, thereby enhancing seed escape. Here we have shown that seed masting can also cause fluctuations in natural selection on seed predators. This fluctuating selection introduced an evolutionary load on seed predator populations, which further enhanced seed escape during mast events because traits in seed predators were adapted to common low-resource conditions and were therefore less prepared to capitalize on rare, resource-rich mast years.

Masting is characterized by several years of low seed production followed intermittently by years of very large seed production (Kelly and Sork 2002). As a result, seed predators frequently experience low-food nonmast years and rarely experience resource-rich mast years. In our system, red squirrel populations experienced five white spruce mast events during the past 30 years. Litter sizes in red squirrels appear to be fairly well adapted to nonmast years. During nonmast years, observed litter sizes (mean = 3.0 offspring) were only slightly less than optimum litter sizes ($\theta_{\text{nonmast}} = 3.4$), and there was only weak directional selection for larger litters, which is consistent with previous estimates of stabilizing selection on litter size in red squirrels around the population mean (Réale et al. 2003). Several explanations have been proposed for this common empirical finding of brood sizes that are smaller than those that would maximize offspring recruitment (Roff 1992). First, fitness costs manifested through fitness components other than offspring recruitment will cause optimum litter sizes on the basis of offspring recruitment to overestimate the true optimum. For example, an optimum litter size estimated on the basis of offspring recruitment might overestimate the true optimum if the production of larger litters reduces maternal survival (Moreau 1944; Charnov and Krebs 1974). However, previous litter size manipulations in red squirrels had no effect on maternal survival (Humphries and Boutin 2000). Second, it is possible that smaller litters maximize long-run fitness, despite lower annual fitness because of “bad-year effects” (Boyece and Perrins 1987). There is a high degree of generation overlap in red squirrels, and adult annual survival ($\sim 0.7$) is typically much higher than juvenile survival (0.26; McAdam et al. 2007), suggesting that arithmetic mean fitness likely provides a reasonable measure of what evolution maximizes in red squirrels (sensu Messina and Fox 2001). Both unmeasured fitness costs of larger litters and bad-year effects will result in an upward bias in optimum litter size relative to the true optimum. Ultimately, the degree to which
higher (to nonmast conditions. ARS suggest that red squirrel litter sizes are fairly well adapted to nonmast years. Nevertheless, the similarity between observed litter sizes and those that maximize ARS suggest that red squirrel litter sizes are fairly well adapted to nonmast years, they are well below the litter sizes that would have maximized offspring recruitment during resource-rich mast years, which represents a lag load (Maynard Smith 1976a) for red squirrels during mast years.

In contrast, optimum litter sizes were substantially higher ($\theta_{\text{opt}} = 5.2$ offspring) than observed litter sizes ($\bar{z}_{\text{litter size}} = 3.3$ offspring) during less common resource-rich mast years. This resulted in directional selection for larger litters during mast years. The episodic production of large amounts of cones by white spruce trees therefore results in fluctuations in the optimum litter size of red squirrels. While red squirrel litter sizes appear to be relatively well adapted to nonmast years, they are well below the litter sizes that would have maximized offspring recruitment during resource-rich mast years, which represents a lag load (Maynard Smith 1976a) for red squirrels during mast years.

Although mast years induced a lag load on red squirrels, mast years are in no way bad for red squirrel populations in an absolute sense. To satiate the ability of red squirrels to harvest spruce cones (Fletcher et al. 2010), trees synchronously produce very large numbers of cones (fig. 1A). This resource-rich environment allows for greatly increased juvenile recruitment (fig. 3), and populations grow dramatically during mast years ($\lambda_{\text{mast}} = 2.03$). Nevertheless, anything that lessens the magnitude of recruitment and population increase of red squirrels during a mast year will enhance the annual fitness of spruce trees through enhanced cone escape. So while mean fitness of red squirrels was much higher during a mast year, it was not as high as it would have been if the squirrels had been able to plastically produce even larger litters that matched the very large optimum litter size during mast years.

