

## The pea and the coconut: seed size in safe sites

Seed size varies by ten orders of magnitude in the global flora (from orchid seeds of less than a microgram to double coconuts of more than ten kilograms). Even within local floras, the range commonly exceeds five orders of magnitude<sup>1</sup>. Variation within species is much smaller, but not negligible. Coefficients of variation are typically greater than 20%, with most of the variation occurring among the seeds produced by individual plants<sup>2</sup>. Some seedlings start life with a larger 'packed lunch' than others.

Other things being equal, larger seeds will produce fitter seedlings, but fewer large seeds can be produced from a fixed quantity of resources. Smith and Fretwell presented an influential model of the evolutionary trade-off between offspring size and number<sup>3</sup>. Their model was formulated as an optimization problem in which parental investment ( $m$ ) increases an offspring's probability of survival ( $s$ ). Parents were predicted to invest a constant amount in each offspring, the amount that maximized  $s/m$  (Fig. 1a). For present purposes, seed size can be interpreted as a measure of parental investment, in which case, the Smith-Fretwell model predicts seeds of uniform size. The optimality criterion implicitly assumes that a seed's contribution to parental fitness is independent of the size of seeds produced by other parents (a seedling's probability of survival is also assumed to be independent of the number and size of its siblings, but that is another issue). If, however, a seed's prospects depend on the size of its competitors, the appropriate mathematical tool is game theory rather than optimization.

In a new paper, Stefan Geritz employs a game-theoretic approach to argue that a uniform seed size is not evolutionarily stable<sup>4</sup>. In his model, seeds undergo an initial period of frequency-independent selection followed by a period of competition within safe sites in which the largest seed wins. The survivors of the initial phase are distributed at random among safe sites. Some sites receive no seeds, some a single seed, some two seeds, and so on. Whether a seed is able to establish in a safe site depends on its own size relative to the size of its neighbors. A population that produced seeds of a single size would be vulnerable to invasion by strategies that included smaller seeds, because the larger number of seeds would increase the chances of reaching otherwise unoccupied sites, and by strategies that included larger seeds,

because the larger seeds would prevail in competition within sites. Thus, a range of seed sizes is expected at an evolutionary equilibrium, with seeds of all sizes yielding the same return per unit cost.

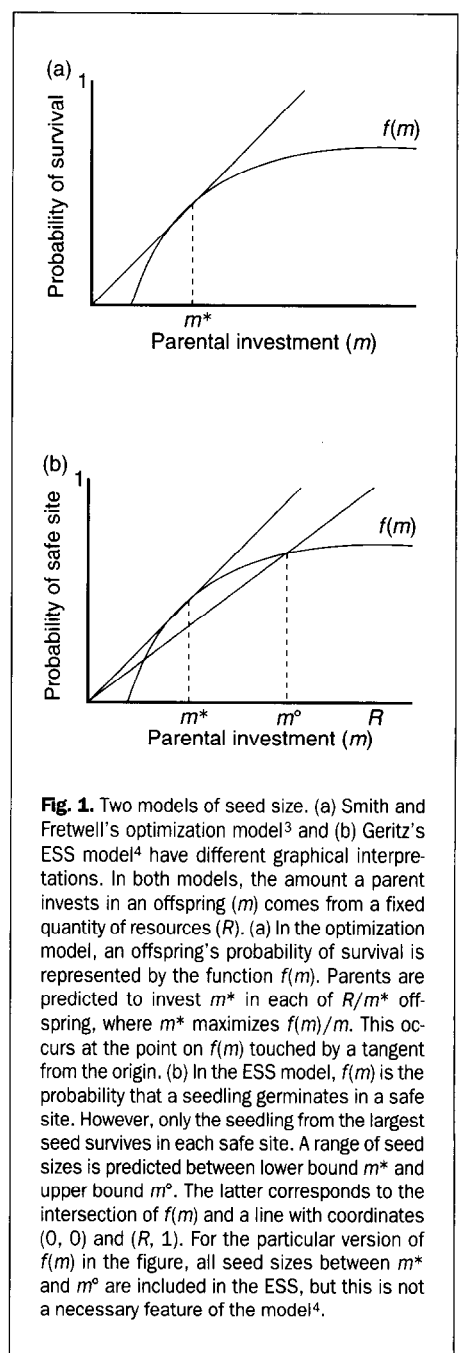
At the evolutionary stable strategy (ESS), the lower bound of the size distribution occurs at a size below which size-dependent, frequency-independent mortality results in fewer expected survivors in safe sites. The upper bound occurs at a size above which there are insufficient survivors in safe sites for parents to replace their numbers, even though the survivors triumph in every site they occupy (Fig. 1b). Within these bounds, frequency-dependence will ensure that a parent producing seeds of a single size would expect one seed, on average, to establish in a site unoccupied by any seed larger than itself. The ESS distribution of seed sizes could be the outcome of a single class of parents, each producing the ESS mixture of seed sizes, or of a mixture of parents (in the appropriate proportions) each producing a single seed size.

