

Anticipatory Reproduction and Population Growth in Seed Predators

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Mast seeding, the intermittent, synchronous production of large seed crops by a population of plants, is a well-known example of resource pulses that create lagged responses in successive trophic levels of ecological communities. These lags arise because seed predators are thought capable of increasing reproduction and population size only after the resource pulse is available for consumption. The resulting satiation of predators is a widely cited explanation for the evolution of masting. Our study shows that both American and Eurasian tree squirrels anticipate resource pulses and increase reproductive output before a masting event, thereby increasing population size in synchrony with the resource pulse and eliminating the population lag thought to be universal in resource pulse systems.

The reproductive output of any species is constrained by the availability of resources required for offspring production. As a consequence, reproductive rates are often correlated with resources available before and during parental care (1–3). All basic consumer-resource population models portray consumer rates of increase as a function of current or past rather than future resource availabilities (4, 5). This has important ecological implications, including boom and bust consumer dynamics in systems characterized by intermittent resource pulses (6, 7).

Seed masting, the intermittent production of large seed crops by a population of plants, is a

well-known example of a resource pulse (7–9). There is growing evidence that the increased reproductive investment necessary for masting is an adaptive response by the plant rather than a simple resource-tracking strategy (8, 10). A widely cited evolutionary explanation for this phenomenon is predator satiation (8, 11). Seed consumers are forced into a starvation-saturation cycle whereby low resources before the masting event prevent the seed predator from increasing reproductive investment until after the resources have come and gone, creating a lagged population response. Although it would appear advantageous for seed predators to anticipate mast years by increasing reproduction and population growth before masting, doing so would require both a reliable cue signaling the upcoming mast event and the capacity to increase reproductive investment before the abundant food supply becomes available. Some insects use environmental cues to emerge in synchrony with seed masts (12, 13), and there are rare examples of vertebrate species using unknown cues to trigger onset of reproduction in mast years only (14, 15). Although many organisms initiate reproduction before regular seasonal resource peaks (16), irregular resource pulses represent a unique challenge to consumers, because they occur infrequently relative to

the generation time of consumers and future resource availability is often not correlated with current or past availability.

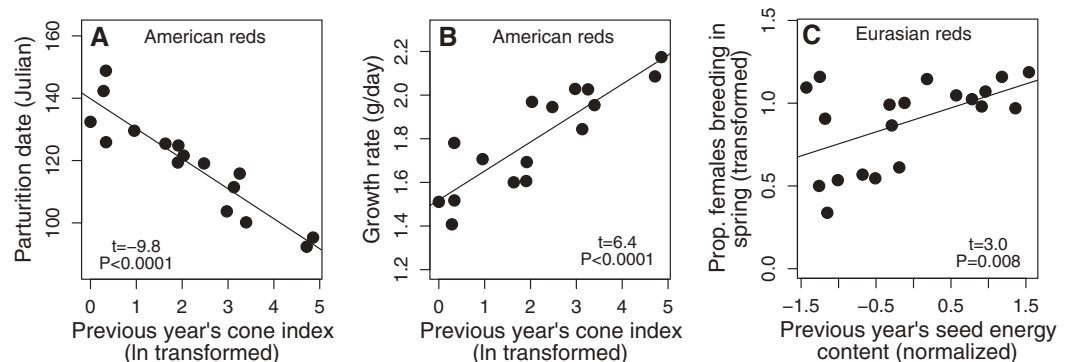
Here, we provide evidence that two species of seed predators do not follow a resource-tracking strategy but instead adjust reproductive investment according to future rather than past seed crops. We studied red squirrels (*Tamiasciurus hudsonicus*, hereafter American reds) in Yukon Canada and Eurasian red squirrels (*Sciurus vulgaris*, Eurasian reds) in Belgium and Italy (17). For American reds, we used complete enumeration to track population size, survival, and reproductive output of individual females in two control populations from 1989 to 2004 (17). For Eurasian reds, we used capture-recapture techniques to collect similar data for two populations in northern Belgium and for a single population in northern Italy over a 3- to 9-year period (17).