By measuring the effects of local squirrel density on annual cone escape by spruce trees, we were able to quantify the benefit to spruce trees of the lag load experienced by red squirrels during mast years. Regardless of how well ARS reflects true fitness in red squirrels, what matters to the annual fitness of spruce trees is the current population density of squirrels available to harvest cones, including newly recruited offspring. As a result, the production of litter sizes that were lower than those that would have maximized offspring recruitment will benefit spruce trees regardless of whether this represents maladaptation in red squirrels in the strict sense. The lag load that we documented for red squirrels during mast years benefits individual spruce trees because the number of spruce cones escaping squirrel predation was negatively related to the local density of red squirrels (table A2). Furthermore, mast years are particularly important for white spruce trees because most spruce recruitment is associated with mast events and the creation of appropriate seed-beds following wildfire (Peters et al. 2005). While our documented effects indicate that mastings induces a lag load on red squirrels, which has a meaningful consequence for the seed escape of spruce trees, we acknowledge that there will be high uncertainty in the magnitude of this effect when uncertainty is compounded across each analysis.

In addition to inducing natural selection on seed predators, mast events might also alter natural selection on seed attributes. For example, Clark’s nutcrackers (Nucifraga columbiana) only imposed selection on cone and seed traits of whitebark pine (Pinus albicaulis) when cone crops were large (Siepielski and Benkman 2007). Squirrels are generally considered to be effective dispersal seed predators, capable of suppressing tree recruitment and densities (Siepielski et al. 2000).

Table 5: Effects of current mast conditions and maternal mast conditions on the recruitment probability of juvenile red squirrels

| Variable                        | Estimate ± SE | z    | P     |
|---------------------------------|---------------|------|-------|
| Intercept                       | −1.93 ± .22   | −8.9 | <.001 |
| Sex (male)                      | −.63 ± .11    | −6.0 | <.001 |
| Maternal mast (yes)             | .02 ± .15     | 1    | .92   |
| Mast (yes)                      | 1.25 ± .45    | 2.8  | .006  |
| Study area (SU)                 | −.26 ± .13    | −2.0 | .04   |
| Maternal mast (yes) ×           | −.22 ± .38    | −.6  | .56   |

Note: For nominal fixed effects, the level corresponding to the parameter is specified. The fitted model was a generalized linear mixed effects model with a binomial error distribution and a logit link function. This model was based on 4,157 juveniles from 1,367 litters in 23 years. Residual deviance = 3,411.2, residual df = 4,149. Random effects: among-litter variance $\sigma^2 = 0.56$.

Table 6: Effects of current mast conditions, population size, and the proportion of the population that was born during a mast year on the population growth rate of red squirrels

| Variable                        | Estimate ± SE | t    | df  | P    |
|---------------------------------|---------------|------|-----|------|
| Intercept                       | 1.04 ± .13    | 7.8  | 26.58| <.001|
| Population size                 | −.004 ± .002  | −2.4 | 31.61| .02  |
| Mast (yes)                      | 1.38 ± .18    | 7.5  | 27.70| <.001|
| Proportion born                  | .23 ± .28     | .8   | 35.26| .41  |
| Study area (SU)                 | .001 ± .06    | .01  | 21.40| .99  |
| Mast (yes) × proportion born    | −1.03 ± .62   | −1.7 | 32.35| .11  |

Note: The analysis was based on 23 years of data (1994–2016) for each of two study areas. The identity of the study area was also fitted as a fixed effect. The model was fitted as a general linear mixed effects model. Degrees of freedom (df) were estimated based on a Satterthwaite approximation using lmerTest. This model was based on 46 observations in 23 years. Random effects: among-year variance $= 0.014$. 
and Benkman 2008) and acting as an agent of selection on seed attributes (Benkman et al. 2003; Molinari et al. 2006). Instead of heavily protecting seeds, white spruce cones ripen and release seed quickly, and we have previously found that red squirrels favor local synchrony of cone ripening in white spruce (Archibald et al. 2012). The degree to which red squirrels impose selection on cone and seed traits in white spruce and whether this differs between mast and nonmast years is, however, not currently known.