Geritz's model is phrased in terms of competition among members of a single species, but safe sites often contain seedlings of several species, and similar logic applies. Thus, interspecific competition within safe sites may help to explain the coexistence, within a single environment, of species with vastly different seed sizes. Seed-size specialists should supplant seed-size generalists because seeds of different sizes are suited to different dispersal modes, different dates of release, different germination strategies, such that a single species would be unable to monopolize the full range of seed sizes. The upper bound of seed size at the ESS increases as the amount of resources available to a parent increases. This would predispose species with larger mature individuals to specialize on larger seeds, suggesting one reason why trees tend to have larger seeds than herbs.

Tilman has investigated models of interspecific competition in spatially structured environments. These models allow the stable coexistence of a potentially unlimited number of plant species on a single resource, provided that trade-offs exist among longevity, competitive ability and colonizing ability. Species with a sufficiently high dispersal rate are able to persist in sites that remain uncolonized by superior competitors<sup>5</sup>. The trade-off between seed size and seed number provides

a plausible reason why the number of sites occupied and competitive ability will often be negatively correlated. Tilman's and Geritz's conclusions converge even though their models were constructed to address different questions.

Parents do indeed face a trade-off between seed size and seed number, but the relative value of producing a few large seeds or many small seeds depends on the kinds of seeds produced by potential competitors (whether of the same or different species). Geritz has shown that competition among seedlings in small local neighborhoods favors a range of seed sizes at evolutionary equilibrium. Seedlings of several species often compete for occupation of the same safe sites, and the empirical evidence suggests that the



**Fig. 1.** Two models of seed size. (a) Smith and Fretwell's optimization model<sup>3</sup> and (b) Geritz's ESS model<sup>4</sup> have different graphical interpretations. In both models, the amount a parent invests in an offspring ( $m$ ) comes from a fixed quantity of resources ( $R$ ). (a) In the optimization model, an offspring's probability of survival is represented by the function  $f(m)$ . Parents are predicted to invest  $m^*$  in each of  $R/m^*$  offspring, where  $m^*$  maximizes  $f(m)/m$ . This occurs at the point on  $f(m)$  touched by a tangent from the origin. (b) In the ESS model,  $f(m)$  is the probability that a seedling germinates in a safe site. However, only the seedling from the largest seed survives in each safe site. A range of seed sizes is predicted between lower bound  $m^*$  and upper bound  $m^o$ . The latter corresponds to the intersection of  $f(m)$  and a line with coordinates  $(0, 0)$  and  $(R, 1)$ . For the particular version of  $f(m)$  in the figure, all seed sizes between  $m^*$  and  $m^o$  are included in the ESS, but this is not a necessary feature of the model<sup>4</sup>.

largest component of variation in seed size occurs between species. Is the adaptive problem of seed size (for individuals of a particular species) dominated by competition with conspecifics or with other species? And does the answer affect the level of variation expected within species? We now have reasons to believe that variation in seed size need not be maladaptive. But does the observed distribution of sizes within species distinguish adaptive from nonadaptive variation? A good model need not provide all the

answers if it succeeds in reframing the questions.

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#### References

- 1 Westoby, M., Jurado, E. and Leishman, M. (1992) **Comparative evolutionary ecology of seed size**, *Trends Ecol. Evol.* 7, 368–372
- 2 Michaels, H.J. *et al.* (1988) **Seed size variation: magnitude, distribution, and ecological correlates**, *Evol. Ecol.* 2, 157–166
- 3 Smith, C.C. and Fretwell, S.D. (1974) **The optimal balance between size and number of offspring**, *Am. Nat.* 108, 499–506
- 4 Geritz, S.A.H. (1995) **Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density**, *Am. Nat.* 146, 685–707
- 5 Tilman, D. (1994) **Competition and biodiversity in spatially structured habitats**, *Ecology* 75, 2–16

## Cooperative lions escape the Prisoner's Dilemma

Lions (*Panthera leo*) are an emblem of cooperation for many people: males united in protecting their pride, females defending their cubs and their territory in exemplary solidarity. This image persists despite empirical work over the past 15 years demonstrating that lion cooperation is more complex, subtle and context-dependent than the distorted representations of the 'Lion King'. The most recent work to emerge from the Serengeti lion population in Tanzania, East Africa, reveals the most disturbing truth yet: lionesses 'cheat' on their pridemates when defending the pride territory against intruding females<sup>1</sup>. This is the latest finding in a productive series of studies using playbacks of recorded lion roars to simulate different levels and types of territorial intrusions<sup>1–3</sup>. Two new papers examine the mechanisms of cooperation in group-territorial lionesses<sup>1</sup> and in coalitions of male lions<sup>2</sup>. They illustrate the difficulty of matching empirical work to existing theoretical models for cooperation.