The natural history of American and Eurasian red squirrels suggests that they are part of a classic consumer-resource pulse system, the key elements being that the resource pulse (seed mast) is highly variable (fig. S1) and is not mature and consumed until autumn, well after the consumer has committed to reproductive investment for that year (17). As a consequence, increased reproductive investment and population growth would not be expected to occur until the following spring, when females enter the breeding season in good condition after having fed on abundant seeds all winter (18). Thus, if red squirrels respond in the manner typical of consumer-resource pulse systems, we would expect reproduction to be constrained by seasonal resource limitation before a masting event but enhanced in the year after the masting event. We found limited evidence for this. For American reds in years after high seed production, females responded by breeding earlier and raising faster-growing offspring than in years after low seed production (Fig. 1, A and B), but the proportion of yearling females breeding and the litter size were not correlated with the previous year's seed crop (table S1). In Eurasian reds, only the proportion of females producing spring litters (Fig. 1C) was positively correlated with food abundance in the previous year, whereas litter

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Fig. 1. Red squirrel life history characteristics that responded to the previous year's food abundance [indexed by cones or seed energy content (17)]. In American reds, parturition date (A) was advanced and juvenile growth rates (B) were higher after years of high cone production. In Eurasian reds, the proportion of females producing spring litters (C) was higher after years of high food abundance. Values shown are yearly averages, and proportions are arcsine square root transformed. See table S1 for statistical results.



size and the proportion of females producing a summer litter were not (table S1).

Reproductive investment was, however, correlated with future seed production (seed production in the current year but not available for consumption until after females have completed the bulk of their reproductive investment). American reds gave birth to larger litters in advance of high food production (Fig. 2A) and were more likely to breed as yearlings (Fig. 2B). The most striking effect was that females produced a second litter after a successful first litter (the equivalent of summer litters in Eurasian reds) in advance of high food production (Fig. 2C). In most cases, females were still lactating with the first litter when they conceived the second (litter one young were 35 to 87 days old, and weaning occurs at 70 days of age), suggesting that the normal physiological inhibition of ovulation by lactation characteristic of mammals (19) had been circumvented. These increases in reproductive effort when taken together resulted in a higher average number of offspring produced per female in advance of high food production (Fig. 2D). In Eurasian reds, summer litters were produced in all years, but the proportion of females doing so was positively correlated with future food abundance (Fig. 2E), as was summer litter size (Fig. 2F). In both species, none of these breeding parameters were correlated with the previous year's food abundance (table S1).

The ability to adjust reproductive output to match future food resources has the potential to alter typical lagged responses between the availability of food resources and the growth of consumer populations. In contrast to assumptions of resource-consumer population models, the summer population growth rates of both American and Eurasian reds were not correlated

with the abundances of food produced the previous autumn (table S1). Instead, summer population growth rates were correlated with future food production (Fig. 3). This increased population growth before the maturation of the seed crop means that population size reached a maximum when the seed crop reached maturity in autumn. These results show that the temporal lag in population growth rate, common to consumer-resource pulse systems, can be circumvented through anticipatory reproductive investment.

The collective anticipatory reproductive responses observed in both systems represent a departure from the simple resource-tracking strategy characteristic of consumers in resource pulse systems. This raises two important questions. First, what cues do American and Eurasian red squirrels use to predict upcoming resources? We can rule out previous food abundance, because seed crop in the previous year was not correlated with seed crop in the current year (for American reds, the relevant statistics are $r = -0.07$, $t_{14} = -0.28$, and $P = 0.78$; for Eurasian reds, they are $r = -0.24$, $t_{18} = -1.0$, and $P = 0.32$). Other studies have suggested that visual (20) or chem-

ical (21) stimuli, possibly linked to reproductive structures [buds, flowers, pollen cones (15)], can trigger onset of reproduction. These structures are also good cue candidates for American and Eurasian reds, because they are consumed by squirrels (17) and are present in advance of and may be correlated with the size of the forthcoming seed crop (22).