In addition to causing temporal changes in the optimum litter size, episodic mast events also introduced a temporal pattern to natural selection on litter size. Importantly, the frequency of mast events and the demography of red squirrels were such that parents and their offspring often experienced environments with different optimum litter sizes and parturition dates (i.e., parents that were born in mast years reproduced almost exclusively in nonmast years; fig. 4B). Both litter size and parturition date are heritable traits in this population (Réale et al. 2003), but we found no evidence of reduced individual fitness or a reduction in population growth rates associated with a mismatch in mast environments experienced by mothers and offspring. Possible feedbacks between ecology and evolution have attracted theoretical and empirical interest (Hairston et al. 2005; Pelletier et al. 2009; Ellner et al. 2011; Schoener 2011) but are challenging to document. Despite the moderately strong natural selection caused by mast events, the magnitude of evolutionary response to one generation of selection on these traits is small and undetectable. The intermittent nature of masting and breeding between cohorts of red squirrels also means that selection for larger litter sizes during mast years will not persist across more than one generation. Ecological effects on offspring recruitment and population growth rate were also very strong. Population size and the availability of mast seed crops (ecological effects) together explained more than 81% of the variation in population growth rates in these populations of squirrels, leaving little scope for evolutionary effects to have measurable effects on population dynamics under natural conditions. So while the population of squirrels experienced a lag load during mast years, we found no evidence that squirrels born during nonmast years experienced a greater lag load during mast years than squirrels born during mast years.

When environments and selection fluctuate within generations (i.e., fine-grained variation), evolutionary models predict reliance on shorter-term environmental cues of upcoming natural selection (Levins 1968; Leimar and McNamara 2015). Red squirrels partially tracked the increased optimum litter size during mast years through phenotypic plasticity. Mean litter sizes were significantly higher during mast years (3.3 offspring) than nonmast years (3.0 offspring; see also Boutin et al. 2006). Since most litters are conceived between January and May but cones produced in the current year are not consumed before mid-June (Boutin et al. 2013), the plastic increase in litter sizes during mast years was anticipatory of upcoming selection rather than a response to elevated food resources (Boutin et al. 2006, 2013). It is currently unclear how red squirrels anticipate upcoming cone production, but they do consume spruce buds (Fletcher et al. 2013), which have already differentiated as vegetative or reproductive buds (although not yet developed into cones) at the time of conception by red squirrels (Boutin et al. 2013). This anticipatory plasticity partially but not completely mitigated the lag load associated with increased optimum litter sizes during mast years. Thus, the large difference in optimum litter size between mast and nonmast years exceeded the tolerance of red squirrels to adjust litter sizes through plasticity (sensu Levins 1968). Following predictions by Levins (1968), red squirrel litter sizes were matched fairly well to nonmast optimum litter sizes, which were experienced much more frequently (p = 25/30 years) but were poorly matched to optimum litter sizes during mast years, which were experienced more rarely (1 − p = 0.17).

Two common ecological explanations for the benefits of a mast seeding strategy are numerical declines in seed predators resulting from multイヤ resource shortages and saturating functional responses generated by handling time constraints during brief resource pulses. Here we have shown evidence of resource-dependent population growth, which together with previous evidence of saturating functional responses in this study system (Fletcher et al. 2010; Archibald et al. 2012) confirms that mast seeding reduces squirrel density in low-resource nonmast years and enhances seed escape in high-resource mast years. However, here we have also provided evidence that fluctuations in optimum litter sizes of red squirrels associated with masting by white spruce causes a lag load in red squirrels. Plastic responses by squirrels to short-term environmental cues of upcoming shifts in optimum litter size allow them to partially mitigate this load. Despite this adaptive plasticity, offspring recruitment remained below that which would have been achieved had greater plasticity allowed squirrels to produce optimum litter sizes during mast years, which further enhanced seed escape by spruce trees during mast events. Although ecological consequences of intermittent mast seed production for seed predators likely remain the primary benefits of mast seed production (Kelly and Sork 2002), here we have provided evidence of an additional benefit to mast seed production. The production of several years of small seed crops can cause natural selection for more frugal life histories in seed predators, leaving them evolutionarily less prepared to take advantage of the additional resources available during more rare mast events. Optimum intermast intervals might therefore be shaped by both the ecological and the evolutionary responses of seed predators to intermittent mast seed production.
Acknowledgments

