How to balance the offspring quality–quantity tradeoff when environmental cues are unreliable

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Maternal effects on offspring size can have a strong effect on fitness, as larger offspring often survive better under harsh environmental conditions. Selection should hence favour mothers that find an optimal solution to the offspring size versus number tradeoff. If environmental conditions are variable, there will not be a single optimal offspring size, as predicted in a constant environment, but plastic responses can be favoured. To be able to adjust offspring size in an adaptive manner, mothers have to use environmental cues to predict offspring environmental conditions. Cues can be unreliable, however, particularly in species where individuals occupy different niches at different life stages. Here we model the evolution of plasticity of offspring size when the environmental cues mothers use to predict the conditions experienced by their offspring are not perfectly reliable. Our results show that plastic strategies are likely to be superior to fixed strategies in a stochastically varying environment when the environmental cues are at least moderately reliable, with the threshold depending on plasticity costs and the difference of resources available to mothers. Plasticity is more likely to occur if resource availability is not too different between environments. For any given scenario, plasticity in offspring size is favoured if offspring survival varies greatly between environmental states. Whenever plastic strategies are optimal, the occurring switches performed by mothers between small and large offspring are predicted to be substantial, as small adjustments are unlikely to reap fitness benefits great enough to overcome the costs of plasticity.

Offspring size is a trait that is closely linked to both offspring and maternal fitness (Bernardo 1996). The optimal solution to the tradeoff between number and size of offspring has been a central topic of life history studies for decades (Lack 1947, Smith and Fretwell 1974, Einum and Fleming 2000). On the one hand mothers are selected to maximize the number of offspring produced, on the other hand they should supply each of their progeny with sufficient resources to guarantee their survival and future reproduction. These conflicting tasks may additionally trade off with the survival of the mother herself. Across many taxa, offspring that are born larger grow faster, attain larger body sizes and have higher survival chances (Fleming and Gross 1990, Sinervo et al. 1992, Fox 1994, Einum and Fleming 1999, Fox and Czesak 2000, Roff 2002, Einum 2003, Marshall et al. 2003), a phenomenon that has been summarized as the 'bigger is better' hypothesis (Sogard 1997).

Smith and Fretwell's often cited study (1974) predicted a unique optimal size of offspring as a solution to the quality–quantity tradeoff, based on two factors: a limited amount of resources available to a mother is split between her offspring, and offspring survival probability is positively related to offspring size. Later studies (Parker and Begon 1986, McGinley et al. 1987) have criticized the assumption that there exists one environment-independent optimal offspring

size. Instead, these authors suggest that environmental circumstances should have a crucial influence on optimal offspring size. Parker and Begon (1986) were the first to point out that if the offspring environment can be anticipated by mothers, they should adjust the size of the offspring accordingly. Several authors have later expanded on their pioneering work, showing that environmental conditions encountered by the offspring select for larger offspring size while favourable conditions allow mothers to produce more and smaller offspring (Parker and Begon 1986; see also Lloyd 1987, McGinley et al. 1987, Braby 1994, Marshall et al. 2006). These studies highlighted the particular benefits of plastic responses in variable environments. Selection should then favour mothers that adaptively adjust offspring size based on environmental circumstances.

Environmental conditions have thus long been recognized to be important in the evolution of optimal offspring size, and environmental variation over time or space is predicted to select for plastic responses in dealing with the quality–quantity tradeoff. Several empirical studies have given support for this theoretical prediction (Jonsson et al. 1996, Fox et al. 1997, Hendrickx et al. 2003, Bashey 2006, Taborsky et al. 2007, Allen et al. 2008, Leips et al. 2009) and have identified the environmental factors linked with offspring size plasticity. For example, seed beetles, *Stator limbatus*,

tailor the size of eggs produced to the respective host plant seeds they lay their eggs on (Fox et al. 1997). Offspring fitness significantly increased with size on one host plant, whereas offspring survival was generally high irrespective of egg size on the second type of host plant seeds. Seed beetles are thus plastic in their tradeoff decisions, and are able to switch between producing large and small eggs depending on the seed type used as substrate. Similarly, Allen et al. (2008) demonstrated offspring size plasticity in a bryozoan species. Larger larvae performed better when competition was strong (high density). Accordingly, mothers produced larger larvae that are better competitors and have higher dispersal ability at higher densities, but a higher number of small larvae at low densities. In a similar experiment, females of the least killifish, *Heterandria formosa* adjusted offspring size to density with mothers at higher densities producing larger offspring (Leips et al. 2009). Another possible mechanism was identified by Taborsky et al. (2007) in a cooperatively breeding cichlid. They showed that mothers can plastically adjust offspring size as a response to perceived predation risk with mothers producing larger offspring when perceived predation risk was higher.

The above-mentioned studies demonstrate that adjusting offspring size in a plastic manner can be adaptive for a mother in a variable environment. Such an adaptive response is only possible if the state of the expected offspring environment can be assessed by the mother. Evaluating environmental conditions becomes considerably more complex, however, in species in which juvenile and adult individuals occupy different niches that are often spatially separated (Werner and Gilliam 1984). Niche separation between life stages can, but does not have to be, associated with differences in body size. Ontogenetic niche shifts can occur as discrete events (e.g. metamorphosis in amphibians or holometabolous insects) or as rather continuous transitions during the growth period. Niche separations of subsequent life stages are ubiquitous in nature and have been demonstrated in a broad range of taxa (reviewed by Werner and Gilliam 1984), for example in fish (Werner and Gilliam 1984, Osenberg et al. 1992, Hjelm et al. 2000), amphibians (Wilson 2005), reptiles (Mushinsky et al. 1982, Eskew et al. 2009), and invertebrates, for example in cephalopods (Rodhouse and Nigmatullin 1996), polychaetes (Hentschel 1998), and insects (Bradshaw and Johnston 1995). Thus, the environmental conditions experienced by a mother when deciding on the size-number tradeoff are not necessarily identical to what her offspring will encounter. To reduce the level of uncertainty, mothers can collect information that will be useful in making decisions (Dall et al. 2005): for example, a butterfly laying eggs may sample the larval environment (the host plant). In a variable environment, however, a certain level of uncertainty is likely to persist even if mothers are able to gain information about the larval environment. Sampling might be incomplete and sometimes erroneous, and time delays between the sampling and the actual encounter of the environment by the offspring could form a source of inaccuracy.

Studies investigating adaptive phenotypic plasticity in offspring size have so far either assumed that mothers possess full information on the postnatal environment of their progeny (essentially juveniles and adults share the same environment, Fox et al. 1997), or that the maternal environment is a good predictor for offspring environmental conditions (Allen et al. 2008) without quantifying how much error being a 'good predictor' might tolerate. In reality, the environment where a mother accumulates and allocates resources for reproduction and the environment her offspring will experience will be correlated to quite different degrees (Bernardo 1996). It is therefore important to include the reliability of cues available to mothers explicitly in the study of maternal allocation decisions. We expect the information available, and hence the reliability of environmental cues, to play an important role in the evolution of phenotypically plastic offspring size.

Here we introduce a conceptual model to investigate under which environmental conditions a plastic determination of offspring size is expected to evolve. In our model we investigate how strongly correlated maternal and juvenile environments have to be, and hence how 'reliable' the environmental cues available to the mother have to be for a phenotypically plastic offspring size strategy to be favoured by selection.

Methods

We model a system where adults and offspring of a species occupy different niches, and juveniles migrate from the juvenile to the adult niche when reaching maturation. For simplicity, we consider a semelparous life history with one reproductive event in a lifetime. This allows us to ignore the third component in the complex three-way tradeoff of offspring size, offspring number and parental survival. We thus focus on the major life history tradeoff of offspring number versus size. We derive optimal solutions to this tradeoff in a setting where adult and juvenile environments may differ from each other, and mothers have incomplete information on which to base their predictions of the environment encountered by the offspring.

