

Comment

Bet-hedging as an evolutionary game: the trade-off between egg size and number

In a recent paper, Olofsson *et al.* (2009) explore the evolution of egg mass in a temporally variable environment using an individual-based simulation model. The model includes realistic assumptions such as density-dependent population growth and a fluctuating minimum size for survival. Their main focus was on the evolution of variation in egg mass both within and between clutches, and they explore whether this variation is adaptive, and if it is, how it should be distributed within and between clutches. Much of their discussion is couched in terms of evolutionary bet-hedging, the idea that a reduction in mean fitness can be selected for provided there is a corresponding decrease in the temporal variance in fitness (Seger & Brockmann 1987). Olofsson *et al.* (2009) identify three possible bet-hedging strategies: (i) conservative bet-hedging (large eggs with little variation in egg mass), (ii) diversified bet-hedging (medium egg mass and large within-clutch egg mass variation), and (iii) coin flipping (medium egg mass and large between-clutch variation in mean egg mass but little within-clutch variation). Olofsson *et al.* (2009) therefore use changes in the mean and variance in egg mass to identify different types of bet-hedging strategies. In this commentary we wish to make three points; (i) in order to be a useful concept, bet-hedging must be defined in terms of the mean and variance in fitness, not trait values, and using trait variation to identify bet-hedging strategies can be very misleading, (ii) the precise way that variation is added to a model is critical, and (iii) diversified strategies can only be understood from the point of view of the genotype (or strategy).

1. CAN TRAIT MEANS AND VARIANCES BE USED TO IDENTIFY BET-HEDGING?

To illustrate the difficulties in using variation in trait values to identify bet-hedging we first describe the Olofsson *et al.* (2009) model in a little more detail and then show that even when the environment is constant there can be selection for variability in egg mass. Rather than relying only on simulation, we use ideas from adaptive dynamics to analyse a constant environment case of their model. The model assumes that there is a minimum egg size required for survival, m_{\min} , and each individual makes a total egg mass M each year; initially we will assume that m_{\min} is constant. Juvenile survival is determined by the total number of juveniles produced independent of their egg size. This is equivalent to density

dependence operating on offspring establishment so we can calculate the evolutionarily stable strategy (ESS) by maximising the number of juveniles (Mylius & Diekmann 1995). Considering a simple model where individuals all produce the same egg mass, we find the ESS egg mass is $\mu_m = m_{\min}$; producing larger eggs results in lower fecundity which reduces fitness, whereas producing smaller eggs increases mortality.

We now explore how adding variation in egg mass affects the numbers of eggs and juveniles produced, where variation is added turns out to be critical.

(a) Effects of within-clutch variation in egg mass

To explore how variation in egg mass influences the number of eggs produced, we first note that from the definition of the mean we have $\mu_m = M/n$, where n is the total number of eggs produced. Consequently, if M and μ_m are fixed then so is n irrespective of the within-clutch variance in egg mass, σ_m^2 . For $\mu_m \geq m_{\min}$ increasing the variance in egg mass will decrease the number of eggs below m_{\min} and so reduce survival, therefore the number of juveniles, n_j is a monotonically decreasing function of σ_m^2 . In this case increasing the within-clutch variance in egg mass cannot increase the number of juveniles (i.e. mean fitness), and so any selection for variation in within-clutch egg mass can be interpreted as selection for evolutionary bet-hedging, since the associated reduction in mean fitness must be accompanied by a reduction in fitness variation.

(b) Effects of between-individuals variation in egg mass (adaptive coin-flipping)

To understand the importance of between-individual variation we consider a limiting case of the original model. We will assume each individual produces eggs of size m (no within-clutch variation), and m varies between individuals. As m varies between individuals, so the number of eggs produced now varies between individuals. For small between-individual variance, σ_b^2 , the expected number of eggs produced prior to mortality is

$$E[n] \approx \frac{M}{\mu_m} \left[1 + \frac{\sigma_b^2}{\mu_m^2} \right], \quad (1.1)$$

from which we conclude that between-individual variation increases the average number of eggs produced (this also follows more generally from Jensen's inequality), so we may see selection for between-individual variation in egg mass (adaptive coin flipping) even in a constant environment.