We thank Agnes MacDonald and her family for long-term access to her trapline and the Champagne and Aishihik First Nations for allowing us to conduct our work within their traditional territory. This research was funded by grants from the Natural Sciences and Engineering Research Council, the National Science Foundation, the Ontario Ministry of Research and Innovation, and Polar Knowledge Canada. We thank the many dedicated fieldworkers who helped to collect the data, A. Sykes and E. Anderson for careful data management, and M. Strimbas-Mackey for coding assistance. Thanks to K. Deasley for assistance with cone counting. R. Norris, J. Fryxell, A. Hendry, A. Newman, J. Travis, anonymous reviewers, and our laboratory groups provided helpful comments on the manuscript. This is a contribution number 97 in the Kluane Red Squirrel Project. The authors declare no competing financial interests. Statement of authorship: A.G.M. developed the concept for the article; S.B. initiated the long-term study and all authors collected the field data; A.G.M. analyzed the data and wrote the article with help from the other coauthors.

Literature Cited

Archibald, D. W., A. G. McAdam, S. Boutin, Q. E. Fletcher, and M. M. Humphries. 2012. Within-season synchrony of a masting conifer enhances seed escape. American Naturalist 179:536–544.

Benkman, C. W., T. L. Parchman, A. Favis, and A. M. Siepielski. 2003. Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. American Naturalist 162:182–194.

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

Bonnet, T., and E. Postma. 2018. Fluctuating selection and its (elusive) evolutionary consequences in a wild rodent population. Journal of Evolutionary Biology 31:572–586.

Boutin, S., A. G. McAdam, and M. M. Humphries. 2013. Antipaternity reproduction in squirrels can succeed in the absence of extra food. New Zealand Journal of Zoology 40:337–339.

Boutin, S., L. A. Wauters, A. G. McAdam, M. M. Humphries, G. Tosi, and A. A. Dhondt. 2006. Anticipatory reproduction and population growth in seed predators. Science 314:1928–1930.

Boyce, M., and C. Perrins. 1987. Optimizing great tit clutch size in a fluctuating environment. Ecology 68:142–153.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. 2nd ed. Springer, New York.

Burt, A. 1995. The evolution of fitness. Evolution 49:1–8.

Charnov, E. L., and J. R. Krebs. 1974. On clutch-size and fitness. Ibis 116:217–219.

Chevin, L.-M., M. E. Visser, and J. Tufto. 2015. Estimating the variation, autocorrelation, and environmental sensitivity of phenotypic selection. Evolution 69:2319–2332.

Cooper, E. B., R. W. Taylor, A. D. Kelley, A. R. Martinig, S. Boutin, M. M. Humphries, B. Dantzer, J. E. Lane, and A. G. McAdam. 2017. Personality is correlated with natal dispersal in North American red squirrels (Tamiasciurus hudsonicus). Behaviour 154:939–961.

Crossner, K. A. 1977. Natural selection and clutch size in the European starling. Ecology 58:885–892.

Dantzer, B., A. E. M. Newman, R. Boonstra, R. Palme, S. Boutin, M. M. Humphries, and A. G. McAdam. 2013. Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. Science 340:1215–1217.

Deasley, K. 2014. Red squirrels cause balancing selection on the length of white spruce cones. MSc thesis. University of Guelph, Ontario, Canada.

Descamps, S., S. Boutin, A. G. McAdam, D. Berteaux, and J.-M. Gaillard. 2009. Survival costs of reproduction vary with age in North American red squirrels. Proceedings of the Royal Society B 276:1129–1135.

Ellner, S. P., M. A. Geber, and N. G. Hairston Jr. 2011. Does rapid evolution matter? measuring the rate of contemporary evolution and its impacts on ecological dynamics. Ecology Letters 14:603–614.

Ellner, S. P., and N. G. Hairston Jr. 1994. Role of overlapping generations in maintaining genetic variation in a fluctuating environment. American Naturalist 143:403–417.

