

Research



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Mast seeding promotes evolution of scatter-hoarding

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Many plant species worldwide are dispersed by scatter-hoarding granivores: animals that hide seeds in numerous, small caches for future consumption. Yet, the evolution of scatter-hoarding is difficult to explain because undefended caches are at high risk of pilferage. Previous models have attempted to solve this problem by giving cache owners large advantages in cache recovery, by kin selection, or by introducing reciprocal pilferage of 'shared' seed resources. However, the role of environmental variability has been so far overlooked in this context. One important form of such variability is masting, which is displayed by many plant species dispersed by scatterhoarders. We use a mathematical model to investigate the influence of masting on the evolution of scatter-hoarding. The model accounts for periodically varying annual seed fall, caching and pilfering behaviour, and the demography of scatterhoarders. The parameter values are based mostly on research on European beech (*Fagus sylvatica*) and yellow-necked mice (*Apodemus flavicollis*). Starvation of scatterhoarders between mast years decreases the population density that enters masting events, which leads to reduced seed pilferage. Satiation of scatterhoarders during mast events lowers the reproductive cost of caching (i.e. the cost of caching for the future rather than using seeds for current reproduction). These reductions promote the evolution of scatter-hoarding behaviour especially when interannual variation in seed fall and the period between masting events are large.

This article is part of the theme issue 'The ecology and evolution of synchronized seed production in plants'.

1. Introduction

Masting, or periodic, synchronized production of abundant seed crops, is a common reproductive strategy of many plants [1,2] and a classic example of a pulsed resource [3,4]. Masting provides foundational, yet unstable resource levels, creating cycles of feast and famine in food webs [5]. These cycles strongly influence the behaviour and life-history strategies of consumers. For example, animals migrate to track populations of masting plants [6], enter diapause to survive lean periods between mast events [7] and increase reproduction in anticipation of masting [8,9]. However, despite decades of research, many impacts of masting on consumers remain poorly understood [5]. Here, we use a mathematical model to show that masting can play an important but overlooked role in the evolution of a widespread animal behaviour: scatter-hoarding.

Scatter-hoarding is defined as caching seeds for future consumption in many small, widely dispersed caches [10]. This caching strategy is used by numerous species of animals, most notably by rodents and corvids [11–13]. Scatterhoarders provide essential seed dispersal services in many ecosystems throughout the world. According to a recent review, there are 1279 species of plants known to rely on this mode of seed dispersal, although this number is certainly underestimated [13]. However, even though scatter-hoarding is so widespread, the evolutionary advantage of this behaviour is not obvious

because the caches are undefended and often suffer very high rates of pilferage [14–17]. Thus, scatter-hoarding appears vulnerable to cheating by non-caching pilferers [18–20].

First attempts to solve this problem focused on the role of the owner's advantage. According to a model by Andersson & Krebs [18], scatter-hoarding can evolve when cache owners are substantially more likely to recover caches than are naive foragers. Empirical estimates of the owner advantage vary widely but appear relatively high in scatter-hoarding birds (particularly those that rely on specialized spatial memory: e.g. [21]) and quite low in mammals. In most studies on rodents, cache owners are only two to four times more likely to recover their caches when compared with naïve individuals ([22–29]; see also [30]). In many systems, the owner's advantage appears to be insufficient to prevent substantial cache loss to pilferage (2–30% lost per day, according to a review by [20], though this rate might vary depending on environmental characteristics like soil moisture: [31]).

A later model by Vander Wall & Jenkins [20] suggested that caching can represent an adaptive, stable strategy when all caches are reciprocally pilfered by scatter-hoarding animals with overlapping home ranges (see also [19]). Under this scenario, caches represent a collective resource used by selfish individuals [20]. The reciprocal pilferage hypothesis predicts that animals are unlikely to avoid pilferage, but can compensate for it by pilfering caches of other individuals. As a corollary, individuals should invest in their pilfering tactics rather than in theft-reducing strategies (but see e.g. [32–38] for examples of potentially costly behaviours aimed to reduce pilferage).

Environmental variability represents an additional, potent mechanism for scatter-hoarding that has been largely overlooked in the existing models. Such variability is pervasive in ecosystems dominated by plants that produce scatterhoarder-dispersed fruits because such plants usually show pronounced masting [39,40]. Examples of scatterhoarder-dispersed masting plants can be found in the tropics [41,42], deserts [43,44] and in temperate zones [45–48]. While studies of masting have often emphasized the benefit of masting to plants in terms of reduced *per capita* seed predation ('predator satiation': [1]), masting also has important effects on consumer population dynamics that can feedback to affect the evolution of caching. In particular, the cycles of satiation and starvation induce striking fluctuations in consumer population size [3,4,49]. Typically, masting triggers a temporary increase in consumer population size followed by a pronounced crash. Thus, when the next mast year comes, seed to consumer ratios is particularly high [1,3].

We use a mathematical model to investigate the influence of mast-related fluctuations in scatterhoarder population size on the evolution of scatter-hoarding. The model mimics interactions between a masting tree and a scatter-hoarding rodent. The scatterhoarders consume or cache harvested seeds and pilfer or recover their own caches over years that differ in both the magnitude of seed fall and the number of competing consumers. Previous models demonstrated that caching is influenced by the owner's advantage in cache recovery and the probability that scatterhoarders survive long enough to use the caches [18–20]. However, both the proportion of recovered seeds and scatterhoarder survival depend on the magnitude of seed fall and the resulting fluctuations in population size [16,50,51]. Thus, we expand on previous models by including the effects of environmental variability resulting from mast seeding on caching behaviour. We do this by

treating the proportion of seeds that are cached, rather than immediately consumed, as an evolving trait and examining how the evolutionarily stable strategy of this caching behaviour varies with: (i) masting intensity, (ii) the frequency of mast years, (iii) the owner's advantage in cache recovery, and (iv) the survival of scatterhoarders. Our results demonstrate that mast-related fluctuations in scatterhoarder population size reduce both the risk of cache loss to pilferers and the reproductive cost of caching (i.e. the cost of caching seeds for future use rather than using seeds for current reproduction), thus promoting the evolution of scatter-hoarding.