The second question is how American and Eurasian reds increase reproductive investment during what has been considered a seasonal resource bottleneck in other consumer-resource pulse systems. One possibility is that the squirrels are in fact following a resource-tracking strategy but that the resource being tracked is an alternative energy source whose abundance is correlated to the upcoming seed crop (23). Immature reproductive structures of trees are unlikely candidates, because they are only consumed in quantity when seed is not available and do not differ in energetic value from vegetative buds, which are always superabundant (24, 25). American reds given buds in feeding trials lost weight (24); in the case of Eurasian reds, daily energy intake was low, time spent active in-

Fig. 3. Summer population growth rates of American (A) and Eurasian (B) reds were positively correlated to future food supply. Values are weekly rates measured between spring and autumn censuses (17).

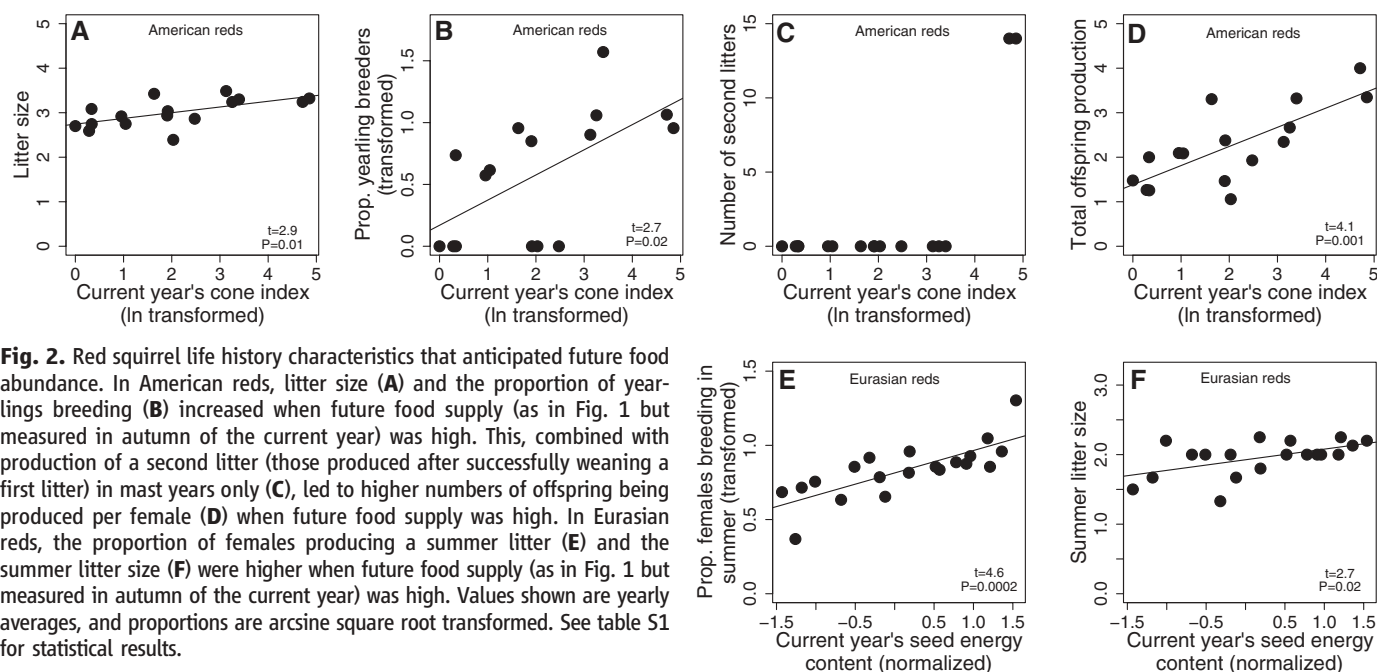
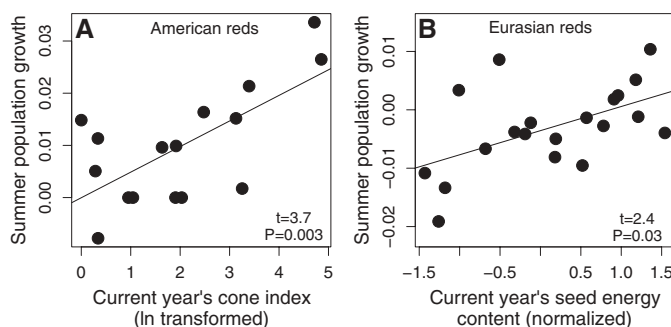