We assume that offspring survival depends on offspring size. We call this trait 'size' in keeping with tradition in the literature, but strictly speaking we refer to offspring mass. Survival also depends on the current environmental state encountered by the offspring. We assume that the offspring environment can take one of two possible states, either 'good', G, or 'poor', P. Hence, we describe offspring survival by two separate functions for the two environmental states. We assume that there is a survival benefit to being large, thus in both environments survival is a monotonously increasing function of size *s*. In addition, for any given size, offspring should survive better if the environmental conditions are good than when they are poor. From the above assumptions it follows that large size can compensate for reduced survival chances when the environment turns poor. For our examples we use the Holling type III function to give the survival probability in 'good' environmental conditions, $S_G(s)$, and in 'poor' conditions: $S_P(s)$,

$$S_P(s) = \frac{s^\alpha}{\beta_P + s^\alpha} \tag{1a}$$

$$S_G(s) = \frac{s^\alpha}{\beta_G + s^\alpha} \tag{1b}$$

Here a determines the shape and β_P and β_G the steepness of the survival functions $S_P(s)$ and $S_G(s)$, respectively. All three parameters take positive values only. To make the labels 'good' and 'poor' biologically feasible we assume $\beta_P > \beta_G$ such that offspring survive better in a good environment. From the above assumptions it follows that $S_G(s) > S_P(s)$ for all $s > 0$, and that survival is zero if size equals zero. Hence, under good environmental conditions, survival probability initially increases faster with size but also attenuates faster than in a bad environment. In other words, the survival benefits of increased size diminish faster with growing size s when the environment is good (Fig. 1).

We assume offspring number n to be negatively proportional to the size of individual offspring. In other words, the larger the offspring produced, the smaller is the number of offspring within a clutch. In keeping with much of the literature on size-number tradeoffs, we assume a simple relationship where the total amount of mass to be allocated to reproduction is split between offspring (Fig. 1).

$$n(s) = \frac{R}{s} \qquad (2)$$

Here, R is the total mass of resources to be divided between offspring. We assume that R depends both on the maternal phenotype and the amount of resources provided by the environment that is available to a mother. As the resources should vary with the quality of the adult environment, we assume that offspring number depends on R_G in a good environment and R_P in a poor environment: $n_G(s) = R_G/s$ and $n_P(s) = R_P/s$.

Given our assumption of semelparity, maternal fitness in a specific environment can be defined as the product of offspring number times offspring survival probability. As we consider variable environmental conditions, we have to weigh these fitness values with the probabilities f or $(1 - f)$ that the respective environmental situation occurs, and the maternal fitness is properly defined as the geometric mean of the fitness values across the two possible environments. In variable environments, and particularly for semelparous life histories, the geometric rather than the arithmetic mean
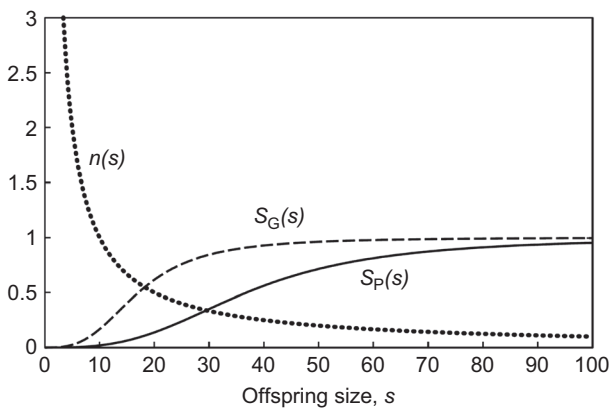
is the suitable fitness measure (Philippi and Seger 1989). We thus define fitness as

$$W(s) = n_G(s)^f \times S_G(s)^f \times n_P(s)^{(1-f)} S_P(s)^{(1-f)} \qquad (3)$$

where f is the probability that the environmental condition experienced by the offspring will be good. If it is certain that the juvenile environmental conditions will be good or poor ($f = 1$ or $f = 0$), $W(s)$ becomes

$$W_G(s) = n_G(s) \times S_G(s) \qquad (4a)$$

or

$$W_P(s) = n_P(s) \times S_P(s) \qquad (4b)$$

respectively. Offspring fitness $W(s)$ as described in Eq. 3 is now a weighted geometric average of these two expressions, with f and $(1-f)$ being the weights.

To reflect our assumption that individuals are born into a juvenile environment but will occupy a different niche as adults (Fig. 2), we define and model the juvenile environment J and the adult environment A separately. We assume that individuals migrate to the adult environment upon reaching maturation, and that both environments fluctuate stochastically between the good and poor states while maintaining a level of autocorrelation. In the simplest scenario (the 'no information scenario'), the juvenile and adult environments are spatially separated and isolated without any information flow or link between the two. More importantly, our model also includes scenarios where adults are able to sample the juvenile environment before deciding on offspring size (the 'sampling scenario'), or alternatively, J and A are physically linked by an external forcing factor such as weather (this allows mothers to 'know' something about J even if they have not sampled J directly; we call this the 'inference without sampling scenario'). These two variants differ only in interpretation. In either case, the adult environment A encompasses all the information available to an adult (including potential sampling of J). In the 'sampling scenario' we simply let the imperfect correlation between A and J reflect the state of knowledge that can be reached in A by sampling J. In the 'inference without sampling scenario' the correlation between J and A has a more direct interpretation: it results from an external forcing (e.g. weather) which indirectly causes a correlation between the juvenile and adult environment (Fig. 2).

Figure 1. Offspring survival probability $S_G(s)$ in a 'good' juvenile environment (dashed), and $S_P(s)$ in a 'poor' juvenile environment (solid), describing how survival in a good vs poor environment increase with offspring size. Size-number tradeoff function $n(s)$ (dotted), describing how number of offspring decreases with offspring size. Parameters: $a = 3$, $\beta_P = 50000$, $\beta_G = 5000$, $R = 10$.
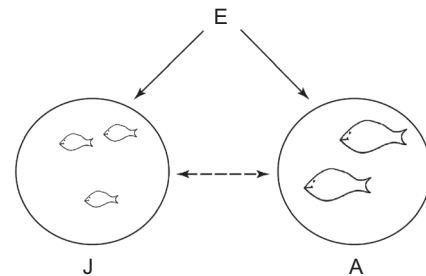

Figure 2. Sketch of environmental components. External environment E, juvenile environment J and adult environment A are set up in a hierarchical way, such that E influences both J and A directly (solid arrows) and an indirect influence arises between J and A (dashed arrows).

To accommodate these assumptions we model an environment consisting of three components with a hierarchical structure: the external environment E, the juvenile environment J, and the adult environment A. Similarly to J and A, the external environment E can be in a 'good' or a 'poor' state. This state creates the forcing that influences both J and A in the following fashion: The juvenile environment J stays in its current state with probability p_j, and switches to the current state of the external environment E with probability $(1-p_j)$. Similarly the adult environment A stays in its current state with probability p_a, and switches to the state of E with probability $(1-p_a)$. There is no feedback from J or A to E, instead the external environment E stays in its current state with probability p_e, and switches to its alternative state with probability $(1-p_e)$.

These environmental dynamics can be described by a simple stochastic process which has a finite number of discrete states and forms a Markov chain. The three components of the environment (E,J,A) can be in state 'good' or 'poor' each, resulting in eight different three-dimensional states altogether. These eight states form the state space Ω of the system,

$$\Omega = \{(P,P,P),(P,P,G),(P,G,P),(G,P,P),(P,G,G),$$
$$(G,G,P),(G,P,G),(G,G,G)\}, \qquad (5)$$

where, for example, state (G,P,G) describes the case that the external environment E is good, the juvenile environment J is poor and the adult environment A is good.

