

How should parents adjust the size of their young in response to local environmental cues?

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Abstract

Models of parental investment typically assume that populations are well mixed and homogeneous and have devoted little attention to the impact of spatial variation in the local environment. Here, in a patch-structured model with limited dispersal, we assess to what extent resource-rich and resource-poor mothers should alter the size of their young in response to the local environment in their patch. We show that limited dispersal leads to a correlation between maternal and offspring environments, which favours plastic adjustment of offspring size in response to local survival risk. Strikingly, however, resource-poor mothers are predicted to respond more strongly to local survival risk, whereas resource-rich mothers are predicted to respond less strongly. This lack of sensitivity on the part of resource-rich mothers is favoured because they accrue much of their fitness through dispersing young. By contrast, resource-poor mothers accrue a larger fraction of their fitness through philopatric young and should therefore respond more strongly to local risk. Mothers with more resources gain a larger share of their fitness through dispersing young partly because their fitness in the local patch is constrained by the limited number of local breeding spots. In addition, when resource variation occurs at the patch level, the philopatric offspring of resource-rich mothers face stronger competition from the offspring of other local mothers, who also enjoy abundant resources. The effect of limited local breeding opportunities becomes less pronounced as patch size increases, but the impact of patch-level variation in resources holds up even with many breeders per patch.

Introduction

How much should a parent invest in each individual offspring, given that greater investment in each entails a decrease in the total number of young produced? This question, often expressed as the trade-off between offspring size and number (Smith & Fretwell *et al.*, 1974; Lloyd, 1987), is a central focus of life history theory (Bernardo, 1996b; Fox & Czesak, 2000; Roff, 2002). Whereas classical theory predicted that parents should always produce offspring of a uniform, optimal size (Smith & Fretwell *et al.*, 1974), empirical data

have shown that offspring size often varies according to the age and/or condition of the parent, as well as the nature of the parental environment (e.g. Meffe, 1987; Einum & Fleming, 2002; Marshall & Keough, 2007; Allen *et al.*, 2008; Räsänen *et al.*, 2008; Leips *et al.*, 2009). Prompted by this data, a number of models have shown that when mothers can anticipate the survival risk that their offspring will endure (Parker & Begon, 1986; McGinley *et al.*, 1987; Fischer *et al.*, 2011), they do, indeed, stand to gain by producing larger offspring when these survival risks are greater (the so-called bigger is better hypothesis: Sogard, 1997; Krist, 2011). This effect may favour production of larger young by mothers exposed to a harsher environment, and/or by more fecund mothers, whose offspring are likely to experience a density-dependent reduction in survival.

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Most current life history models, however, focus on the evolution of offspring size strategies in well-mixed populations. Even those models that focus on adjustment of offspring size in response to varying environmental conditions have not explicitly considered the spatial and temporal pattern of environmental variation. Here, we address this lack by developing a spatially explicit model of parental investment in a patch-structured population, where resource availability and survival risk may vary from patch to patch and from one generation to the next. In this framework, parental investment can be considered as a social trait (see also Lion & Van Baalen, 2007; Van Cleve *et al.*, 2010) that affects the fitness of others in a patch, analogous to the more abstract helping and harming traits whose evolution in viscous populations has been studied in great detail (Taylor, 1992; Gardner & West, 2006; Johnstone & Cant, 2008; Lion & Gandon, 2009; Lion *et al.*, 2011; Rodrigues & Gardner, 2012). Just as local kin competition can influence helping and harming behaviour, we show that it can also influence parental investment, leading to some novel and surprising predictions about the ways in which mothers should respond to local environmental conditions.

The model

Model description

To study the evolution of resource-dependent offspring size in a variable environment, we make use of a demographic kin selection model (Taylor & Frank, 1996; Rousset, 2004; Lion *et al.*, 2011; Rodrigues & Gardner, 2012), of which a formal description is provided in the Appendix. Consider an ‘infinite island’ population with haploid inheritance that reproduces sexually, with nonoverlapping generations. The population is structured into discrete territories, each containing n male and n female breeders. Female breeders vary in the (nonheritable) amount of resources they have to invest in reproduction, with variation in resources occurring either at the individual level or at the patch level. In the former case, when variation occurs at the individual level, each female receives either a high amount of reproductive resources x_h with probability q_h or a low amount of reproductive resources x_l with probability $1 - q_h$. Hence, the number of female breeders n_h that received a high amount of resources in a given territory ($0 \leq n_h \leq n$) is a binomially distributed variable, $n_h \sim \text{Bin}[n, q_h]$. When resources vary at the level of the patch, all females in a particular patch receive either a high amount of reproductive resources x_h with probability q_h or a low amount of reproductive resources x_l with probability $1 - q_h$. We will show that the scale of resource variation strongly affects the degree of individual differences in offspring size plasticity.