Fig. 2. Red squirrel life history characteristics that anticipated future food abundance. In American reds, litter size (A) and the proportion of yearlings breeding (B) increased when future food supply (as in Fig. 1 but measured in autumn of the current year) was high. This, combined with production of a second litter (those produced after successfully weaning a first litter) in most years only (C), led to higher numbers of offspring being produced per female (D) when future food supply was high. In Eurasian reds, the proportion of females producing a summer litter (E) and the summer litter size (F) were higher when future food supply (as in Fig. 1 but measured in autumn of the current year) was high. Values shown are yearly averages, and proportions are arcsine square root transformed. See table S1 for statistical results.

creased, and body mass was lower when squirrels were feeding on these items as compared with feeding on seed (26, 27). Lastly, food supplementation experiments of American reds have failed to produce increases in litter size or a second litter, providing strong evidence that the increased reproductive investment observed in our study cannot be triggered by increased energy availability alone (17, 28, 29). We hypothesize that, rather than following a resource-tracking strategy where reproductive investment is determined by current resource amounts, reproductive rates are driven by future fitness payoffs. During years of low seed production, competition among juveniles for available resources is intense, and, although litter augmentation experiments in American reds show that females are capable of supporting larger litters (30), they refrain from doing so because offspring recruitment is low (30). However, when mast years occur, competition among juveniles is reduced, and females produce more offspring, which successfully recruit into the population (31, 32). Further, the increased production of young by females in mast years does not come with any obvious cost to the female, because overwinter survival is not reduced after years of increased reproductive investment (for American reds, offspring production in the previous year versus proportion of adult females surviving to spring has slope = -0.023 ± 0.034 , $t_{15} = -0.7$, and $P = 0.51$; for Eurasian reds, proportion of estrous females in the previous year versus adult female survival to spring has slope = 0.37 ± 0.27 , $t_{15} = 1.4$, and $P = 0.19$).

If masting has evolved as a swamp-and-starve adaptation against seed predation, then anticipatory reproduction and population growth represent a potent counteradaptation by the predators. Given that increased reproductive output in these systems coincides with low current but high future resources, our results suggest that reproductive investment in these systems is more responsive to future fitness prospects than present energetic constraints. The evolution of seed masting in trees is also driven by the survival prospects for progeny rather than simple resource tracking, suggesting an intriguing parallel in reproductive strategies of trees and the predators that consume their seed.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/314/5807/1928/DC1
Materials and Methods

SOM Text

Fig. S1

Table S1

References

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Human Catechol-*O*-Methyltransferase Haplotypes Modulate Protein Expression by Altering mRNA Secondary Structure

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Catechol-*O*-methyltransferase (COMT) is a key regulator of pain perception, cognitive function, and affective mood. Three common haplotypes of the human *COMT* gene, divergent in two synonymous and one nonsynonymous position, code for differences in COMT enzymatic activity and are associated with pain sensitivity. Haplotypes divergent in synonymous changes exhibited the largest difference in COMT enzymatic activity, due to a reduced amount of translated protein. The major *COMT* haplotypes varied with respect to messenger RNA local stem-loop structures, such that the most stable structure was associated with the lowest protein levels and enzymatic activity. Site-directed mutagenesis that eliminated the stable structure restored the amount of translated protein. These data highlight the functional significance of synonymous variations and suggest the importance of haplotypes over single-nucleotide polymorphisms for analysis of genetic variations.

The ability to predict the downstream effects of genetic variation is critically important for understanding both the evolution of the genome and the molecular basis of human disease. The effects of non-synonymous polymorphisms have been widely characterized; because these variations

directly influence protein function, they are relatively easy to study statistically and experimentally (1). However, characterizing polymorphisms located in regulatory regions, which are much more common, has proved to be problematic (2). Here, we focus on the mechanism whereby polymorphisms of the catechol-*O*-methyltransferase (*COMT*) gene regulate gene expression.

COMT is an enzyme responsible for degrading catecholamines and thus represents a critical component of homeostasis maintenance (3). The human *COMT* gene encodes two distinct proteins: soluble COMT (S-COMT) and membrane-bound COMT (MB-COMT) through the use of alternative translation initia-

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