2. Methods

(a) Modelling approach

We consider a population of scatterhoarders that experience three distinct periods of seed availability in each year: autumn, winter/spring and summer. During the autumn, seeds become available, and scatterhoarders gather and either immediately consume or cache them. Energy from consumed seeds contributes to reproduction while cached seeds may be recovered for use during the subsequent winter/spring. During the winter/spring, scatterhoarders are sustained by seeds from their own caches or seeds they pilfer from the caches of other scatterhoarders. As caching behaviour may not always be favoured, we implicitly assume the availability of other winter resources that prevent population extirpation. During the summer, scatterhoarders survive and reproduce using resources other than seeds. Caching behaviour for an individual is represented by the threshold T , such that the individual consumes up to T seeds during the autumn and caches the rest. We determine the conditions under which caching behaviour is favoured by solving for the evolutionary stable strategy (ESS) of T . The central conundrum is that the strategy of scatter-hoarding appears vulnerable to cheating by non-caching pilferers, who may invade the population and outcompete caching individuals. If the population is monomorphic for a particular caching threshold, then this threshold value is an ESS if this population cannot be invaded (outcompeted) by individuals with any other threshold value.

(b) Model description

During autumn (period 1), there is a seed fall of $S(t)$ from the primary seed source. Seeds are gathered at a rate proportional to the density $n_1(t)$ of scatterhoarders during this period. The proportionality constant a_1 corresponds to the *per capita* (i.e. per scatterhoarder) seed harvest rate. Seeds are also lost to other sources (e.g. competitors, germination, decay, etc.) at a rate of L_1 . If all seeds are gathered or lost to other sources by the end of the autumn, then the amount of seed gathered per individual equals:

$$G(t) = \frac{a_1 S(t)}{L_1 + a_1 n_1(t)}.$$

All seeds above a threshold, T , are cached by individuals for later in the year. The seeds which are not cached, $\min\{G(t), T\}$, are used for survival and reproduction. The number of offspring produced by an individual, $R_1(t)$, at the end of the autumn is a saturating function of $\min\{G(t), T\}$, with a maximal number of offspring b and a half-saturation constant h (i.e. h is the amount of resources required to produce $b/2$ offspring). The fraction of adults surviving from the first period (autumn) to the second period of the year (winter/spring) equals s_1 . Thus, the total density $n_2(t)$ of individuals entering winter/spring equals:

$$n_2(t) = [R_1(t) + s_1]n_1(t) \text{ where } R_1(t) = \frac{b \min\{G(t), T\}}{h + \min\{G(t), T\}}.$$

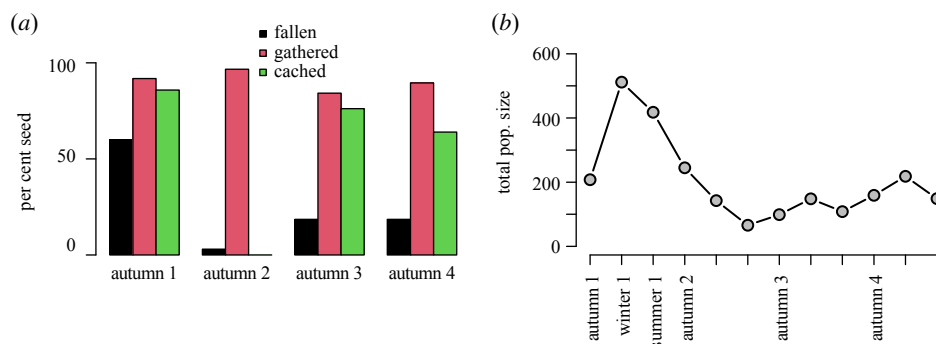


Figure 1. The annual dynamics of autumn seeds (a) and seasonal population dynamics (b) when masting years occur every 4 years. Both (a) and (b) correspond to a stable, periodic solution of the model. In (a), the per cent of seeds that fall each year from all of the seeds in 4 year masting intervals years are plotted as black bars; the first year corresponds to the masting year that is followed by years of lower seed fall. The per cent of fallen seed that are gathered each year correspond to the red bars, while the per cent of gathered seed that is cached are the green bars. In (b), the total population densities vary intra- and inter-annually; the highest densities occur in the winter/spring period of the masting year after which the population densities crash to lower densities. Parameter values as described in the main text with a sixfold owner's advantage in cache recovery. (Online version in colour.)

The main resource available to individuals during winter/spring is the total size of seed caches $\max\{G(t) - T, 0\}n_1(t)$. Cache owners who survived gather their cached seed at a rate proportional to the size of their seed caches. This proportionality constant a_2 corresponds to the *per capita* rediscovery and use rate of their caches. All other individuals are assumed to pilfer seed from others' caches at a *per capita* rate a_{pil} . Seeds are lost to other sources at a rate of L_2 . If all cached seeds are gathered or lost by the end of winter/spring, then the fraction of caches recovered by its owner given that the owner survived from autumn to winter/spring is:

$$M(t) = \frac{a_2}{L_2 + a_2 + a_{pil}(n_2(t) - 1)},$$

while the fraction of caches that was pilfered by each non-owner is:

$$O(t) = \frac{a_{pil}}{L_2 + a_2 + a_{pil}(n_2(t) - 1)}.$$

For seed caches whose owner died, the fraction that was recovered by a living non-owner is:

$$D(t) = \frac{a_{pil}}{L_2 + a_{pil}n_2(t)}.$$

The total amount of cached seed gathered by a surviving individual from autumn is the amount of seed recovered from its own caches plus the amount of seeds pilfered from the caches of other surviving individuals and the caches of deceased individuals:

$$C_{\text{survivor}}(t) = \max\{G(t) - T, 0\}[M(t) + O(t)(s_1n_1(t) - 1) + D(t)(1 - s_1)n_1(t)].$$