Our next aim is to calculate how often each of the eight possible states occur in the system. This allows us to derive the correlation between the J and A environments based on the parameters p_e, p_j and p_a. To derive the frequencies of these states, we have to analyse the stochastic process describing the dynamics of the environment. The Markov transition probabilities t_{ij} define the frequencies of state changes from state i to state j for all possible values $i = 1,\dots,8$ and $j = 1,\dots,8$. The transition probabilities are summarized in the transition matrix $\mathbf{M} = (t_{ij})_{i,j}$ which is given below.

It is worth emphasizing that it is not the actual state of the three environmental components E, J and A that determines the probability of the three-dimensional state in D, as we did not assign probabilities to states but to switches between states (our p parameters). The probability that the adult environment matches the poor state of the external environment while the juvenile environment differs from these by being in a good state (this is expressed as $D(P,G,P)$ is thus equal to $D(G,P,G)$ in which the adult environment once again reflects the external environment but this time by both being in a good state, and again the juvenile environment differs, now by being poor. In both cases the adult environment A and the external environment E are in the same state, while J is in the alternative state. This logic applies to all such pairings, and hence, the eight probability values in D split up into four pairs and summing up one of each pair gives a probability of 0.5,

$$D(P,G,G) + D(G,G,G) + D(P,P,G) + D(G,P,G) = 0.5 \qquad (7)$$

The numerical values of the elements of D are useful for deriving the following three biologically meaningful expressions: the probability $f_{G|G}$ that the offspring will experience a good environment given that the adult environment is good, $f_{G|P}$ that the offspring environment is good even though the adult environment is bad, and the environmental reliability r,

$$f_{G|G} = \frac{D(P,G,G) + D(G,G,G)}{D(P,G,G) + D(G,G,G) + D(P,P,G) + D(G,P,G)}$$
$$= 2(D(P,G,G) + D(G,G,G)) \qquad (8)$$

$$f_{G|P} = \frac{D(P,G,P) + D(G,G,P)}{D(P,G,P) + D(G,G,P) + D(P,P,P) + D(G,P,P)}$$
$$= 2(D(P,G,P) + D(G,G,P)) = (1 - f_{G|G}) \qquad (9)$$

$$\mathbf{M} = \begin{pmatrix}
p_e & 0 & 0 & p_a(1-p_e)p_j & 0 & p_a(1-p_e)(1-p_j) & (1-p_a)(1-p_e)p_j & (1-p_a)(1-p_e)(1-p_j) \\
(1-p_a)p_e & p_a p_e & 0 & 0 & 0 & 0 & (1-p_e)p_j & (1-p_e)(1-p_j) \\
p_e(1-p_j) & 0 & p_e p_j & 0 & 0 & p_a(1-p_e) & 0 & (1-p_a)(1-p_e) \\
1-p_e & 0 & 0 & p_a p_e p_j & 0 & p_a p_e(1-p_j) & (1-p_a)p_e p_j & (1-p_a)p_e(1-p_j) \\
(1-p_a)p_e(1-p_j) & p_a p_e(1-p_j) & (1-p_a)p_e p_j & 0 & p_a p_e p_j & 0 & 0 & 1-p_e \\
(1-p_e)(1-p_j) & 0 & (1-p_e)p_j & 0 & 0 & p_a p_e & 0 & (1-p_a)p_e \\
(1-p_a)(1-p_e) & p_a(1-p_e) & 0 & \mathbf{0} & 0 & 0 & p_e p_j & p_e(1-p_j) \\
(1-p_a)(1-p_e)(1-p_j) & p_a(1-p_e)(1-p_j) & (1-p_a)(1-p_e)p_j & 0 & p_a(1-p_e)p_j & 0 & 0 & p_e
\end{pmatrix} \qquad (6)$$

The stable distribution D of the Markov chain will give the desired frequency of each state. D is a 1×8 vector determining the equilibrium distribution of the eight states given above and it can be calculated by finding the normalized leading eigenvector of the matrix $\mathbf{M}$. While it is possible to find an analytical solution for the stable distribution D, the expressions are unwieldy (the expressions are available from the authors on request).

$$r = 2[D(P,G,G) + D(G,G,G) + D(G,P,P)$$
$$+ D(P,P,P)] - 1 = 2f_{G|G} - 1 \qquad (10)$$

Our measure of reliability r describes the correlation between the states of A and J, with values ranging from $r = 0$ (nothing can be deduced about the state of J when knowing the state of A, i.e. the 'no information scenario') to $r = 1$ (A and

J are always in the same state). For a system where adults are able to sample the juvenile environment (the 'sampling scenario'), r can be interpreted as the accuracy of an adult's estimate of the juvenile environment. This is best reflected by presenting examples. Consider a case where p_e is high, such that the external environment is highly autocorrelated (it switches state infrequently), and both p_j and p_a are very low, meaning that the adult and juvenile environmental states are mostly copies of the external environment rather than autocorrelated with their own past state. Intuitively, this means that reliability should be high, as both the adult and juvenile environment are similarly forced by the external environment. Numerical values confirm this intuition: for example $p_e = 0.9$, $p_a = p_j = 0.1$ leads to high reliability $r = 0.96$. For the 'sampling scenario' this means that estimates are very accurate. Alternatively, under the equally valid 'inference without sampling' interpretation, the close correlation between juvenile and adult environments indicates that adults can base their decision on the fact that the states of J and A are almost always identical. But if, for example, $p_e = 0.4$ and $p_a = p_j = 0.9$, the reliability becomes $r = 0.04$ and reproductive decisions should take into account that A and J will often be in different states (they are only rarely updated to match the external environment).

Results

In our results, we consider two kinds of optima: we consider 'optimal offspring size' under various conditions but also 'optimal plasticity', which we define as the difference between optimal offspring sizes when the environment is good and when it is poor (usually the environment here refers to the adult environment because this is the one that the mother is able to measure). When the optimal size of offspring is identical across these environmental conditions, the model will indicate that optimal plasticity is zero (no size difference).

Fitness maxima under certainty and dependency on resources

The fitness function given in Eq. 3 has a maximum at some positive offspring size (fitness $W(s)$ is greater than zero for positive offspring size s, and since $W(0) = 0$ and $\lim_{s \to \infty}(W(s)) = 0$), which means that mothers are expected to balance the size-number tradeoff at an intermediate size. We first consider the special case where adults have complete information about the conditions their offspring will encounter ($f = 1$ or $f = 0$). In this case the optimal size of offspring can be calculated by setting the first derivative of the fitness functions in Eq. 4a and Eq. 4b to zero. Maternal fitness is then maximized at offspring size $\hat{s}_{f=1} = (\beta_G a - \beta_G)^{1/a}$ or $\hat{s}_{f=0} = (\beta_P a - \beta_P)^{1/a}$ when the mother knows for sure that the offspring environment will be good or poor, respectively. These optimal sizes do not depend on R, the total amount of resources available to a mother. This result is in agreement with earlier findings in optimal offspring size theory, and in our model it holds generally (i.e. not only for the case of complete information) as R cancels out when setting the derivative of Eq. 3 equal to zero.

We next proceed to comparing good and poor conditions. Our assumptions that offspring benefit more from large size in poor environments are reflected in $\beta_G < \beta_P$ and $a > 1$, and it follows that $\hat{s}_{f=1} < \hat{s}_{f=0}$. The model thus produces the expected outcome that the optimal offspring size is smaller when offspring are guaranteed to experience good conditions than when they are guaranteed to experience poor conditions. It is in the interest of the mother to take advantage of higher survival in her offspring and invest in producing more of them, or – expressed as the flipside of the same argument – a mother is expected to buffer offspring survival against adverse conditions by investing more in fewer offspring.