Upon receiving x_k resources, $k = \{h, l\}$, each female breeder mates with a randomly chosen male in her local environment. She subsequently produces a number of x_k/m_{ki} offspring, where m_{ki} denotes the size of her young (assumed to be under maternal control), which depends on both her resource level x_k and the current environmental state i of the territory. After birth, each offspring either disperses to a random patch with probability d or remains on its natal patch with probability $1 - d$. We assume that dispersal is cost free.

Territories differ in their environmental quality, which affects the size-dependent survival $f_j(m_{ki})$ of juveniles after dispersal into environment j . The current model considers two types of territory $j = \{g, b\}$ (‘good’, ‘bad’), and the survival probability of a juvenile with any given size is higher in the good environment: $f_g(m_{ki}) > f_b(m_{ki})$. Because there are two possible levels of maternal resources (high and low) and two possible environmental qualities (good and bad), a maternal strategy must specify offspring size, m_{ki} , for all four possible combinations of resource level and environmental state; these four size values are summarized in the vector $\mathbf{m} = [m_{hg}, m_{lg}, m_{hb}, m_{lb}]$.

After the survival stage, the surviving offspring of each sex compete for the n breeding positions in the patch. Subsequently, the quality of each local environment may change from type j to ℓ with probability $s_{j \rightarrow \ell}$, after which the reproductive cycle repeats. All in all, our model thus includes two sources of variation: (i) spatiotemporal variation between patches in size-dependent survival of juveniles $f_j(m_{ki})$ and (ii) variation in the amount of resources x_k that a mother obtains (Fig. 1).

Assuming that evolution proceeds through the successive substitution of small-effect mutations, the rate of evolutionary change in offspring size trait m_{ki} is proportional to the marginal rate of change in the fitness W_i of individuals occupying environment i , with respect to the trait in question. Using a neighbour-modulated fitness approach, this selection gradient is given by

$$\frac{dW_i}{dm_{ki}} = \left[\frac{\partial W_i}{\partial m_{ki}} + R_{\text{loc},i}^f \frac{\partial W_i}{\partial \hat{m}_{ki}^f} + R_{\text{loc},i}^m \frac{\partial W_i}{\partial \hat{m}_{ki}^m} \right] \Big|_{\mathbf{m}=\hat{\mathbf{m}}^f=\hat{\mathbf{m}}^m=\bar{\mathbf{m}}}. \quad (1)$$

The first part within square brackets reflects the fitness effect of a change in the focal parent’s size trait m_{ki} , whereas the second and third parts reflect the fitness effects of a change in the mean size trait of local females on a focal female and on a focal male, respectively, where the average offspring size trait among females in the focal’s patch is denoted \hat{m}_{ki}^f for a focal female and \hat{m}_{ki}^m for a focal male; the population-wide average size trait is denoted \bar{m}_{ki} . The second and third terms are weighted by the coefficients $R_{\text{loc},i}^f$ and $R_{\text{loc},i}^m$, which denote the relatedness of local females to a focal female or to a focal male.