Eshel, I., and W. D. Hamilton. 1984. Parent-offspring correlation in fitness under fluctuating selection. Proceedings of the Royal Society B 222:1–14.

Fisher, R. A. 1930. The genetical theory of natural selection. Oxford University Press, Oxford.

Fletcher, Q. E., M. Landry-Cuerrier, S. Boutin, A. G. McAdam, J. R. Speakman, and M. M. Humphries. 2013. Reproductive timing and reliance on hoarded capital resources by lactating red squirrels. Oecologia 173:1203–1215.

Fletcher, Q. E., S. Boutin, J. E. Lane, J. M. LaMontagne, A. G. McAdam, C. J. Krebs, and M. M. Humphries. 2010. The functional response of a hoarding seed predator to mast seeding. Ecology 91:2673–2683.

Gomulkiewicz, R., and R. D. Holt. 1995. When does evolution by natural selection prevent extinction? Evolution 49:201–207.

Gomulkiewicz, R., and D. Houle. 2009. Demographic and genetic constraints on evolution. American Naturalist 174:E218–E229.

Grant, P., and B. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin’s finches. Science 296:707–711.

Hairston, N., S. Ellner, M. Geber, and T. Yoshida. 2005. Rapid evolution and the convergence of ecological and evolutionary time. Ecology Letters 8:1114–1127.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomologist 91:293–320.

Humphries, M. M., and S. Boutin. 2000. The determinants of optimal litter size in free-ranging red squirrels. Ecology 81:2867–2877.

Janzen, D. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2:465–492.

Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology Letters 7:1225–1241.

Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: why, how, where? Annual Review of Ecology and Systematics 33:427–447.

Kerr, T. D., S. Boutin, J. M. LaMontagne, A. G. McAdam, and M. M. Humphries. 2007. Persistent maternal effects on juvenile survival in North American red squirrels. Biology Letters 3:289–291.
Kingsolver, J. G., S. E. Diamond, A. M. Siepielski, and S. M. Carlson. 2012. Synthetic analyses of phenotypic selection in natural populations: lessons, limitations and future directions. Evolutionary Ecology 26:1101–1118.

Krebs, C. J., J. M. LaMontagne, A. J. Kenney, and S. Boutin. 2012. Climatic determinants of white spruce cone crops in the boreal forest of southwestern Yukon. Botany 90:113–119.

Kuznetsova, A., P. Bruun Brockhoff, and R. Haubo Bojesen Christensen. 2015. lmerTest: tests in linear mixed effects models. R package version 2.0-29. https://cran.r-project.org/web/packages/lmerTest/index.html.

Lack, D. 1947. The significance of clutch-size. I. Intraspecific variation. Ibis 89:302–352.

LaMontagne, J. M., and S. Boutin. 2007. Local-scale synchrony and variability in mast seed production patterns of Picea glauca. Journal of Ecology 95:991–1000.

LaMontagne, J. M., S. Peters, and S. Boutin. 2005. A visual index for estimating cone production for individual white spruce trees. Canadian Journal of Forest Research 35:3020–3026.

Lande, R. 1979. Quantitative genetic-analysis of multivariate evolution, applied to brain-body size allometry. Evolution 33:402–416.

Lande, R., and S. Arnold. 1983. The measurement of selection on correlated characters 37:1210–1226.

Lane, J. E., A. G. McAdam, and A. Charmantier. 2015. Post-weaning parental care increases fitness but is not heritable in North American red squirrels. Journal of Evolutionary Biology 28:1203–1212.

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

Leimar, O., and J. M. McNamara. 2015. The evolution of trans-generational integration of information in heterogeneous environments. American Naturalist 185:E55–E69.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, NJ.

MacColl, A. D. C. 2011. The ecological causes of evolution. Trends in Ecology and Evolution 26:514–522.

Maynard Smith, J. 1976a. What determines the rate of evolution? American Naturalist 110:331–338.

———. 1976b. A comment on the Red Queen. American Naturalist 110:325–330.