Because individuals that were born at the end of the autumn had no opportunity to cache, the total amount of cached seed gathered by these individuals in the spring/winter is only the amount pilfered from the caches of either surviving or deceased individuals:

$$C_{\text{new}}(t) = \max\{G(t) - T, 0\}[O(t)s_1n_1(t) + D(t)(1 - s_1)n_1(t)].$$

If s_2 is the fraction of individuals surviving to summer (period 3), then the density of individuals entering summer equals

$$n_3(t) = [R_2(t) + s_2]n_2(t),$$

where $R_2(t)$ is the population-level *per capita* fecundity corresponding to the weighted combination of reproductive contributions of

individuals surviving from autumn and new individuals born at the end of autumn (for simplicity, we assume the same value of h for surviving and newborn individuals):

$$R_2(t) = \frac{b C_{\text{survivor}}(t)}{h + C_{\text{survivor}}(t)} \frac{s_1}{R_1(t) + s_1} + \frac{b C_{\text{new}}(t)}{h + C_{\text{new}}(t)} \frac{R_1(t)}{R_1(t) + s_1}.$$

During this final period of the year (summer), individuals rely on other resources with availability A to reproduce and survive with probability s_3 (these resources represent alternative foods, such as fungi, invertebrates or seeds of other plant species; adjusted to obtain population dynamics consistent with patterns observed in the field). Thus, the density of individuals entering the autumn of the next year equals

$$n_1(t + 1) = [R_3(t) + s_3]n_3(t),$$

where $R_3(t)$ is the *per capita* reproduction. We model this *per capita* reproduction using a Beverton–Holt function:

$$R_3(t) = \frac{\beta}{1 + \alpha n_3(t)},$$

where β is the maximal summer fecundity and α determines the strength of intraspecific competition. By composing the equations across the three periods of the year, the yearly update rule for population densities at the beginning of autumn is $n_1(t + 1) = [R_3(t) + s_3][R_2(t) + s_2][R_1(t) + s_1]n_1(t)$.

We modelled seed fall $S(t)$ in the autumn as a periodic function of time where the period P corresponds to the time between masting years. In the masting years, $S(t) = S_{\text{high}}$, next year $S(t) = S_{\text{min}}$ (typically, seed crops produced after mast years are particularly scant: [52,53]), then $S(t) = S_{\text{low}}$ until another mast year. Our analysis assumes that the average seed output, $(S(1) + S(2) + \dots + S(P))/P$, is fixed and what varies is the proportion of total seed output in the masting year. Higher intensity of masting means more seeds during the masting year, but concomitantly fewer seeds in other years (as opposed to just increasing seed output in masting years with no effect on seed production in other years). Similarly, when we vary the number of years between masting events, the average seed output remains the same (i.e. longer intermast interval corresponds to higher seed production in mast years).

Figure 1 illustrates the typical dynamics of the model for the baseline parameters described below. In this figure, seed masting occurs every 4 years (figure 1a) and leads to a stable, 4-year population cycle (figure 1b). Population densities (figure 1b) exhibit seasonal as well as yearly variation. Highest densities are reached at the end of the masting year (year 1) and crash

to low densities in the ensuing years (years 2–4). For lower caching thresholds, caching occurs in all years except the year after a masting event (green bars in figure 1a). Table A1 in the electronic supplementary material, Appendix A lists all parameters for the model and their meaning.

(c) Model parameters

The parameter values are based mostly on research on European beech (*Fagus sylvatica*) and yellow-necked mice (*Apodemus flavicollis*). *Apodemus* mice are among the most important seed predators and scatterhoarders in Eurasia (e.g. [38,54–56]). While we found it useful to base our parameter estimates on a specific, reasonably well-studied system, we also performed a global sensitivity analysis for our main conclusions (electronic supplementary material, Appendix B). Specifically, for each of main results, we reran the simulations 100 times with each parameter, call it x , chosen independently from a uniform distribution on the interval $[x/1.5, 1.5x]$.

The parameters a_1 and L_1 (per capita harvest rate and seed loss) may be reduced to the single parameter L_1/a_1 . Rearranging the equation for the amount of seeds gathered G yields $L_1/a_1 = (1 - G/S_0)n_1/(G/S_0)$. The parameters n_1 and n_2 were taken to be the average species-wide density for *A. flavicollis*: 17.7 individuals ha^{-1} [57]. Estimates of the proportion of seeds removed from the forest floor (G/S_0) tend to be variable with Zwolak *et al.* [16] reporting 78% seed removal during mast years and 91% seed removal during non-mast years for *A. flavicollis*, and Le Louarn & Schmitt [58] reporting 61% and 74% seed removal by *Apodemus sylvaticus* during two different years. We selected the average value of 76% as our estimate of seed removal. Thus, $L_1/a_1 = 5.59$. In all cases where L_1 and a_1 were treated as separate parameters, we used $a_1 = 1$ and set L_1 equal to our choice for L_1/a_1 .