When mothers face uncertainty when determining optimal offspring size fitness becomes a weighted geometric average of the two fitness functions under certainty, with the probabilities that the offspring environment is 'good' versus 'poor' forming the weights. The probabilities that the offspring environmental conditions are 'good' versus 'poor' are given by $f_{G|G} = (1+r)/2$ and $f_{G|P} = (1–r)/2$, respectively. We get separate fitness functions for the two environmental states a mother might currently face. Maternal fitness hence becomes

$$W_G(s) = n_G(s)^{(1+r)/2} \times S_G(s)^{(1+r)/2} \times n_P(s)^{(1-r)/2} S_P(s)^{(1-r)/2} \quad (11a)$$

$$W_P(s) = n_G(s)^{(1-r)/2} \times S_G(s)^{(1-r)/2} \times n_P(s)^{(1+r)/2} S_P(s)^{(1+r)/2} \quad (11b)$$

for a 'good' and 'poor' adult environment, respectively, where r is the reliability. These two fitness functions reach their maxima at two different optimal offspring sizes which we call $\hat{s}_G$ and $\hat{s}_P$ (Fig. 3).

The two fitness functions and hence also their maxima approach each other when we increase the autocorrelation within the juvenile and adult environments while keeping the external autocorrelation constant (Fig. 3). To quantify this effect, we define the 'optimal degree of phenotypic plasticity' in offspring size as the difference between optimal offspring sizes in the 'poor' and 'good' adult environment, $\hat{s}_P - \hat{s}_G$ (the horizontal distance between the stars indicating the fitness optima in Fig. 3). When the maxima are far apart, it is optimal for a mother to be highly plastic. Plasticity is strongest – i.e. the size difference of offspring produced in different environments is at its largest – when mothers can perfectly predict the juvenile environment (i.e. when reliability $r = 1$; see vertical dashed lines in all panels of Fig. 3). Plasticity will always disappear when the two fitness functions are identical, since this automatically produces $\hat{s}_G = \hat{s}_P$. This occurs not only in the special case where there is no difference in survival in 'good' and 'poor' environments (in which case the labels 'good' and 'poor' lose their meaning), but also in a much more general case where the probability that the offspring environment is good is independent of the current state of the adult environment (reliability $r = 0$). Note that the same value of r might result from different combinations of autocorrelation probabilities (p_a, p_j and p_e, Fig. 4).

The fitness equations for 'good' and 'poor' adult environmental states predict optimal plasticity based on the reliability r. All combinations of autocorrelations p_a, p_j and p_e that lead to the same value of r produce the same level of optimal plasticity. This means that very different
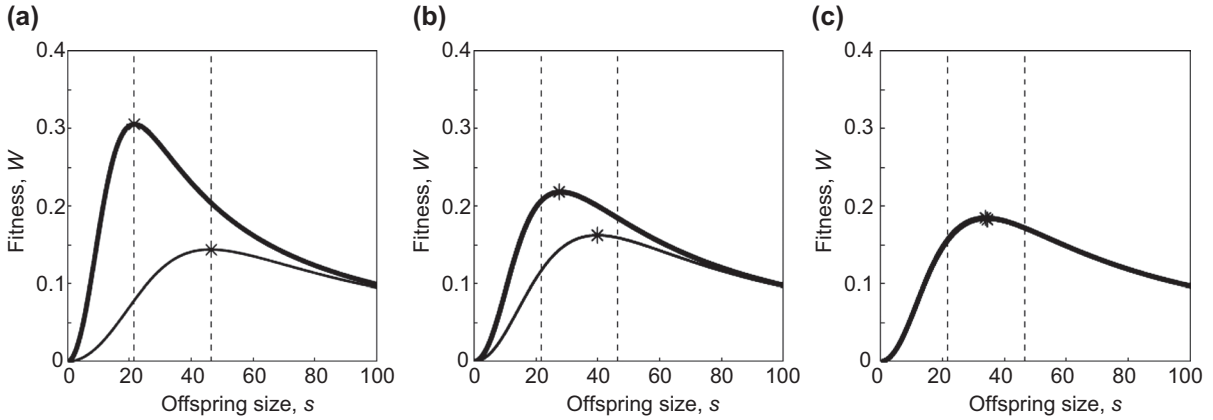
Figure 3. Example fitness functions. Maternal fitness depending on offspring size for different combinations of autocorrelation values p_e, p_j and p_a when adult environment is 'good' (thick) and when adult environment is 'poor' (narrow). Stars indicate the maxima of the fitness functions. Vertical dashed lines show optimal offspring size in a certainly 'good' (right vertical dashed line) and certainly 'bad' (left vertical dashed line). Parameters: (a) $p_e = 0.31$, $p_j = p_a = 0.07$; (b) $p_e = 0.31$, $p_j = p_a = 0.31$; (c) $p_e = 0.31$, $p_j = p_a = 0.93$; Other parameters: $a = 3$, $\beta_B = 50000$, $\beta_G = 5000$, $R_G = R_P = 10$.

environmental situations can give rise to the same reliability and consequently the same plasticity (Fig. 4). Optimal plasticity is always zero for zero reliability (the 'no information scenario'), and grows with increasing reliability r (Fig. 4a): in other words the better mothers can estimate the offspring environment, the greater the difference in offspring sizes (for given survival functions). However, this relationship is generally not linear. The shape of the function describing how plasticity depends on reliability can vary from almost linear to sigmoid for different choices of parameters in the survival functions (Fig. 4a). The same reliability value can result from different combinations of environmental autocorrelation values: because reliability increases with growing p_e and with decreasing p_j and p_a, a smaller p_e (more frequent switching of the external environment) can be compensated by even smaller p_j and p_a (juvenile or adult environments follow the external environment more faithfully) such that reliability as a whole remains intact (Fig. 4b).

Because of these relationships between reliability and the environmental autocorrelations, we can rephrase our above findings and state that optimal plasticity also increases with growing autocorrelation of the external environment (increasing p_e) and with decreasing p_j and p_a, that is when the juvenile and adult environments mostly follow the external environment rather than their own autocorrelation (Fig. 5). This is a direct consequence of the monotonous relationship between reliability and plasticity (i.e. each value of reliability predicts a unique value for plasticity regardless of which combination of p_e, p_j and p_a values produced the current level of reliability; compare Fig. 5 with Fig. 4a). High p_e indicates that the external force fluctuates slowly, and this together with low values for the autocorrelations p_a and p_j lead to juvenile and adult environments which track the external environment E fast enough for high reliability. This makes good predictions possible and ultimately leads to a high optimal degree of plasticity in offspring size.
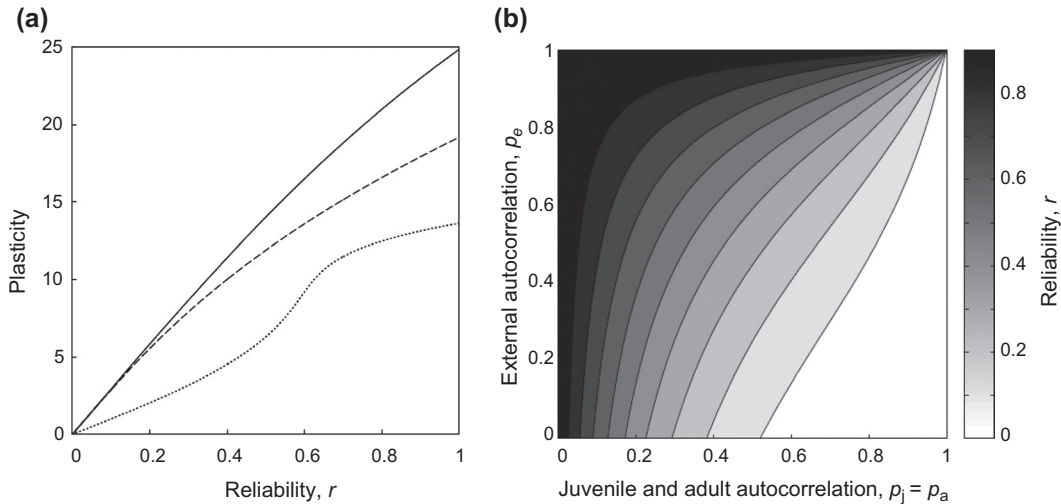