The evolutionary basis for cooperation has received much theoretical attention since the theories of kin selection and reciprocal altruism emerged in the 1960s and 1970s. Cooperation between non-relatives remains the greater puzzle, and the most popular metaphor for the problem has been the two-person Prisoner's Dilemma game<sup>4</sup>. A strong temptation to exploit a cooperative protagonist together with a low (sucker's) payoff for being exploited oneself makes defection the best solution to any round of the game. However, if a pair of individuals play each other repeatedly (Iterated Prisoner's Dilemma – IPD) cooperative strategies can evolve under certain conditions. Participants must interact

a large but unknown number of times, no information can be exchanged during encounters, and participants must be able to 'score-keep' and 'punish' defectors. Consequently, they base their decision for each round of the game on the history of past encounters<sup>4</sup>.

The best known strategy, tit-for-tat (TFT), came to prominence in a computer tournament. Tit-for-tat strategists begin by cooperating, but retaliate against cheating by withholding further cooperation<sup>4</sup>. However, TFT players are not invulnerable: participants may be locked into a series of mutual defections by mistakes. Also, a population of TFT players can be invaded passively by individuals who always cooperate, and this population in turn can be invaded by unconditional defectors<sup>5</sup>. Pavlov is a more robust strategy: pavlovians cooperate if the previous round was either mutual defection or mutual cooperation, but they will continue to defect if their partner cooperates persistently. Therefore, Pavlov strategists accommodate occasional mistakes and are able to exploit unconditional cooperators<sup>5</sup>.

Considerable work has gone into refining and extending models dealing with the IPD, possibly at the expense of other approaches to cooperation<sup>6</sup>. For example, theoreticians have questioned whether any strategy can be a pure evolutionary stable strategy (ESS)<sup>7</sup>, tested the performances of new strategies in the game<sup>5</sup>, and investigated the effects of different degrees of mobility by participants and non-random interactions on game outcomes<sup>8</sup>. Empirical work has lagged behind. Evidence for reciprocity has come from a variety of taxa but the data have been received with some scepticism. The most contested

example, predator inspection by fish, is claimed to be a case of the IPD where participants in the game play TFT<sup>9</sup>. Critics have suggested that selfish grouping effects<sup>10,11</sup> or predator deterrence<sup>12</sup> are more plausible explanations.

Evidence from a long-term study of the Serengeti lions by Craig Packer and his colleagues indicates that, contrary to popular belief, lions do not live in groups because of the benefits of communal hunting<sup>13</sup>. Female-grouping patterns are best explained as facilitating cooperative defence of cubs against infanticidal males and defence of territory against other females<sup>13</sup>. Males form coalitions (with relatives or non-relatives) and cooperate to take over and maintain residence in a pride<sup>2</sup>. However, while animals may be in social groups for other reasons, they could still hunt in groups if there are mutualistic advantages in doing so<sup>14</sup>. For example, lions are more likely to participate in hunts of large or hard-to-catch prey<sup>14,15</sup>, when the involvement of an additional hunter markedly improves the probability of capture. A lion will only join in a hunt for short-term benefits; reciprocity is not involved<sup>15</sup>.

Lions advertise territory ownership by roaring<sup>2,3</sup>; territorial intrusions can be simulated by playing the recorded roars of strangers to the residents. Females respond to female intruders in a risk-sensitive manner: they are less likely to approach when the odds (ratio of challengers to defenders) are unfavourable<sup>3</sup>. Lionesses approach in single-file, and individuals at the front of the response expose themselves to a greater risk of attack and injury than those at the back, although all members of the group benefit from successfully repelling the intruders<sup>1</sup>. This situation resembles an IPD: defecting (lagging behind) while your partner cooperates (goes forward) results in the highest payoff, but mutual defection is less rewarding than mutual cooperation. Being at the front of the response while your partner lags behind incurs the sucker's payoff<sup>1</sup>.