The parameters a_{pil} and L_2 may similarly be reduced to L_2/a_{pil} . Zwolak *et al.* [16] estimated the recovery of seeds from artificial caches to be 54% during non-mast years and 5% during mast years, which we assumed to be roughly equivalent to the proportion of seeds recovered from an abandoned cache ($D/\max(G(t) - T, 0)$). We then estimated L_2/a_{pil} to be between 15.1 and 336.3. In our analysis, we set this value to the upper end of this range (300) as this leads to more conservative estimates of when caching evolves. In all cases where L_2 and a_{pil} were treated as separate parameters, we used $a_{pil} = 1$ and set L_2 equal to our choice for L_2/a_{pil} .

We let $a_2 = 3$ (when $a_{pil} = 1$). This value approximates the results of several studies on scatter-hoarding rodents [25–28] that documented seed removal rates by cache owners and naïve foragers. However, we explored scenarios with both higher and lower cache owner's advantage (see Results).

We assumed a maximum litter size of 11 individuals [59], with one breeding event per period (2–3 litters per year: [60]). Assuming that half the population are female and half of the individuals born are female, this yields $b = 5.5$.

The half-saturation constant for mid-year reproduction (h) was set as 124 seeds offspring $^{-1}$ multiplied by half the maximum number of offspring (b). This value was calculated on the basis of energy contents of beech seeds [61], energy requirements of yellow-necked mice (0.60 kcal g^{-1} : [62]; average body mass of yellow-necked mice is 28.3 g: AnAge) and typical costs of reproduction-related energy expenditure in small mammals (25% increase in energy expenditure during gestation and 200% increase during lactation: [63–67], given the length of gestation and lactation in yellow-necked mice (26 and 22 days, respectively: AnAge). Note that the link between food availability and reproduction limits winter breeding to masting events (which are known to result in winter reproduction in our and related study systems: [50,62,68,69]).

We used 77.5% as the yearlong monthly survival rate (calculated from data on winter survival in [50]: see also [62] for similar

values). We assumed that each period lasts four months, yielding $0.775^4 = 36.1\%$ as the survival rate for each period (s_1 , s_2 and s_3). Winter survival rates in Pucek *et al.* [50] are similar to monthly summer survival rates reported or calculated from other studies (e.g. [70,71]), thus we assumed equal survival across all seasons in our initial scenario, but examined how relaxing this assumption affects caching rates (see Results).

In principle, food availability affects both reproduction and survival in a manner that depends on life-history allocation. That is, an organism can allocate most of its energy budget to enhanced survival or enhanced reproduction, or a blend of the two. Predicting this life-history allocation is complex [72], thus rather than attempt to predict the optimal allocation (which should depend on optimal caching and vice versa), we draw on the natural history of the system to argue that as a first pass, it is more important to examine how food consumption affects fecundity as opposed to survival. An increase in food consumption clearly increases fecundity. By contrast, we assume that the consumer has alternative food sources (see above) that are sufficient to allow it to survive adequately even if it does not allocate any additional energy from the focal seed source towards survival. We further assume that allocating extra energy to increased survival is not very effective (in our system) because survival also depends heavily on predation, disease, etc. [73]. In this scenario, survival depends little on the amount of the focal seed source consumed. This is also in line with numerous empirical studies reporting that rodents allocate extra energy to increase reproductive output rather than survival (meta-analysed by [74]). In addition, a critical point for relating food to demography is that in short-lived, fecund animals such as rodent scatterhoarders, elasticity for survival is low whereas elasticity for reproduction is higher [75], which means that even if survival does vary, this variation does not affect population growth as much as do changes in reproduction. Accordingly, we focus on effects of food on reproduction and simplify the analysis by assuming that survival is a parameter that is constant across years. However, we do vary survival across all years (see Results).

(d) Numerical methods

To identify the evolutionary stable caching strategies, we examined whether a small mutant subpopulation using the caching threshold T_m can invade a resident population using the caching threshold T . When the mutant subpopulation densities $m_i(t)$ in each of the periods $i = 1, 2, 3$ are sufficiently small, the effect of the mutant population on the resident population and itself is negligible. Hence, the dynamics of the mutant in the initial phase of invasion can be approximated by the mutant's growth rate when the population is composed entirely of residents. We now describe these dynamics.

As the mutant and resident individuals only differ in their caching strategy, the amount of seeds gathered in year t by a mutant individual equals the amount of seeds gathered $G(t)$ by a resident individual. As for the resident dynamics, yearly update of the mutant's autumn density is of the form

$$m_1(t+1) = [Q_3(t) + s_3][Q_2(t) + s_2][Q_1(t) + s_1]m_1(t),$$

$Q_1(t)$ corresponds to the number of offspring produced by a mutant individual during the autumn and only differs from the resident in its threshold T_m :

$$Q_1(t) = \frac{b \min\{G(t), T_m\}}{h + \min\{G(t), T_m\}},$$

$Q_2(t)$ corresponds to the number of offspring produced by a mutant individual during the winter/spring given by a weighted combination owing to the fraction of individuals that survived from the autumn and individuals born in the autumn:

$$Q_2(t) = \frac{b C_{m,\text{survivor}}(t)}{h + C_{m,\text{survivor}}(t)} \frac{s_1}{Q_1(t) + s_1} + \frac{b C_{\text{new}}(t)}{h + C_{\text{new}}(t)} \frac{Q_1(t)}{Q_1(t) + s_1},$$