Figure 4. (a) Optimal plasticity in offspring size as a function of reliability for different parameters in the survival functions. Solid line: $a = 3$, $\beta_P = 50000$, $\beta_G = 5000$; dashed line: $a = 2$, $\beta_P = 500$, $\beta_G = 10$; dotted line: $a = 5$, $\beta_P = 500000$, $\beta_G = 500$. (b) Reliability as a function of the external autocorrelation p_e, juvenile p_j and adult p_a autocorrelation, for $p_a = p_j$.
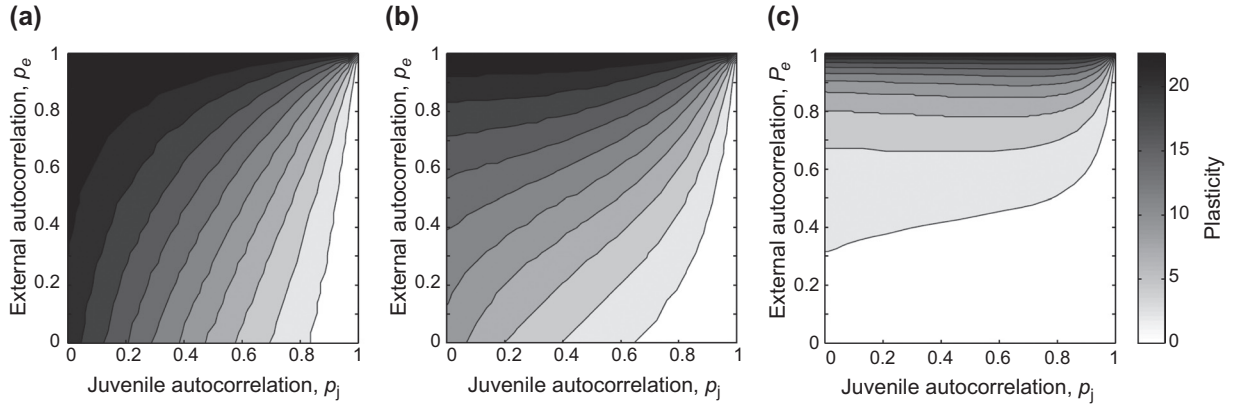
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Figure 5. Optimal degree of phenotypic plasticity in offspring size as a function of the of the external autocorrelation p_e, and juvenile autocorrelation p_j, for three different levels of adult environmental autocorrelation and for the almost linear reliability-plasticity relationship shown in Fig. 4a, solid line. (a) $p_a = 0.1$; (b) $p_a = 0.5$; (c) $p_a = 0.9$; Survival parameters as in Fig. 4a, solid line: $a = 3$, $\beta_P = 50000$, $\beta_G = 5000$.

If the juvenile environment is strongly autocorrelated as is the external environment, for example $p_j = 0.9$, $p_e = 0.9$, the optimal degree of plasticity can change rapidly when varying one of the parameters slightly (the contour lines lie very close to each other in the upper right corners of each panel in Fig. 5). The area in parameter space where optimal plasticity drops to zero (mothers are expected to exhibit no plasticity) is at its widest when p_a is large, i.e. when the adult environment follows its own autocorrelation rather than forms a useful predictor of the offspring environment (Fig. 5).

The effect of survival

Our survival functions have three parameters, which makes it desirable to simplify the analysis by introducing dimensionless variables. This reduces the number of independent parameters. We define a new variable $x = \dfrac{s}{b}$ such that x measures size relative to b, where $b = \sqrt[a]{\beta_G}$. The survival functions can thus be rewritten as $S_G(x) = \dfrac{x^a}{1+x^a}$ and $S_P(x) = \dfrac{x^a}{\gamma^a + x^a}$, where $\gamma = \sqrt[a]{\beta_P/\beta_G}$. The size-number tradeoff function n then becomes $n(x) = \dfrac{R/b}{x}$. As the total amount of resources available to a mother does not affect optimal offspring size (see explanation above) but affects fitness through offspring number, dividing R by b has no effect on optimal offspring size.

The new parameter γ is always greater than 1. It describes by how much an offspring has to be larger in the poor environment to reach the same survival probability ('midpoint') as an offspring of relative size 1 who resides in a good environment. At the midpoint size γ, an offspring survives in the poor environment with probability 1/2: $S_P(\gamma) = 1/2$. The midpoint of good survival is 1, $S_G(1) = 1/2$. The slopes of the survival functions at their midpoints are

$$\xi_P = S_P{}'(\gamma) = \frac{a}{4\gamma} \tag{12a}$$

$$\xi_G = S_G{}'(1) = \frac{a}{4} \tag{12b}$$

for 'poor' and 'good' survival, respectively. In addition to determining the midpoint of S_P, γ also determines the ratio of the slopes at the midpoints of the survival functions, $\gamma = \xi_G/\xi_P$. We now switch to using ξ_G as a shape parameter instead of a, as ξ_G has a more straightforward interpretation than a: it measures how fast survival increases with size at the midpoint. We finally have two remaining parameters that, in addition to the autocorrelations, describe the system: ξ_G, the slope at the midpoint of the survival in a good environment and γ, the midpoint of the survival in a poor environment.

We next want to analyze how these parameters in the survival functions affect optimal plasticity. We focus on the special case where the reliability r is 1, which is achieved when when p_a, $p_j = 0$, such that both the adult and the juvenile environment never deviate from the external environment E. Maximal reliability $r = 1$ is then reached for any choice of p_e, which means that mothers can perfectly predict offspring environmental conditions. By analyzing this special case we will be able to show how maximum possible plasticity (the horizontal distance between the vertical dashed lines, Fig. 3) depends on the survival parameters. We find that optimal plasticity increases with an increase in the midpoint γ. Since the midpoint is a measure of how much larger an offspring has to be in the poor environment to reach an equivalent survival value as in the good environment, this result makes intuitive sense. The more there is reason to compensate and buffer offspring against adverse conditions, the larger the optimal plastic response. Interestingly, optimal plasticity first decreases but then increases with increasing slope ξ_G (Fig. 6).

Plasticity costs

The above results suggest that the more precise a mother's estimate of the expected offspring environment, the more plasticity in offspring size she should exhibit, although this relationship can be nonlinear. We next wish to take into account that the ability to adjust offspring size flexibly requires mothers to maintain additional sensory and information processing machinery. Keeping track of the environmental state, processing this information and conducting the necessary physiological adjustments, which is required when applying a plastic strategy, can cause additional costs
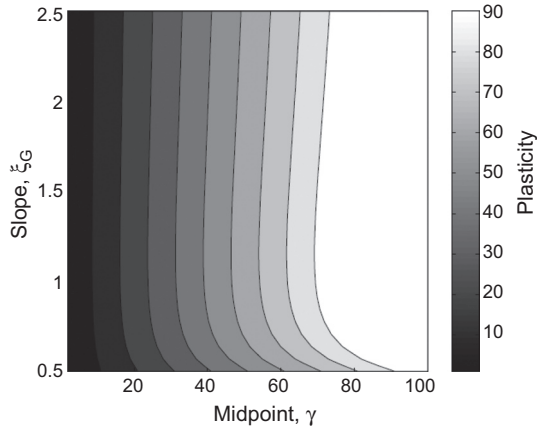
Figure 6. The effect of the two parameters in the juvenile survival functions, *slope* ξ_G and *midpoint* γ on the optimal degree of phenotypic plasticity. Other parameter: $r = 1$.