In order to see how this translates into fitness in a constant environment we need to calculate the number of

The accompanying reply can be viewed on page 1153 or at <http://dx.doi.org/doi:10.1098/rspb.2009.2023>.

juveniles produced. If a particular female produces eggs of mass m (where necessarily $m < M$), then she produces M/m eggs that all survive if $m > m_{\min}$, and all die otherwise. So for any probability distribution of egg sizes $\varphi(m)$,

$$n_J = \int_{m_{\min}}^M \left(\frac{M}{m}\right) \varphi(m) dm. \quad (1.2)$$

As an example, we can take $\varphi(m)$ to be a Gaussian distribution with mean μ_m and standard deviation σ_b , constrained to take values $\leq M$; and this is the distribution we use for numerical work. As in the case of within-clutch variation, in a constant environment the ESS egg mass is m_{\min} , and when $\mu_m = m_{\min}$ adding any variability in egg mass reduces fitness, as all eggs smaller than m_{\min} die, and producing larger eggs reduces fecundity. However, when $\mu_m > m_{\min}$ there is an ESS level of between-clutch variation in egg mass even when the environment does not vary from year to year (figure 1*a*). As there is no variability in the environment this cannot be the result of bet-hedging, so why is between-clutch variability in egg mass selected? To understand this, it must be remembered that fitness is determined by the number of juveniles produced, as a result of competition between juveniles being independent of their egg masses, and so there is an enormous advantage to producing small eggs because this increases number of eggs produced (Jensen's inequality, equation (1.1)). However, producing variable egg masses always incurs a cost because a fraction of the clutches will have eggs that are smaller than the minimum mass required for survival (m_{\min}). The extent of these costs and benefits depends on how far the mean eggs mass (μ_m) is from m_{\min} and the size of σ_b . When $\mu_m \approx m_{\min}$ there is little benefit in between-clutch variation in egg mass, as variability results in the production of clutches of large eggs, which reduces the number of juveniles produced, while the production of clutches of small eggs results in increased mortality (figure 1*b*). In contrast when $\mu_m \gg m_{\min}$ between-clutch variation in egg masses is highly beneficial as it increases the number of eggs through nonlinear averaging, with little cost in terms of mortality from producing clutches with eggs smaller than m_{\min} .

To explore how mean egg mass (μ_m) influences the arithmetic mean and variance of fitness when the threshold m_{\min} is temporally variable, we produced a stochastic version of the above model, again excluding within-clutch variance. Following Olofsson *et al.* (2009), the minimum viable egg size varies among years according to a lognormal distribution. We iterated this model over a large number of generations and used equation (1.2) to calculate both the mean (figure 1*c*) and variance (figure 1*d*) in the number of juveniles (i.e. fitness) as a function of μ_m . This clearly shows that increasing mean egg mass (μ_m) initially increases mean fitness whereas the variance in fitness decreases over almost the entire range of μ_m . This means that bet-hedging (which requires both decreasing mean and variance in fitness) can only be invoked for large egg masses (approx. $\mu_m > 0.5$). For this simple model the mean egg mass that maximizes arithmetic fitness is 0.5, in good agreement with Olofsson *et al.* (2009) simulation results (0.57–0.68). We repeated the same analysis for a second stochastic model with only within-clutch variation and obtained very similar results,

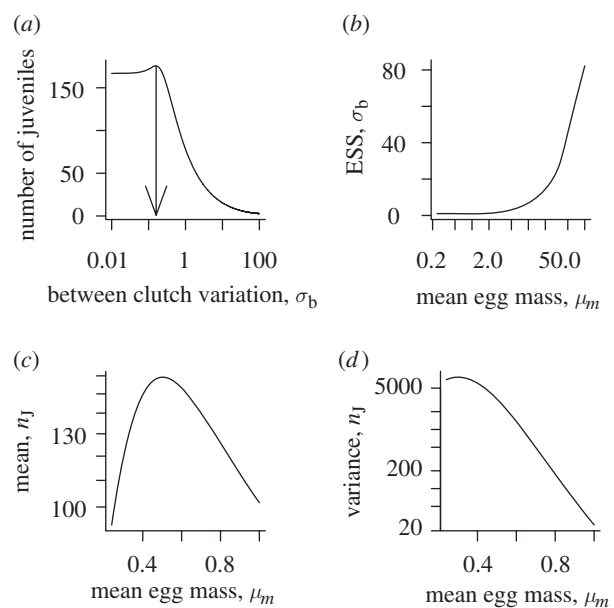


Figure 1. (a) The number of juveniles produced as a function of the between-clutch egg mass variability, σ_b . The arrow marks the ESS value which is approximately 0.13. (b) The ESS between-clutch egg mass variability (σ_b) plotted against mean egg mass μ_m . Other parameters, from Olofsson *et al.* (2009) are $M = 100$, $m_{\min} = 0.34$ and $\mu_m = 0.65$. (c,d) Plots of the arithmetic mean and variance in the number of juveniles produced from the stochastic model with m_{\min} varying from year to year (mean $m_{\min} = 0.34$, variance $m_{\min} = 0.02$).

although the egg mass that maximizes arithmetic mean fitness is slightly lower (approx. 0.45) because there is no effect of nonlinear averaging.