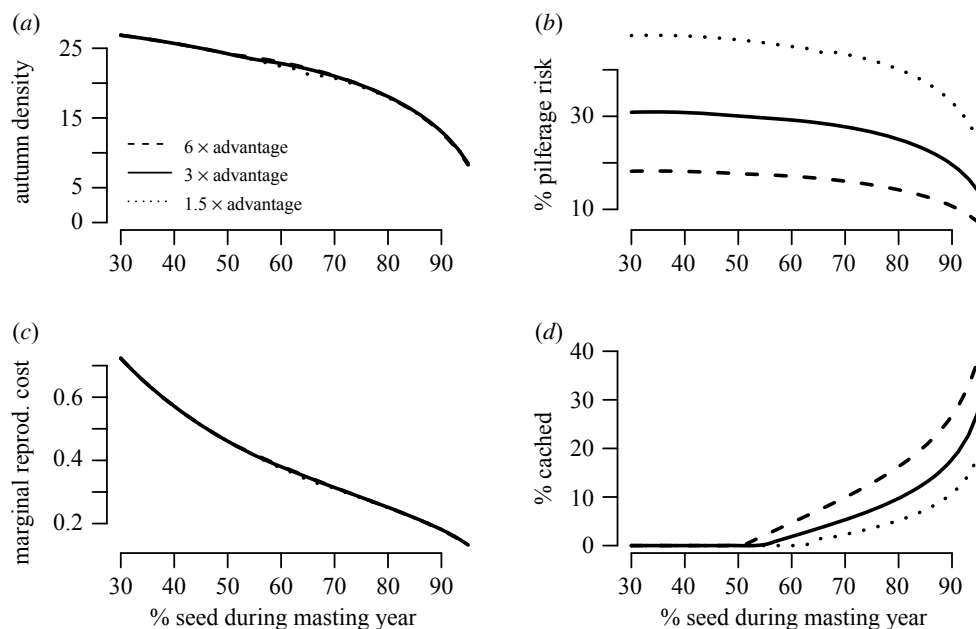


Figure 2. Mast year autumn population density in individuals ha^{-1} (a), pilferage risk, defined as the probability that cached seed would be pilfered (b), marginal reproductive costs of caching (c), and proportion of seeds cached rather than eaten (d) as a function of masting intensity (expressed as the percentage of total seed production that occurs during mast years), with mast occurring every fourth year. Dashed, solid and dotted lines represent the magnitude of owner's advantage in cache recovery (owners 6, 3 and 1.5 times more likely to discover their own caches relatively to naïve foragers). All dependent variables are given at the evolutionary stable caching strategy and its associated periodic population dynamics.

where $Q_2(t)$ differs from $R_2(t)$ only in its first term owing to surviving individuals with the mutant caching strategy: $C_{m,survivor}(t) = \max\{G(t) - T_m, 0\}M(t) + \max\{G(t) - T, 0\}[O(t)(s_1n_1(t) - 1) + D(t)(1 - s_1)n_1(t)]$. Finally, the number of offspring produced by a mutant over the summer is the same as the resident, i.e. $Q_3(t) = R_3(t)$.

Whether the mutants playing strategy T_m are able to invade the residents, playing the strategy T , or not depends on their long-term *per capita* growth rate:

$$s(T, T_m) = \lim_{t \rightarrow \infty} \frac{1}{t} \log [Q_3(t) + s_3][Q_2(t) + s_2][Q_1(t) + s_1],$$

provided the limit exists. Over the parameter space (see previous section) that we simulated, the population dynamics always converged to a periodic solution whose period kP is a multiple k of the seed masting period P . Typically, this multiple was 1 or 2 or 4, the latter two corresponding to period-doubling bifurcations. We developed R code to efficiently approximate these periodic solutions. For these periodic solutions of the resident dynamics, the long-term *per capita* growth rate of mutant strategy T_m against resident strategy T equals

$$s(T, T_m) = \frac{1}{kP} \sum_{t=1}^{kP} \log [Q_3(t) + s_3][Q_2(t) + s_2][Q_1(t) + s_1].$$

A strategy T is an ESS for caching if $s(T, T_m) < 0$ for all strategies $T_m \neq T$. To find ESSs for caching, we derive in the electronic supplementary material, Appendix C an explicit expression for the fitness gradient $(\partial s / \partial T_m)(T, T)$, when the resident population is playing threshold strategy T . When the fitness gradient is positive, mutants with a higher threshold strategy than the residents can invade while mutants with a lower threshold strategy fail [76]. When the fitness gradient is negative, the opposite occurs. As mutants with larger or smaller thresholds fail when invading a resident population playing the ESS, the fitness gradient equals zero at an ESS. Hence, we identified ESSs by iteratively solving for thresholds T at which the fitness gradient $(\partial s / \partial T_m)(T, T)$ is zero (figure C1 in the electronic supplementary material, Appendix C).

Our results focus on the fraction of seeds cached (F) rather than the caching threshold (T), as this quantity is easier to interpret. The relationship between these two measures of caching is given by $F = \max\{0, (G(t) - T/G(t))\}$. As the amount of seeds gathered $G(t)$ varies from year to year, the percentage of seeds cached when playing the ESS also varies from year to year. We also examine pilferage risk and the marginal reproductive cost of caching. Pilferage risk is the probability (expressed as a per cent) that a seed is pilfered from a surviving individual's cache during winter/spring and equals $100(n_2(t) - 1)O(t)$. If F_m denotes the percentage of seeds cached by mutant individuals, then the marginal reproductive cost of caching equals the infinitesimal reduction in reproductive output for a mutant individual caching an infinitesimal amount of seeds rather than consuming them, i.e. $-(dQ_1/dF_m)|_{F_m=0} = bhG(t)/(G+h)^2$.

3. Results

Increasing intensity of masting results in decreased autumn scatterhoarder population density (i.e. the density that enters masting events; figure 2a). This occurs because reproduction is a saturating function of seeds gathered and the reproductive gains of higher seed availability during masting years are outweighed by the reproductive losses owing to lower seed availability during non-mast years.