(DeWitt et al. 1998, Van Buskirk and Steiner 2009). Hence, we compare the fitness of a plastic strategy with the fitness of a fixed strategy under the assumption that a plastic strategy comes with costs that the fixed strategy is able to avoid. The long-term fitness of an offspring size strategy is given by the geometric mean of the fitness in a good and a poor environment, both weighted equally, as the long-term distribution of good versus poor environments is balanced.

$$W_{plast}(s_G, s_P) = \left((R_G - c) \times (R_P - c) \times \frac{1}{s_G s_P} \times S_G(s_G)^{(1+r)/2} \right.$$
$$\left. \times S_P(s_G)^{(1-r)/2} \times S_G(s_P)^{(1-r)/2} \times S_P(s_P)^{(1+r)/2} \right)^{1/2} \quad (13)$$

$$W_{fix}(s) = \left(R_G \times R_P \times \frac{1}{s^2} S_G(s) \times S_P(s) \right)^{1/2} \quad (14)$$

The fitness of the plastic strategy W_{plast} is a function of two size variables: offspring size in a good environment, s_G and offspring size in a poor environment, s_P, whereas the fitness of a fixed strategy W_{fix} is determined by a single offspring size variable s. The amount of resources available to a mother is R_G in a good and R_P in a poor environment. We assume that plasticity costs c reduce the amount of resources to be allocated. Although plasticity costs can be reflected in many different components of fitness, our choice (a fecundity cost) makes sense in our assumed organism that reproduces only once. Reflecting the idea that the costs arise through the need to maintain the plastic machinery, we assume that the cost c is constant across environmental situations.

We now introduce the resource ratio t, $t = R_P/R_G$. This ratio describes the availability of resources in a poor environment relative to the resources in a good environment. We similarly consider the cost fraction u such that $c = u \cdot R_G$. This allows us to specify plasticity costs c for both environments as a fraction of R_G, with t and u taking values between 0 and 1.

We consider the same scenarios as in our above treatments, but we now note that the most realistic values of t are likely

to differ between interpretations. Specifically, in the 'sampling scenario', we include the case of $t = 1$ which means that adult resource availability does not vary with the state of the adult environment A. This means that A simply reflects the information that a mother has about the juvenile environmental as a result of sampling; there is no need for her own resources to reflect the outcome of the sampling. On the other hand, in the 'inference without sampling scenario', it makes sense that the resource level of mothers simultaneously indicates the status of her environment, which would correspond to $t < 1$.

Using the cost fraction u and resource ratio t, we can now simplify the plastic and fixed fitness functions given above. We are interested in whether optimal plasticity or no plasticity has the higher long term fitness for a given parameter combination. Since this is a question of relative rather than absolute fitness values, we can cancel out R_G and drop the square root, leading to

$$\bar{W}_{plast}(s_G, s_P) = (1 - u) \times (r - u) \times \frac{1}{s_G s_P} S_G(s_G)^{(1+r)/2}$$
$$\times S_P(s_G)^{(1-r)/2} \times S_G(s_P)^{(1-r)/2} \times S_P(s_P)^{(1+r)/2} \quad (15)$$

$$\bar{W}_{fix}(s) = r \times \frac{1}{s^2} S_G(s) \times S_P(s) \quad (16)$$

What is relevant for our analysis is the sign of $\Delta W = \bar{W}_{plast} - \bar{W}_{fix}$ since it determines which one of the two strategies has the higher long-term fitness. The fitness difference ΔW being greater than zero identifies situations where mothers should adjust offspring size plastically, whereas where $\Delta W < 0$, evolving fixed offspring size is the superior option. The higher the costs of plasticity, the less favourable it is to be plastic (Fig. 7). Nevertheless, when reliability is high, plasticity is the superior strategy even if adjustment costs are high ('plastic area', white in Fig. 7).

While the above results are perhaps obvious, it is more interesting to note that the resource ratio t strongly influences whether it is optimal for mothers to adjust offspring size. The more balanced maternal resource availability is in a poor versus good environment (the closer the resource ratio t is to 1), the larger the area in parameter space where a plastic offspring size strategy is favoured ('plastic area', white in Fig. 7a–c). This may appear counterintuitive: for given costs of plasticity, we expect more plasticity when environments differ from each other relatively little.

How can this be explained? The difference in environments that is indicated by t does not refer to offspring survival differences, but to maternal resources. The 'reason' to adjust thus stays constant, but the relative payoff of producing offspring through poor conditions decreases when t declines. The situation is somewhat analogous to source-sink populations that largely adapt to source conditions because these matter much more to future generations; good performance in sinks becomes largely irrelevant when sinks contribute little to future generations (the details thus depend on migration from sinks back to sources, Holt 1996). Thus, in our context, only when the poorer environment is likely to contribute relatively
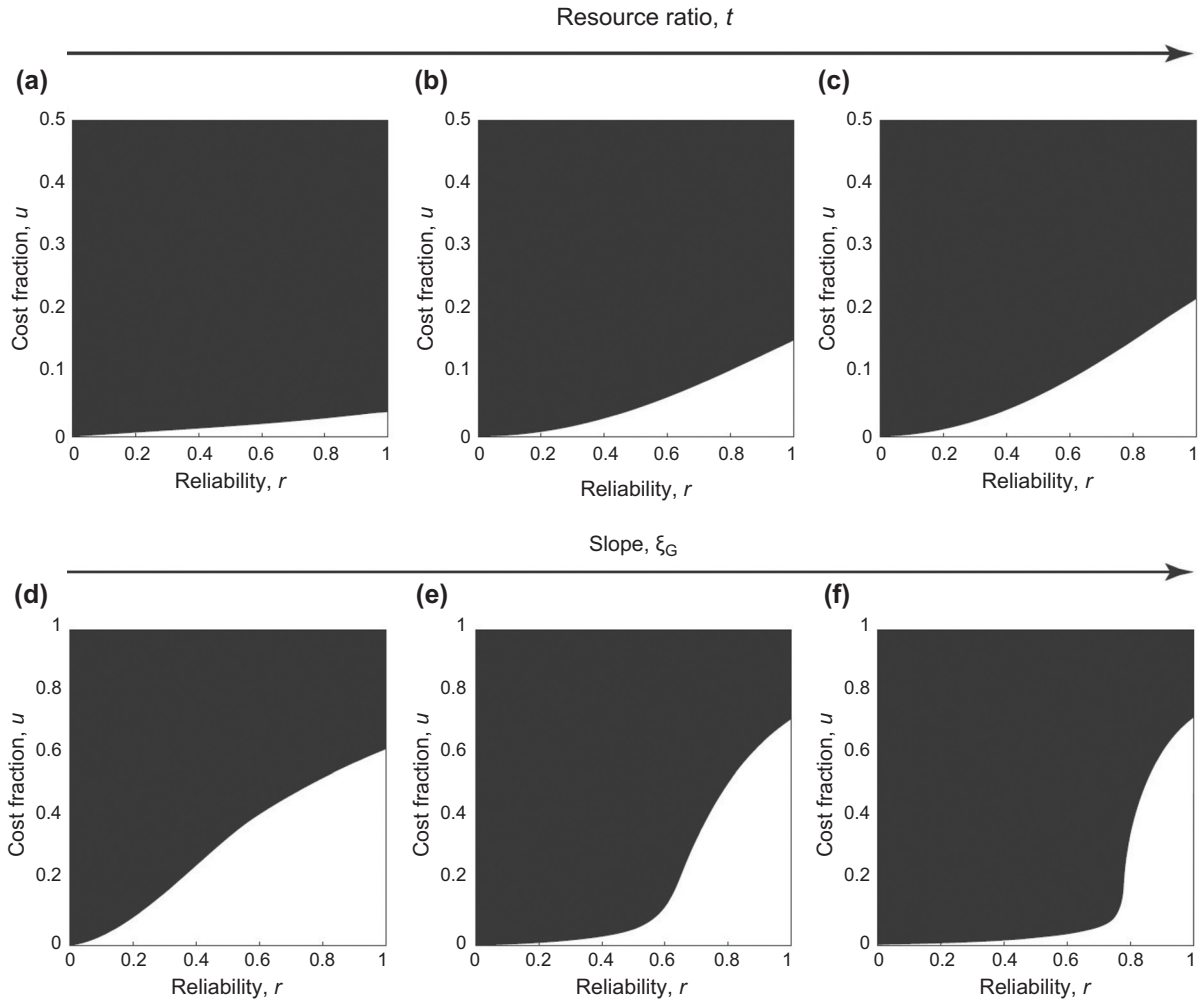
Figure 7. Plastic versus fixed offspring size strategies. Each of the six panels shows where the fixed strategy (black area) or the plastic strategy (white area) has higher fitness, depending on reliability r (horizontal axis) and cost ratio u (vertical axis). First row (a, b and c): resource ratio t increases from left to right (a) $t = 0.1$, (b) $t = 0.5$, (c) $t = 0.9$, other parameters: $\xi_G = 0.75$, $\gamma = 3$. Second row (d, e and f): slope ξ_G increases from left to right (c) $\xi_G = 0.5$, (d) $\xi_G = 1.25$, (e) $\xi_G = 2$, other parameters $r = 0.8$, $\gamma = 45$.