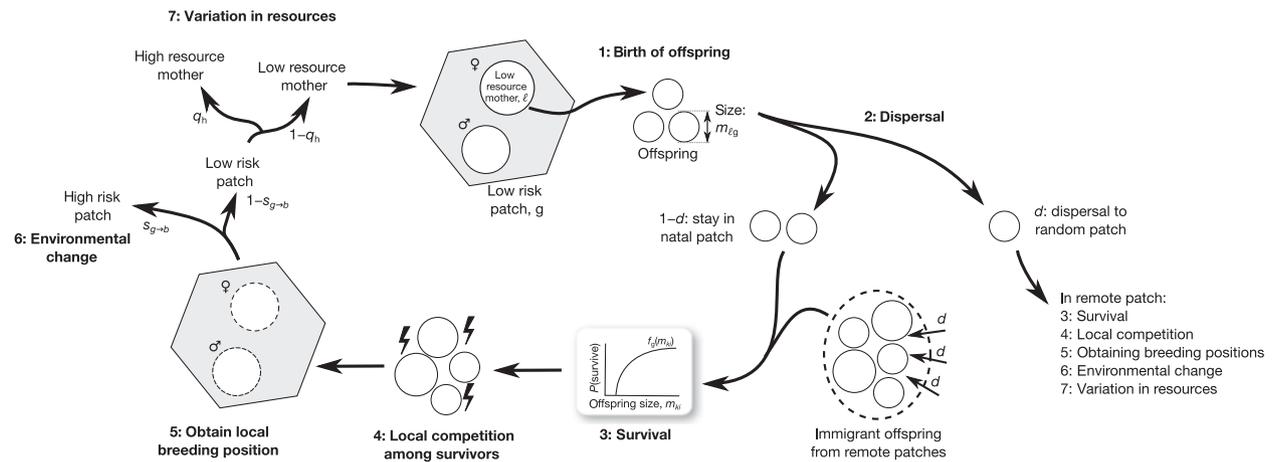


Fig. 1 Transitions between the different life cycle stages. For sake of simplicity, we depicted a single breeding pair per patch ($n = 1$) and focus on one of the infinitely many patches. Stage 1: birth and determination of offspring size m_{ki} , dependent on the level of local level of risk (for this particular patch: low risk) and the level of maternal resources (for this particular mother: low resources). Stage 2: dispersal: juveniles remain in the local patch with probability $1-d$ and leave with probability d . Stage 3: all juveniles in a particular patch (i.e. natively born offspring and incoming migrants) have a size-dependent survival probability $f_g(m_{ki})$, dependent on risk level g of the local patch. Stages 4,5: all surviving juveniles compete for local breeding positions. Stage 6: due to environmental change, the patch may change towards a high-risk patch with probability $s_{g \rightarrow b}$ or remains a low-risk patch with probability $1 - s_{g \rightarrow b}$. Stage 7: each mother becomes a high-resource mother with probability q_h , whereas she becomes a low-resource mother with probability $1 - q_h$. The degree of resources obtained by each mother is nonheritable. After stage 7, the life cycle continues.