Increasing masting intensity also reduces the risk that a cached seed would be pilfered (figure 2b), particularly when a high proportion of seeds are produced during mast years. The responses of pilferage risk and autumn density are correlated (see also, figures 3 and 4) because lower population density means fewer pilferers.

Furthermore, increasing masting intensity is associated with a decline in marginal reproductive costs of caching—the cost of caching seeds for future use rather than using seeds for current reproduction (figure 2c). Lower population densities and higher seed abundance during mast years mean more seeds per individual. Because reproduction

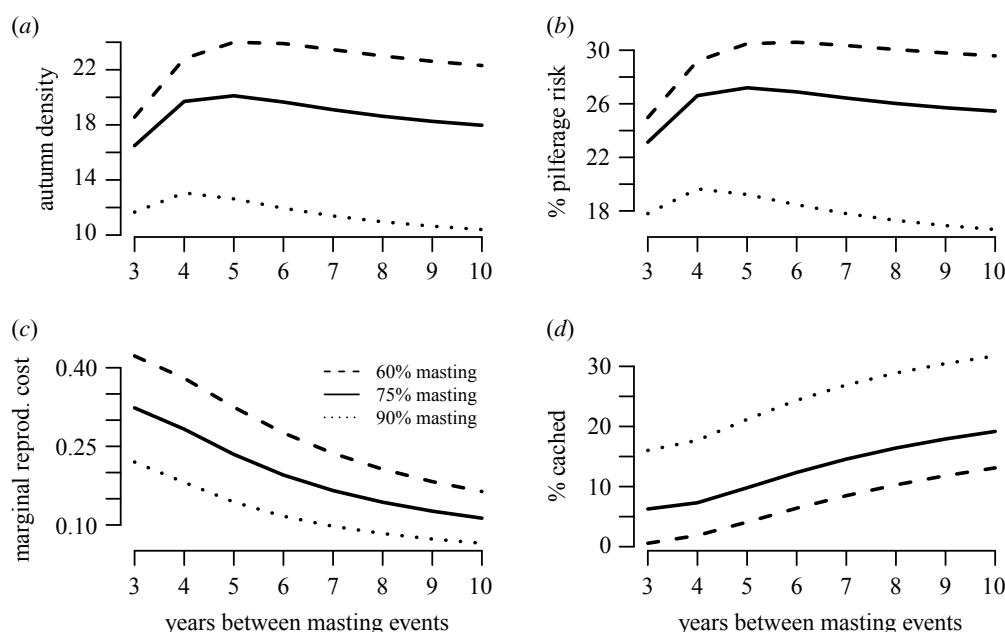


Figure 3. Mast year autumn population density (a), pilferage risk (b), marginal reproductive costs of caching (c), and proportion of seeds cached rather than eaten (d) as a function of masting interval. Dashed, solid and dotted lines represent masting intensity (60, 75 or 90% of total seed production occurring during mast years). All dependent variables are given at the evolutionary stable caching strategy and its associated periodic population dynamics.

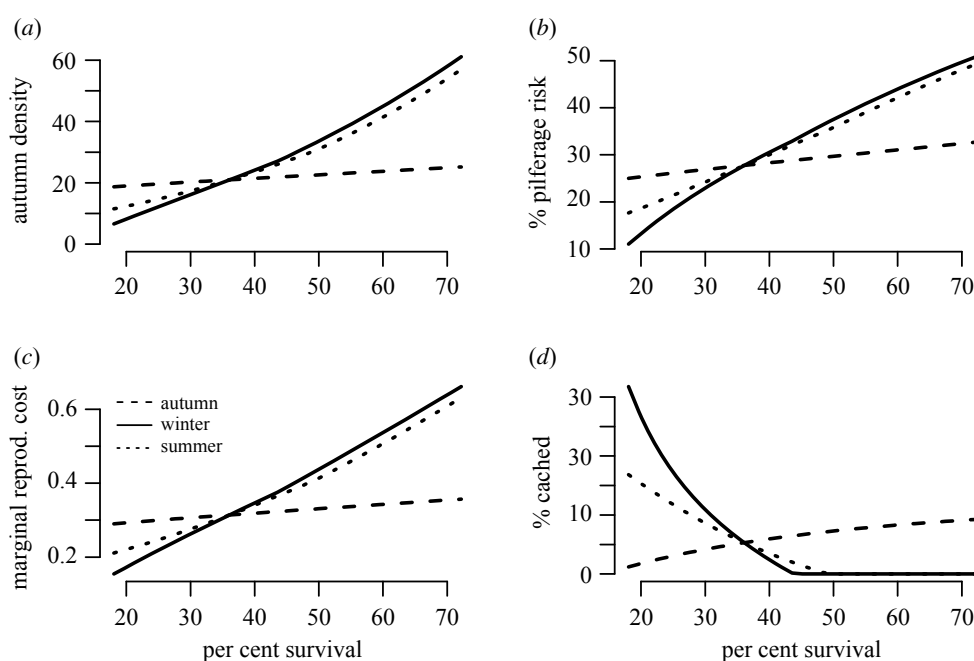


Figure 4. Mast year autumn population density (a), pilferage risk (b), marginal reproductive costs of caching (c), and proportion of seeds cached rather than eaten (d) as a function of scatterhoarder survival. Dashed, solid and dotted lines denote responses to changes in autumn, winter/spring and summer survival, respectively. All dependent variables are given at the evolutionary stable caching strategy and its associated periodic population dynamics.

is a saturating function of seeds consumed, the marginal reproductive cost of caching declines as seed abundance increases.

As a result of reduced pilferage risk and marginal costs, increasing masting intensity causes an accelerating increase in the ESS proportion of seeds cached rather than eaten (figure 2d).

