

Invited reply

What is bet-hedging, really?

Bet-hedging is defined as a strategy that reduces the temporal variance in fitness at the expense of a lowered arithmetic mean fitness. After a few technical points, we will here argue that this definition of bet-hedging is badly suited for models with density- and/or frequency-dependent fitness. A strict interpretation cannot be employed; possibly, a modified definition is necessary.

Technical point one: between- and within-clutch variation are not interchangeable

Rees *et al.* (2010; hereafter RMC) correctly conclude that between-clutch variation (coin flipping) in our model actually decreases genotype-wide mean egg mass, simply because the individuals that choose a strategy with a lighter (and hence smaller) egg will produce more eggs. This fact was overlooked by us and we are grateful to RMC for pointing that out. It means, among other things, that our parameter μ_m is *not* the true mean egg mass unless between-individual variation is zero ($\sigma_b = 0$). It also means that between- and within-clutch variation are not interchangeable in our model. Instead, a relative dominance of between-clutch variation yields a total distribution of egg masses skewed towards smaller eggs. This explains the existence of an intermediate ESS solution—a point ESS instead of a line of constant variance. Selection, albeit weak, was operating on the third and higher moments of the egg mass distribution.

Technical point two: between-clutch variation is not due to selection of the mean

RMC use juvenile production as a proxy for fitness to argue that some of the variation in egg mass present in our ESS solutions may be due to selection for decreased mean egg mass. However, mean egg mass is an unconstrained parameter in our model and its direct evolution should eliminate any further selection pressure. It is in fact possible to show analytically that the strategy maximizing arithmetic mean juvenile production in our model is to produce eggs with mass 0.42, with no variation of egg mass at all. This fixed, non-diversified strategy could thus serve as a benchmark strategy to which all evolved strategies should be compared (but see below).

Technical point three: bet-hedging is not so difficult to identify...

Given a variable environment, natural selection will act to maximize the geometric mean fitness of an evolving

organism. The strategy that maximizes the arithmetic mean is not interesting from an evolutionary perspective, unless it happens to coincide with the maximal geometric mean solution. The two solutions coincide in a constant environment and sometimes in a variable environment—it can, for example, occur if there is only a discrete set of strategies available. In our case, we have a three-dimensional continuous trait space of possible strategies, and it is safe to assume that any internal solution will not simultaneously maximize both the arithmetic and the geometric mean. Any internal ESS is thus by necessity a bet-hedging strategy, as it does not maximize the arithmetic mean fitness. This reasoning is valid if all three variables are evaluated together, or just one by one (like RMC evaluate mean egg mass (RMC, fig. 1*c,d*)).

... but density dependence makes bet-hedging difficult to define

In our model, eggs first have to survive current environmental circumstances (m_{\min}) to become juveniles, and next compete among other juveniles to become new recruits to the population. If, for simplicity, we assume all eggs have the same mass m , the juvenile production per adult is given by

$$b_J = b_0 s_e(m, m_{\min}),$$

where b_0 is the number of eggs per adult ($b_0 = M/m$) and $s_e(m, m_{\min})$ is the survival probability of an egg with mass m in an environment described by m_{\min} (in our case $s_e(m, m_{\min})$ is a step function). The number of new recruits per adult, the net birth rate, becomes

$$b = b_J s_J(b_J N) = b_0 s_e(m, m_{\min}) s_J(b_0 s_e(m, m_{\min}) N),$$

where $s_J(b_J N)$ is the density-dependent survival among juveniles and N is adult population size.

The main point here is that there is dependence between egg survival and juvenile survival—they both depend on m_{\min} . A benign year yields many surviving eggs and therefore strong competition among juveniles, which means there is a negative correlation between juvenile production (b_J) and juvenile survival (s_J). This has evolutionary consequences. As an example, the arithmetic mean net birth rate is given by

$$E(b) = E(b_J s_J) = E(b_J) E(s_J) + Cov(b_J, s_J),$$

where the last term is the covariance. It follows that juvenile production is not a valid fitness proxy, as maximizing $E(b_J)$ is not equivalent to maximizing $E(b)$. More importantly, this shows frequency dependence in our model. The fitness of a given strategy depends on the variation in juvenile competition, which in turn depends on which strategy currently dominates the

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population. More precisely, the fitness of a rare strategy will depend on the correlation between its juvenile production and the juvenile survival of the dominating strategy.

In general, it is not uncommon that density dependence in variable environments gives frequency-dependent selection (e.g. Turelli & Petry 1980; Bulmer 1985). With frequency dependence, the fitness of a strategy is not fixed, but depends on what other strategies are currently present in the population. To determine whether a particular strategy is a bet-hedging strategy is not unambiguous as it will depend on circumstances. Bulmer (1985) has a lucid example of a perennial plant strategy competing with an annual. In some parameter settings, both the perennial and annual strategies are bet-hedging (risk-avoiding) while common, but not while rare.

A strict, generally applicable definition of bet-hedging thus has to specify in which environment a strategy should be evaluated; for example, the environment given when it dominates itself, or perhaps when some standard, default strategy is the most abundant. Second, it has to be specified with which strategy to compare, as 'the strategy with highest arithmetic mean fitness' is no longer defined.

An alternative approach is to leave things as they are, let the ambiguity remain and not be so strict about it. Bulmer (1985) labels a strategy as bet-hedging if it can be said to avoid risk (variable fitness in one life stage or

the other), without any comparison of arithmetic means. We think it is perfectly sensible to regard our ESS solutions as bet-hedging strategies, but no matter what they are called, it is an interesting result that variation in egg size within as well as between clutches (and mixtures thereof) is a possible adaptation to a variable environment.

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