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

McAdam, A. G., S. Boutin, B. Dantzer, and J. E. Lane. 2019. Data from: Seed masting causes fluctuations in optimum litter size and lag load in a seed predator. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.j5s6h0.

McAdam, A. G., S. Boutin, A. K. Sykes, and M. M. Humphries. 2007. Life histories of female red squirrels and their contributions to population growth and lifetime fitness. Ecoscience 14:362–369.

Messina, F. J., and C. W. Fox. 2001. Offspring size and number. Pages 113–127 in C. W. Fox, D. A. Roff, and D. J. Fairbairn, eds. Evolutionary ecology. Oxford University Press, New York.

Mezey, J. G., and D. Houle. 2005. The dimensionality of genetic variation for wing shape in Drosophila melanogaster. Evolution 59:1027–1038.

Molinari, A., L. A. Wauters, G. Airolidi, F. Cerinotti, A. Martinoli, and G. Tosi. 2006. Cone selection by Eurasian red squirrels in mixed conifer forests in the Italian Alps. Acta Oecologica 30:1–10.

Moreau, R. E. 1944. Clutch-size: a comparative study, with special reference to African birds. Ibis 86:286–347.

Morrissey, M. B., and J. D. Hadfield. 2012. Directional selection in temporally replicated studies is remarkably consistent. Evolution 66:435–442.

Nienstaedt, H., J. Zasada, R. Burns, and B. Honkala. 1990. Pages 165–185 in Silvics of North America. Vol. I. Conifers. Picea glauca (Moench) Voss white spruce.

Nosil, P., R. Villoutreix, C. F. de Carvalho, T. E. Farkas, V. Soria-Carrasco, J. L. Feder, B. J. Crespi, and Z. Gompert. 2018. Natural selection and the predictability of evolution in Timema stick insects. Science 359:765–770.

Pelleiter, F., D. Garant, and A. Hendry. 2009. Eco-evolutionary dynamics. Philosophical Transactions of the Royal Society B 364:1483–1489.

Peters, V., S. Macdonald, and M. Dale. 2005. The interaction between masting and fire is key to white spruce regeneration. Ecology 86:1744–1750.

Phillips, P., and S. Arnold. 1989. Visualizing multivariate selection. Evolution 43:1209–1222.

Price, K., and S. Boutin. 1993. Territorial bequeathal by red squirrel mothers. Behavioral Ecology 4:144–150.

Rausher, M. D. 1992. The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. Evolution 46:616–626.

Rèale, D., D. Berteaux, A. G. McAdam, and S. Boutin. 2003. Lifetime selection on heritable life-history traits in a natural population of red squirrels. Evolution 57:2416–2423.

Roff, D. A. 1992. The evolution of life histories. Chapman & Hall, London.

Schoener, T. 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. Science 331:426–429.

Siepielski, A. M., and C. W. Benkman. 2007. Extreme environmental variation sharpens selection that drives the evolution of a mutualism. Proceedings of the Royal Society B 274:1799–1805.

———. 2008. Seed predation and selection exerted by a seed predator influence subalpine tree densities. Ecology 89:2960–2966.

Silvertown, J. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society 14:235–250.

Sinervo, B., E. I. Svensson, and T. Comendant. 2000. Density cycles and an offspring quantity and quality game driven by natural selection. Nature 406:985–988.

Smith, C., and S. Fretwell. 1974. The optimal balance between size and number of offspring. American Naturalist 108:499–506.

Solomon, M. E. 1949. The natural control of animal populations. Journal of Animal Ecology 18:1–35.

Thomson, C. E., and J. D. Hadfield. 2017. Measuring selection when parents and offspring interact. Methods in Ecology and Evolution 8:678–687.

Wade, M. J., and S. Kalisz. 1990. The causes of natural selection. Evolution 44:1947–1955.

Williams, C. T., J. E. Lane, M. M. Humphries, A. G. McAdam, and S. Boutin. 2014. Reproductive phenology of a food-hoarding mast-seed consumer: resource- and density-dependent benefits of early breeding in red squirrels. Oecologia 174:777–788.

Yang, L., J. Bastow, K. Spence, and A. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

Special Feature Editor: Joseph Travis