2. HOW YOU ADD VARIABILITY MATTERS

In their model Olofsson *et al.* (2009) allow the mean egg mass (μ_m) to fluctuate from year to year which generates what they call adaptive coin-flipping. However, it appears from their description of the model that this variability is applied 'independently of other individuals' which means that for a particular genotype there is no between year variability in mean egg mass—the expected value is always μ_m . At the genotype level, ignoring the effects of nonlinear averaging, both Olofsson *et al.*'s (2009) adaptive coin-flipping of mean clutch size from year to year, and their within-clutch variability in egg mass achieve the same result. To compute the fitness of a genotype in a given year, we have to consider the offspring production per individual averaged over a large number of individuals having the genotype in question. If therefore doesn't matter whether each mother chooses a single random value of m from a distribution and produces eggs that are all size m , versus each mother choosing a different random value of m (from the same distribution) for each of her eggs. Either way produces exactly the same distribution of egg sizes for the genotype, and therefore exactly the same expected fitness for the genotype. As a consequence of this the ESS variance in egg mass $\tilde{\sigma}_m^2$ can be produced from any combination of within-clutch variation, σ_m^2 , or adaptive coin-flipping, σ_b^2 . As $\tilde{\sigma}_m^2 = \sigma_m^2 + \sigma_b^2$ we expect to see a line of equal fitness with slope approximately -1 in the σ_m^2, σ_b^2 plane; for

the parameters from Olofsson *et al.* (2009) we have $0.0169 = \sigma_b^2 + \sigma_m^2$ and so the line of equal fitness is $\sigma_b^2 = 0.0169 - \sigma_m^2$, which is very close to what Olofsson *et al.* (2009) found from their individual-based simulations (see their fig. 2a).

3. DISCUSSION

We have demonstrated that using trait means and variances to identify bet-hedging strategies can be very difficult, especially when there are (i) non-linearities in the model, and (ii) changes in average trait values result in increasing mean fitness. The presence of non-linearities means that variability in traits can influence the mean demographic rates (i.e. fecundity or offspring survival) and therefore mean fitness. Identifying which aspects of Olofsson *et al.*'s (2009) results are the consequence of bet-hedging rather than shifts in mean demographic rates or mean fitness, is therefore difficult. However, the decomposition approach used by Rees *et al.* (2004) might be useful in this respect.

If we assume Olofsson *et al.*'s model is true can we use trait values to identify bet-hedging? We know that the ESS egg mass, assuming no variation in egg mass and a constant environment, is m_{\min} so if we observe that the mean egg mass is greater than m_{\min} can this be interpreted as conservative bet-hedging? Increasing mean egg mass clearly decreases the variance in fitness (figure 1d), as required for a bet-hedging interpretation. However, up to an egg mass of approximately 0.5 increases in mean egg mass also increase mean fitness (figure 1c), and so making difficult to separate the effects of increases in mean fitness from bet-hedging. We suspect bet-hedging does play a role in evolution of egg mass in Olofsson *et al.*'s (2009) model, but the effects might be smaller than they claim. For example a strategy maximizing mean fitness would have an egg mass of approximately 0.5, which is not much smaller than that found in Olofsson *et al.*'s (2009) simulations (0.57–0.68). The additional increase in egg mass observed in their results is probably a consequence of bet-hedging. Likewise if we assume a mean egg mass of approximately 0.5 then through nonlinear averaging we would predict a between-clutch variance of approximately 0.02, which is close to what Olofsson *et al.* (2009) find. However, for within-clutch egg mass variance we predict that increases in variability always decrease mean fitness, and so the presence of within-clutch variability at the ESS is almost certainly a consequence of bet-hedging.

It is generally unwise to assume a particular model is correct, and in order to do this one needs to carefully look at the model assumptions. For example, Olofsson *et al.* use a minimum size threshold for survival and this is probably unrealistic, and because this is drawn from a continuous distribution with no upper bound, in some years all offspring will die. In order for the population to persist some adult survival from year to year is therefore essential. The model also makes other strong assumptions, for example that offspring size only affects

survival, and subsequent competition between juveniles is independent of their size. Whether this is a reasonable assumption is difficult to assess. For example, Falster *et al.* (2008) assume that small differences in offspring size can influence competition between established plants many years after recruitment, although others think this is unlikely (Rees & Venable 2007; Venable & Rees 2009).

In summary one cannot realistically hope to identify bet-hedging using trait values alone, except in simple cases where variation enters the model linearly and so cannot change mean demographic rates or arithmetic mean fitness. Explicit calculation of the mean and variance in fitness is needed to demonstrate that optimal strategies are determined by bet-hedging, and these calculations must be compared to a sensible baseline case, for example, the constant environment model considered here. In many systems we suspect there will be a combination of factors acting and in these cases the development of new methods to decompose the contributions of the different factors are required.

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