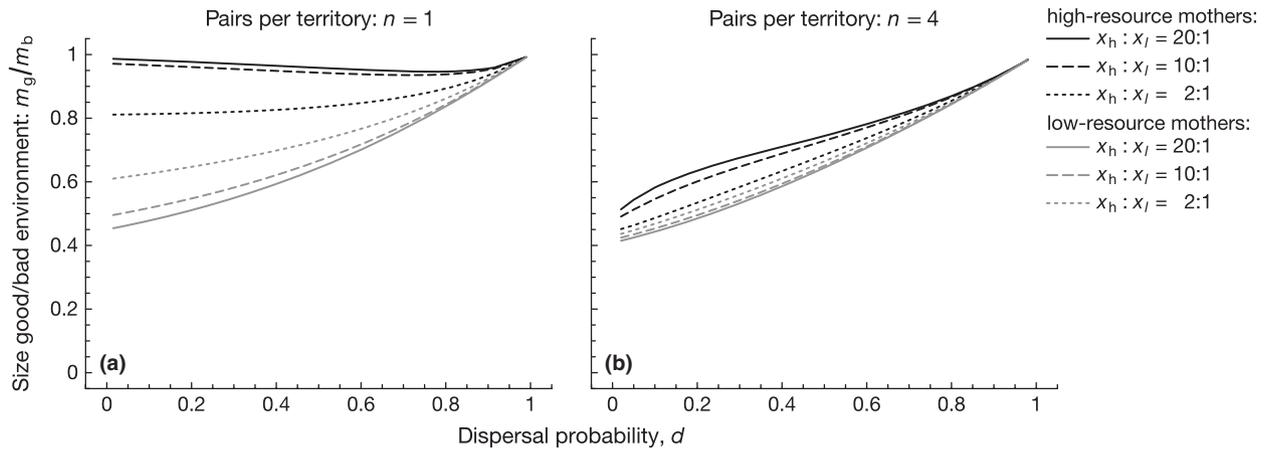


Fig. 2 Limited dispersal and the evolution of offspring size m in low-risk environments m_g relative to high-risk environments m_b , when variation in maternal resources x occurs between mothers inhabiting the same patch. In case of limited dispersal $d < 1$, low-resource mothers (grey lines) are selected to produce offspring that differ more strongly in size across both levels of risk (hence lower ratios m_g/m_b), relative to high-resource mothers in high-risk environments (who have higher ratios m_g/m_b). The relative divergence between high- and low-resource mothers becomes more pronounced when (i) dispersal is limited, (ii) the number of individuals per patch is limited (cf. panel a vs. b) and (iii) when the amount of resources of high- vs. low-resource mothers x_h/x_l increases. Parameters: $s_{g \rightarrow b} = 0.2$, $s_{b \rightarrow g} = 0.2$, $q_h = 0.2$, $c_g = 0.5$, $c_b = 0.05$, $x_h = 10$, $m_{min} = 2$.

Expressions for W_i and for $R_{loc,i}^f$ and $R_{loc,j}^m$ are derived in the Appendix. Using equation (1), we can then solve for the candidate ESSs of each of the four offspring size traits, by numerically finding the point where the selection differentials for all four offspring size traits vanish. In addition, we used individual-based simulations to confirm that these optima are, indeed,

evolutionary endpoints at which no evolutionary branching occurs.

Parameters

The survival $f_j(m_{ki})$ of offspring of size m_{ki} in environment j is given by the function $f_j(m_{ki}) = 1 - exp$

$[-c_j(m_{ki} - m_{\min})]$, in which m_{\min} represents the minimally viable offspring size and c_j reflects the environment-dependent intensity of size-dependent survival. Given our previous assumption $f_g(m_{ki}) > f_b(m_{ki})$, this implies that $c_g > c_b$. Other functional forms, $f_j(m_{ki}) = (m_{ki} - m_{\min}) / ((1/c_j) + (m_{ki} - m_{\min}))$ and $f_j(m_{ki}) = -c_j^2 (m_{ki} - m_{\min})^2 + c_j(m_{ki} - m_{\min})$, were also explored, but as these gave qualitatively similar results, we do not show these additional results here. The main assumption contained within these expressions for $f_j(m_{ki})$ is that returns on additional investment in offspring size (above the minimum viable size) are diminishing (e.g. Smith & Fretwell *et al.*, 1974; Parker & Macnair, 1978; Parker & Begon, 1986; Lloyd, 1987; McGinley *et al.*, 1987). Although many empirical studies have shown a positive relationship between increased parental investment and offspring fitness (i.e. bigger is better) (Bernardo, 1996b; Fox & Czesak, 2000; Krist, 2011), only a few have actually tested whether increased investment per offspring is met with diminishing returns on offspring fitness (see Gotthard *et al.*, 2007 for a similar discussion). Studies that have performed so, however, have found that increased investment is, indeed, met with decelerating returns (Carrière & Roff, 1995; Nasution *et al.*, 2010).

We solve numerically for the optimal offspring sizes given different levels of dispersal d , relative strengths of juvenile survival $c_g : c_b$ (see Fig. S1), equilibrium frequencies of good q_g vs. bad $1 - q_g$ environment patches (where $q_g = s_{b \rightarrow g} / (s_{b \rightarrow g} + s_{g \rightarrow b})$), relative amounts of reproductive resources $x_h : x_\ell$ and the global frequency of high-resource patches (see Fig. S2).

Results

Figure 2 shows how high- and low-resource mothers should optimally adjust the size of their young when living in a good, low-risk environment, m_g , relative to the size of young produced in a bad, high-risk environment m_b . The offspring size ratio between good and bad environments m_g/m_b is always equal to or less than one, because in accordance with the 'bigger is better hypothesis', offspring facing a good environment will benefit less from a larger size than offspring facing a poor environment (e.g. Parker & Macnair, 1978; Parker & Begon, 1986). The lower the ratio of m_g/m_b , the more responsive parents are to differences in offspring survival between the high- and low-risk environments (i.e. $m_b \gg m_g$).