Higher recovery advantage by cache owners reduces pilferage risk (dashed versus solid versus dotted lines, figure 2a), but has little effect on population densities and marginal

reproductive costs in the autumn of masting years. Consequently, higher owner advantage selects for greater caching.

More years with poor seed crops between masting events lower marginal reproductive costs (because there are more seeds per individual) (figure 3c) but can increase or lower densities of individuals entering the autumn of a masting year (figure 3a) which increases or lowers the risk of seed pilferage (because more or fewer individuals enter winter) (figure 3b). Collectively, the lower reproductive costs outweigh the effects of pilferage risk and select for more

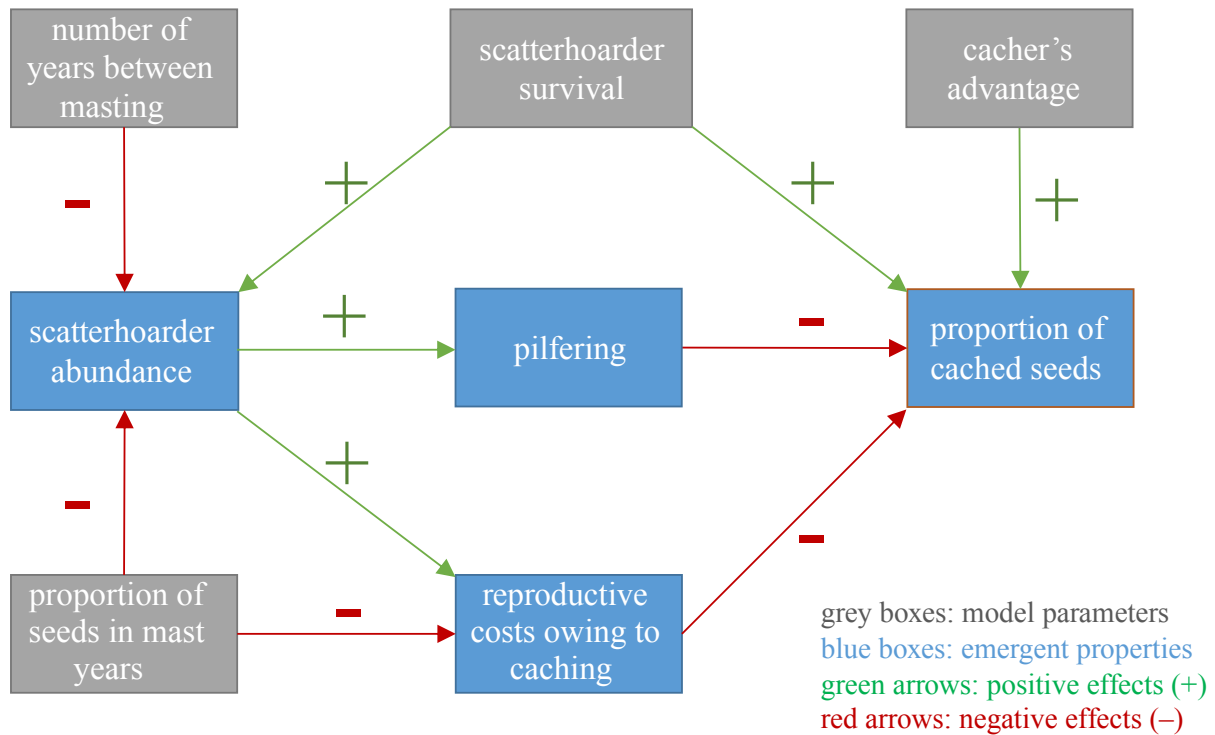


Figure 5. Relationships between input parameters (masting interval and intensity, expressed as the proportion of seeds produced during mast years, scatterhoarder survival and cacher's advantage in cache recovery) and emergent properties of the model (scatterhoarder population density, the proportion of cached seeds that are pilfered, reproductive costs of caching and the quantity of interest: the proportion of seeds cached by scatterhoarders). (Online version in colour.)

caching (figure 3*d*). Varying masting intensity (60, 75 or 90% of seeds produced during mast years: dotted, solid or dashed line in figure 3) affects the magnitude of these changes in the manner consistent with figure 1, with only minor effects on the shape of responses to the masting interval.

Increasing the survival of scatterhoarders leads to increases in autumn population density, pilferage risk and marginal reproductive costs of caching (figure 4). These effects are the strongest owing to increases in winter survival, intermediate owing to summer survival and the weakest owing to autumn survival. This is likely because after masting the greatest concentration of births occurs in the autumn and winter, resulting in the winter population having a higher percentage of new individuals (who are not subject to mortality during the previous period) than the summer and autumn populations. Thus, an increase in mortality in the autumn affects a smaller proportion of the population than an increase in mortality in the winter or summer. Despite increasing marginal reproductive costs and pilferage risk, increasing autumn survival, unlike winter/spring or summer survival, selects for more caching. This occurs because, unlike summer or spring/winter survival, autumn survival increases the likelihood that an individual caching in the autumn will survive to the winter/spring to make use of their cache.

4. Discussion

The fact that masting causes strong fluctuations in populations of seed-eating animals has been well known for a long time [3,49,77,78], yet the traditional research focus has been on how the satiation-starvation cycle reduces seed losses to pre- and post-dispersal seed predators. More recently, researchers suggested that seed masting is one of the means by which plants manipulate behaviour of their dispersers [79,80].