much to future generations (when it is relatively similar to the good environment), will we expect much plasticity to adapt to it (Fig. 7a). Note that if the resource ratio t is 0, the plastic area disappears completely. This corresponds to the case of zero resources in the poor environment, and a fixed offspring size strategy adjusted to the good conditions becomes automatically optimal.

The parameters of the survival functions, the slope ξ_G and the midpoint γ, influence both the size and shape of the area in parameter space where mothers should be plastic (Fig. 7d–f). We numerically investigated the effect of the slope ξ_G and midpoint γ on the shape of the plastic area for the following parameter ranges, $\xi_G \in [0.5, 2.5]$, $\gamma \in [2, 100]$. We found that for any choice of parameters, the plastic area is located around the corner of parameter space where reliability is 1, costs are 0 and the resource ratio is 1. Its size and shape depend on the particular choice of ξ_G and γ (Fig. 7d–f). As a general trend the plastic area expands with growing γ and decreasing ξ_G for the intervals investigated, which means that plasticity evolves most likely when offspring in poor environments need much larger sizes to survive, and when offspring survival improves relatively slowly with increasing

size. The latter relationship is context-dependent, though: for some particular choice of t and u the dependency on ξ_G is non-monotonous (i.e. it can both decrease and increase over the range of possible offspring sizes).

Where plasticity begins to be favoured, it is conceivably possible that plasticity begins in a mild form, i.e. with a small offspring size difference between environments. Alternatively, as soon as the threshold is reached where plasticity is favoured the optimal plasticity (the size difference) could immediately be considerable. The latter case proves optimal in our model. At the threshold plasticity jumps to a considerable large level and thereafter, with increasing reliability r, it increases continuously within the plastic area (Fig. 7, compare Fig. 4a). In the presence of costs, tiny shifts in offspring size are not optimal, as they are outcompeted by fixed strategies (Fig. 7, compare Fig. 4a).

Discussion

In this study, we identify environmental conditions under which offspring size plasticity is expected to evolve. We find

that plastic strategies are likely to be superior to fixed strategies in a variable environment when plasticity costs are low, the reliability of environmental cues available to a mother is high, and the resource availability of mothers does not differ too strongly between environments. Large differences in the dependency of juvenile survival on offspring size in the different offspring environments also favours plastic offspring size strategies. If there are costs to maintaining a plastic machinery, then whenever plastic strategies are found, the occurring shifts in offspring size are predicted to be substantial.

The classical results of Lack (1947) and Smith and Fretwell (1974), which predicted a unique offspring size to be optimal were extended to heterogeneous environments by McGinley et al. (1987) and Parker and Begon (1986), who first mentioned the potential benefits of plastic strategies. In particular, Parker and Begon (1986) considered the effect of maternal body size and competition within a clutch on optimal offspring size jointly, and found that mothers should adjust egg size depending on their own phenotype. Theory predicts that organisms should be plastic when they are exposed to variable environmental conditions, when costs of plasticity are low and when environments provide reliable cues (Levins 1968, Via and Lande 1985, Gomulkiewicz and Kirkpatrick 1992, Moran 1992). Translating these requirements to transgenerational phenotypic plasticity, which is the subject of this study, our results confirm that the evolution of plasticity requires sufficiently reliable cues available to mothers to enable her to predict environmental conditions of her offspring (Marshall and Uller 2007).

In his influential review on the maternal effect of propagule size, Bernardo (1996) criticized that so far, optimality models often neglected the ecological context of mothers (but see Parker and Begon 1986, who accounted for the quality of the adult feeding habitat). He pointed out that conditions during which mothers allocate resources might be uncorrelated with the conditions her offspring will experience, as those environments might be separated in time or space (Bernardo 1996). Our study contributes to closing this gap. We investigate how the correlation between adult and offspring environment influences optimal offspring size and plasticity in this trait. Our approach is novel in that we quantify the reliability of environmental cues necessary to allow plasticity to evolve; we also distinguish between variation in resources that the mother has and the quality of the offspring environment, which may vary independently.

By treating environmental reliability as a variable, we are able to analyze the benefits of plastic strategies versus fixed strategies for the entire range of environmental scenarios, from full synchrony between adult and juvenile environments to random independent fluctuations of the two. We model juvenile and adult environments separately, but our model is capable of describing the entire possible range of scenarios, from complete spatial separation and no information flow between juvenile and adult environments to a situation where juveniles and adults co-occur in the same environment.

Our model results demonstrate that even in environments that are heterogeneous in space and time it is not always selectively favoured to be plastic. We found that plasticity is less likely to evolve if maternal resource availability drops to a very low level when the adult environment is in a poor state and this is correlated with poor juvenile survival chances. This can be explained in an analogous manner as adaptation in source–sink systems (Holt 1996): it is not as 'valuable' to adapt well to environments that offer little fitness prospects as it is to perform well in good environments.

In the example of the seed beetle *Stator limbatus*, maternal nutritional status is clearly not linked to juvenile environmental conditions as juvenile survival is influenced by the type of host seeds mothers use as substrate for their clutch (Fox et al. 1997, 1999). In bryozoans (Allen et al. 2008), on the contrary, maternal food availability is correlated with juvenile survival conditions. Bryozoans are suspension feeders and higher adult density translates into lower space and food availability for mothers and lower post-settlement success and survival chances for their offspring (Allen et al. 2009). In a number of other animals, including cladocerans (Perrin 1989, Guisande and Gliwicz 1992) and guppies (Bashey 2006) mothers produce larger offspring under reduced food availability. Those studies illustrate that plasticity can be favoured even if maternal resource availability is correlated with juvenile survival. According to our results, plasticity becomes less favourable the lower maternal resource availability is under poor environmental conditions relative to resource availability under good environmental conditions. The fitness benefits mothers can gain from adjusting their offspring to poor conditions is then lower because of low resource availability.