The first feature to notice in Fig. 2 is that offspring size plasticity based on maternally perceived risk is absent (i.e. $m_g/m_b = 1$) when all young disperse away from their natal site to a random patch (i.e. when $d = 1$), because in this case, the quality of the mother's local environment is uncorrelated with the quality of the remote environment that offspring will encounter (see also Parker & Begon, 1986; Fischer *et al.*, 2011). By con-

trast, when $d < 1$ and at least some offspring remain in their natal patch, mothers almost always adjust the size of their young in response to their current environment (i.e. m_g/m_b), because for these philopatric offspring, the maternal environment is informative about the conditions that they are likely to encounter. The lower the rate of dispersal, that is, the smaller the value of d , the more philopatric young are produced and the more sensitive mothers should be to the local environment.

The second, more interesting insight to be gained from Fig. 2 is that optimal environmental plasticity in offspring size depends on the level of maternal resources. The model predicts that high-resource mothers (black lines) should be less sensitive to good vs. bad environments than should low-resource mothers (grey lines): for high-resource mothers, the ratio m_g/m_b is closer to unity than for low-resource mothers, whose offspring in good environments are up to 42% smaller compared to offspring in poor environments, for the parameters considered in Fig. 2.

This difference in plasticity between high-resource and low-resource mothers is most apparent when only one breeding pair occupies each individual patch ($n = 1$, Fig. 2a). When multiple individuals breed on the same patch ($n > 1$) and these breeders vary among each other in their level of resources (within-patch resource variation), resource-based differences in plasticity rapidly decay with an increasing number of breeders per patch (Fig. 2b). However, when all breeders in a single patch receive the same level of resources (between-patch resource variation), substantial differences in plasticity between high- and low-resource females persist (Fig. 3) even for a large number of breeding pairs per patch ($n = 20$, Fig. 3b).

In Figure 4, we examine the impact of changes on the global frequency q_b of high-risk patches. The qualitative prediction that low-resource mothers should respond more strongly to local risk than should high-resource mothers (i.e. that low-resource mothers should have smaller ratios m_g/m_b) is unaffected by this model parameter, but quantitatively, resource-based differences in maternal responsiveness are most pronounced when the frequency of high-risk patches is relatively low. We have also explored the impact of changes in the global frequency of high-resource patches q_h , and although the relevant figure is left to the Supplement (Fig. S2), we find once again that the qualitative difference in responsiveness between high- and low-resource mothers is unaffected by this parameter value, although the effect of maternal resources is most pronounced when high-resource patches are rare.

Discussion

Our model suggests that mothers who differ in their level of resources should respond in different ways to environmental risk. Specifically, Figs 2 and 3 show that

resource-poor mothers should produce much larger young in poor compared to good offspring environments, whereas resource-rich mothers should produce offspring of a more constant size regardless of the local level of risk. These differences in parental plasticity between resource-rich and resource-poor mothers are, however, sensitive to the scale of resource variation. When resources vary among individual mothers that breed in the same patch (within-patch resource variation), differences in plasticity between high- and low-resource mothers rapidly decrease with the number of individuals n that breed within a patch (Fig. 2b). By contrast, when resource levels are similar for all female breeders within a single patch (between-patch resource variation), differences in plasticity between high- and low-resource mothers are robust and persist even at large patch sizes (Fig. 3).

Differences in maternal sensitivity to local environmental risk arise in the current model because higher-resource mothers accrue more of their fitness through dispersing young (for whom information about local risk is not informative), whereas lower-resource mothers accrue relatively more fitness through philopatric young (for whom local information about risk is essential). To understand why high-resource mothers are more dependent on dispersing young than are low-resource mothers, consider the relationship between fecundity and fitness accrued through dispersing and philopatric offspring: fitness accrued through dispersing young increases linearly with maternal fecundity (because there are potentially infinitely many patches available to dispersing offspring), whereas fitness accrued through philopatric young is bounded by the number n of breeding positions available in the local patch and thus

approaches a plateau at high fecundity. As a result, dispersing young constitute a disproportionately large share of a high-resource mother's fitness. By contrast, a low-resource mother's fitness returns through philopatric offspring are less likely to saturate, because a low-resource mother produces only few offspring. Therefore, philopatric offspring constitute a relatively larger share of a low-resource mother's fitness, in comparison with a high-resource mother's fitness. This relatively greater dependence on philopatric offspring makes low-resource mothers more sensitive to cues of local risk than high-resource mothers, which explains why variation in maternal resources underlies differences in maternal responsiveness.