According to this reasoning, satiation of current energy needs induces granivores to cache seeds for future use [79]. Here we show that the effects of masting on population dynamics and caching behaviour are mutually dependent. By decreasing the degree of pilfering, the satiation-starvation cycle owing to more extreme seed masting events may promote the evolution and maintenance of seed caching behaviour. Thus, the decrease in seed predation, increase in *per capita* scatterhoarder satiation and reduction in pilfering pressure may each represent an important pathway by which the scatterhoarder satiation-starvation cycle induced by masting may improve plant recruitment (figure 5). These nuanced interactions between plant and seed predator emphasize the importance of studying the feedbacks between population dynamics and behavioural evolution.

Our results suggest that when seed production is highly variable, seed caching can evolve even when cache owners have little advantage over naive foragers in seed recovery (compare with [18]). However, the mechanism that we describe is not mutually exclusive with other evolutionary explanations of scatter-hoarding. It can promote this behaviour in synergy with the cache owner's advantage [18] and reciprocal pilferage [20].

The costs of cache loss to pilferers are reduced in our model because periods of intense seed production coincide with low densities of scatterhoarders—and thus few potential pilferers (see [81] for experimental data demonstrating that the magnitude of cache pilferage is determined by the abundance of scatterhoarders). When there is pronounced masting with relatively long intervals between masting events, densities of scatterhoarders entering the start of the next large masting event are low (figures 2 and 3). Consequently, individuals are able to collect enough seeds to satiate their reproductive needs. As the yearly fitness is determined by the geometric mean of their fitness across the seasons and this geometric mean decreases with variation [82–84], the

benefits of reducing seasonal variation in fitness by increasing winter/spring reproduction (fuelled by cached seeds) outweigh the diminishing returns of increasing reproduction in the autumn (fuelled by immediate seed consumption).

Our results make a prediction that plants dispersed by scatterhoarders should have a high interannual variation of seed production (typically measured with the coefficient of variation, CV) relatively to plants dispersed by other means. This appears to be the case, at least when plants dispersed by scatterhoarders (synzoochorously) are compared to plants dispersed by frugivores (endozoochorously) [2,39,85]. When explaining this pattern, researchers emphasized contrasting selective pressures acting on these groups of plants. Avoiding the risk of satiating frugivores was suggested as a factor that stabilizes seed production in plants dispersed endozoochorously. On the other hand, variable seed production in synzoochorous plants was interpreted as an adaptation that enabled reducing seed mortality caused by animals that act as seed predators and only incidentally disperse seeds [39]. However, we suggest that the high CV of plants dispersed by scatterhoarders can also be linked to the caching behaviour of scatterhoarders (see also [86] for a model exploring the connection between caching behaviour and seed trait evolution).

If, as our simulations suggest, masting intensity and mast interval are important for seed caching, then changes in plant masting patterns might affect the dynamics of seed caching, and therefore also the recruitment in plant populations. Our model is loosely based on the European beech—*Apodemus* mice system [16,62]. Several studies have suggested that the European beech has shown more frequent masting in recent years, probably owing to global warming [53,87–89]. This could shift the beech-rodent interactions towards antagonism, with higher rodent abundances (predicted also by [90]), more seed consumed and fewer cached (recall that caching declines with more frequent masting: figure 3). On the other hand, a recent meta-analysis of global data suggests that masting has become more pronounced ([91]; see also [92]). Such a change could make seed caching more profitable for granivores (higher intensity of masting promotes caching: figure 2). However, extreme interannual variation in seed crops might lead to a decline and even extinction in granivore populations, owing to the difficulty in tracking resource levels.

Moreover, any environmental change that affects scatterhoarder population dynamics could alter caching behaviour and, thereby, impact seed mortality. For example, we found that increased scatterhoarder survivorship during the winter or summer may select against caching behaviour by increasing population densities entering the masting years (figure 4). Thus, changes in winter or summer conditions that are favourable for mice could harm seedling recruitment both directly by increasing seed predation and indirectly by discouraging seed caching. By contrast, autumn conditions that are favourable for mice are likely to improve seedling

recruitment because increased autumn survivorship of scatterhoarders selects for more caching.

Just like every model, the one presented here simplifies reality. For example, in many ecosystems different masting species co-occur. Such species often mast synchronously owing to shared climatic drivers [2,46,47,93,94]. If seed production is synchronous, the consequences for scatterhoarders will be similar to masting by one tree species. However, if masting is asynchronous, its outcome might be similar to reducing masting interval (figure 3d), i.e. the selective pressure to cache seeds will be weaker.

Furthermore, populations of scatterhoarders that have relatively high survival and low reproduction (e.g. corvids) might not fluctuate in response to masting as strongly as do populations of more productive scatterhoarders, such as chipmunks [9], squirrels [95,96] or mice [50,68,97]. However, even in species such as corvids, masting can affect the benefits of caching through similar mechanisms, i.e. reduced risk of interspecific seed pilferage (owing to decreased abundance of sympatric rodents: e.g. [25]) and lower marginal reproductive costs of caching.

Examining ultimate causes and ecological determinants of caching behaviour will help to understand former selective pressures on synzoochorous plants, current dynamics of seed dispersal and future alterations in seed dispersal patterns caused by global changes. Our study provides a step in this direction and suggests several promising avenues for prospective research. For example, future work should address the evolution of caching reaction norms instead of the simple threshold for caching considered here. Additionally, the evolution of caching strategies could be different when individual variation in personalities or, more generally, phenotypes of seed-dispersing animals [98,99] is taken into account. Finally, future studies could examine these interactions from the plant perspective, for example by determining masting patterns that maximize seedling recruitment.

Data accessibility. The code for the main functions of the model, model results and sensitivity analyses are available in the electronic supplementary material [100].

Authors' contributions. R.Z. and S.J.S. conceived the study. S.J.S. and D.C. developed and analysed the model with feedback from R.Z. and A.S. R.Z. wrote the first draft of the manuscript. All authors critically revised the draft and approved the final version of the article.

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