When maternal resource availability differs greatly between poor and good environments, our model predicts that plastic strategies are only favoured if juvenile survival or performance also differs strongly between poor and good conditions. The above mentioned empirical study on bryozoans (Allen et al. 2008) fits this prediction of our model, as in this study increased larval size leads to a significant fitness benefit when competition is intermediate. If juvenile survival is similar in both environments, our results predict that mothers exhibiting a conservative, fixed offspring size strategy have higher fitness. In any case, our results suggest the intriguing, empirically testable prediction that variation in maternal resources might select against plasticity while variation in offspring survival changes promotes plasticity (all else being equal).

Although here we modelled a particular environmental scenario with a hierarchical structure, our results are applicable to a much broader range of environmental settings. The chosen structure where adult and juvenile environments track an external environment with some time lag serves as an example that illustrates how a correlation between juvenile and adult habitats can arise. However, for our further analyses it does not matter how this correlation is caused, as we proceed to investigate how the reliability of environmental cues would select for fixed or plastic offspring size strategies. Our results can hence be applied to any other environmental configuration, where adults can predict juvenile conditions, and where a correlation between the adult and juvenile environment exists.

We predict adaptive differences in offspring size to be of significant extent. Tiny switches should not be selected for if plasticity costs are independent of the level of the adjustment. As soon as sampling and information processing occurs, a

plastic genotype has to pay the resulting plasticity costs. The benefits to be possibly gained from small switches might hence not be able to outweigh the effort of maintaining the whole adjustment machinery. Empirical studies demonstrating adaptive plasticity in offspring size fit this prediction very well. Killifish increase their egg size by 26% (dry weight) in a harsh environment (Leips et al. 2009), bryozoans increase offspring size by 13.5% (Allen et al. 2008), cichlids increase offspring mass by 29% (B. Taborsky unpubl.) and in the classic seed beetle example switches are also large: beetles increased egg size by 30% (mass, Fox et al. 1999). In contrast, another seed beetle, *Callosobruchus maculatus*, responds to changes in density in the maternal environment by very small switches in egg width only (1–3%) (Kawecki 1995). Kawecki explained this response as a residue of a much larger response which was possibly lost in generations of rearing under laboratory conditions.

Many, though not all, of our results are based on the idea that plasticity is costly to maintain. In their recent review, Van Buskirk and Steiner (2009) quantified costs of plasticity and found them generally to be mild. They suggest several possible reasons for this – including the option that plastic organisms might experience selection to reduce the costs of plasticity. Our results hint at an additional possibility. If costs of plasticity are high, our model does not predict 'mild' plasticity, but the complete absence of plasticity. An organism displaying no plasticity is unlikely to have studies of plasticity conducted on it, and one may then end up with a dataset of real organisms displaying only mild costs of plasticity.

Our results suggest that improving the overall quality of either the maternal phenotype or her environment should not affect optimal offspring size. As long as optimal offspring size does not interfere with thresholds imposed by maternal morphology it should hence be independent of the maternal phenotype. This result is in line with most theory on offspring size (Parker and Begon 1986, Lloyd 1987, Hendry et al. 2001) in that only offspring number is affected by varying maternal resource availability. Nevertheless, in many species there is a significant within-population variation in offspring size that often correlates with female size (Roff 2002). A popular explanation is that this arises from morphological constraints of the mother, as smaller females can only produce smaller offspring (Congdon and Gibbons 1987, Sinervo and Licht 1992, Clark et al. 2001, Rollinson and Brooks 2008), for example, because of limited pelvic aperture width (Congdon and Gibbons 1987, Sinervo et al. 1991). On the other hand, models incorporating the influence of the maternal phenotype and the juvenile competitive environment jointly or assuming that larger mothers can select better quality environments for their offspring (Parker and Begon 1986, Hendry et al. 2001) predict that offspring size should vary with maternal phenotype.

There are a number of limitations to our model. The first limitation is that while we allowed mothers to adjust offspring size, we assumed constant offspring size within a brood which implies no possibility to adaptively adjust the variation of offspring size within a brood. Adjusting the within-brood variation in offspring size constitutes an alternative strategy that has been called 'diversified' bet-hedging, as opposed to 'conservative' bet-hedging, which simply stands for elevated mean offspring size (Einum and Fleming 2004; note that the use of bet-hedging terminology is relevant in the latter case because larger offspring survive poor environmental conditions, which reduces fitness variance across environments). By now, there is both theoretical (Slatkin 1974, Philippi and Seger 1989, Marshall et al. 2008, Olofsson et al. 2009) and empirical (Crean and Marshall 2009) support for the idea that within-brood variation in offspring size can function as an adaptive strategy for dealing with unpredictably variable environments. In this study, we have shown that the precision with which mothers are able to predict conditions that their offspring will experience influences the evolution of plasticity. For unpredictable environmental conditions, our model predicts a constant offspring size strategy to be optimal. It is conceivable that a diversified bet-hedging strategy could have a selective advantage over a fixed offspring size strategy in certain unpredictably varying environments. In a comparative study on marine invertebrates, Marshall et al. (2008) examined variation in offspring size among mothers of different species with either non-dispersing offspring (where mothers can predict offspring environmental conditions) or dispersing offspring (where mothers cannot predict offspring environmental conditions). Marshall et al. (2008) found high levels of among-mother variation in offspring size in species with non-dispersing offspring. This suggests that plasticity in offspring size occurs where mothers can predict offspring environmental conditions well, which is in line with our results. They also detected low among-mother variation in species with dispersing offspring but high within-mother variation, suggesting bet-hedging as a possible explanation (Marshall et al. 2008). It would be an interesting topic for future work to integrate the option of within-brood variation into the theoretical investigations in addition to comparing plastic and fixed offspring size strategies, as we did here.

Additionally, our model does not explicitly consider density as a factor potentially affecting offspring survival. High density itself has been considered to form a poor environment in experiments on offspring size plasticity (Allen et al. 2008, Leips et al. 2009; but see also Plaistow et al. 2007 for an example where mothers fail to adjust in response to density). Our model is thus valid at least up to the point where maternal decisions do not themselves alter the local density too much (i.e. competition occurs over larger scales). Considerations of local density should also take into account competition between relatives. Parker and Begon (1986) explicitly consider the difference between sib competition and more general competition, and Plaistow et al. (2007) show empirically that sib competition can also create shifts over the life history of a mother: in soil mites younger offspring have to compete with older, larger siblings, which makes it adaptive for mothers to shift from producing large broods to producing large offspring over their lifetime.

The monotonous increase of juvenile survival probability with increasing offspring size has been criticized in the literature, stating that juvenile survival should instead peak at a size reflecting maximum viability (e.g. a maximum egg size defined by the maternal morphological constraints) and from there on decrease rapidly (Hendry et al. 2001). Physiological and morphological thresholds of mothers could be easily incorporated in the model; these are likely to be

system-specific and should therefore be considered in models more directly inspired by a specific biological system.

An interesting extension of this model would be to allow mothers to use other cues but the ones that can be obtained their current environment. Under certain conditions, cues obtained from a female's own juvenile environment might allow rather precise predictions about the offspring environment, and empirical evidence is accumulating that such strategies can be successful (Taborsky 2006a, 2006b, Vijendravarma et al. 2009). Moreover, it would be interesting to investigate further environmental structures differing from the hierarchical structure we analyzed here, and investigate how they can possibly give rise to a correlation between adult and juvenile environments and thereby affect the reliability of environmental cues.

We conclude that the level of plasticity in offspring size should be expected to increase with the reliability of environmental cues, whereas for low levels of reliability fixed strategies are superior. Any plastic switches between large and small offspring are predicted to be of significant extent. Moreover our model predicts that the more juvenile survival conditions differ between environments, the higher is the likelihood that plasticity in offspring size can evolve.

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