The effect described above depends upon the limited number of breeding positions available to philopatric young as compared to dispersing young. The strength of this effect therefore diminishes as patch size increases, which explains why, when resources vary at the individual level, differences in plasticity between high- and low-resource mothers are negligible for large values of n . But how can we explain the observation that when resources vary at the patch level, such differences persist even at large patch sizes? Under these circumstances, the fitness that a higher-resource mother gains through philopatric offspring is constrained not only by the limited number of breeding spots available in the local patch, but also by greater competition from the offspring of other local mothers, all of whom will also be enjoying abundant resources (and consequently high fecundity). Conversely, the fitness that a lower-resource mother gains through philopatric offspring will be enhanced by reduced competition from the offspring of other local mothers, all of whom will

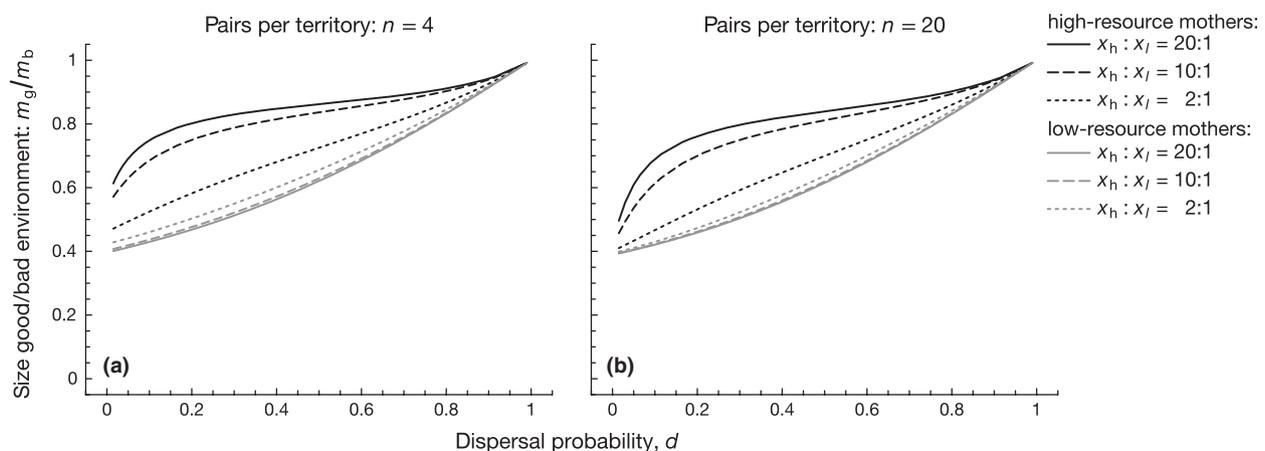


Fig. 3 Limited dispersal and the evolution of offspring size m in low-risk environments m_g relative to high-risk environments m_b , when variation in maternal resources x occurs between patches. In comparison with the case of within-patch variation of maternal resources (Fig. 2b) in which differences between high-resource and low-resource mothers rapidly decay with increasing number of breeders per patch n , between-patch resource variation maintains any differences in responsiveness between high-resource and low-resource mothers for high levels of n (e.g. panel b). Parameters: $s_{g \rightarrow b} = 0.2$, $s_{b \rightarrow g} = 0.2$, $q_h = 0.2$, $c_g = 0.5$, $c_b = 0.05$, $x_\ell = 10$, $m_{\min} = 2$.

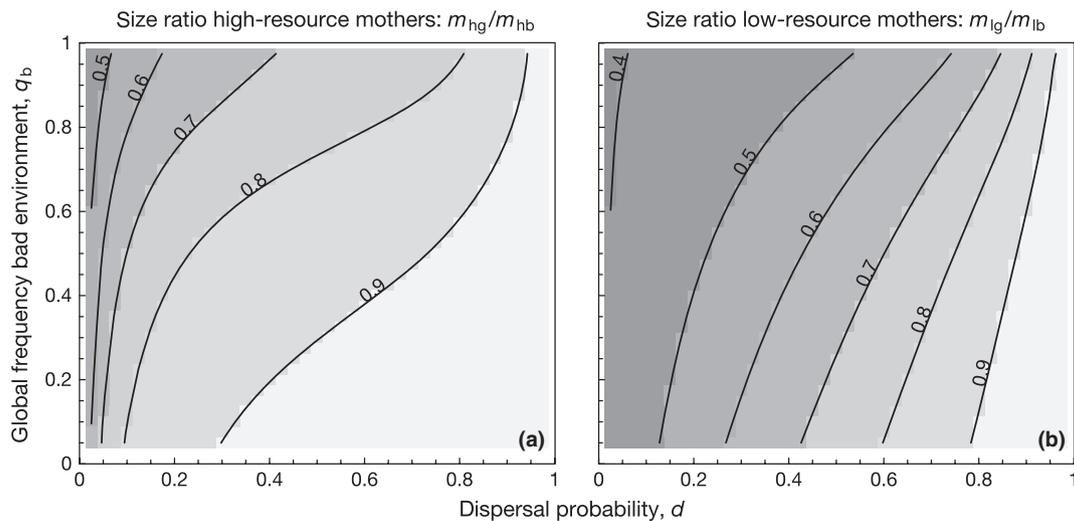


Fig. 4 The effect of the global frequency q_b of the bad, high-risk environment on offspring size produced in the good relative to the bad environment m_g/m_b . Panel a: m_g/m_b produced by high-resource mothers. Panel b: m_g/m_b produced by low-resource mothers. Interestingly, when dispersal is limited, high- and low-resource mothers always differ in their sensitivity ($m_{hg}/m_{lb} \neq m_{lg}/m_{lb}$) for any frequency of the bad environment. However, low frequencies of the high-risk environment are more conducive to resource-based differences in maternal sensitivity than higher frequencies. Parameters: $\bar{s} = [\log_{10}(s_{g-b}) + \log_{10}(s_{b-g})]/2 = 0.1$, $q_h = 0.2$, $c_g = 0.5$, $c_b = 0.05$, $x_t = 10$, $m_{\min} = 2$.

also be suffering from resource shortages. The correlation between resource availability and the intensity of local competition means that even when patches are large, higher-resource mothers accrue relatively more of their fitness through dispersing young and so should be less sensitive to local environmental conditions.

Many empirical studies have shown that parents can adjust the size of their offspring in response to a wide array of cues, such as maternally perceived predation risk to offspring (Tollrian, 1995; Shine & Downes, 1999; Giesing *et al.*, 2011; Segers & Taborsky, 2011), perceived competition among offspring (Bashey, 2006; Allen *et al.*, 2008; Leips *et al.*, 2009), the social environment (Taborsky *et al.*, 2007) and various aspects of maternal condition (e.g. Quinn *et al.*, 1995; Morris, 1998; Berg *et al.*, 2001; Marshall *et al.*, 2010). Less attention has, however, been given to variation between mothers in their responsiveness (in terms of adjusting offspring size) to such cues. Our model shows that mothers may be expected to vary (according to their condition) in their levels of transgenerational responsiveness, giving rise to individual differences in offspring size reaction norms analogous to individual differences in within-generational plasticity (see Nussey *et al.*, 2007; Dingemanse *et al.*, 2010, for reviews). To our knowledge, only a single study has assessed variation among mothers in their offspring size reaction norms when responding to anticipated cues of offspring risk (Segers & Taborsky, 2012): in the mouthbrooding cichlid *Eretmodus cyanostictus*, all maternal genotypes increase the size of their offspring in the presence of a predator cues, but

some maternal genotypes appear to do so more strongly than others (e.g. Fig. 5 in Segers & Taborsky, 2012). It remains a question for future research to determine whether such variation among mothers in offspring size plasticity is a widespread pattern. For example, the cladoceran *Daphnia* may be a suitable model system to test for variation among mothers in offspring size plasticity, because recent studies have found resource-dependent variation in maternal plasticity in the context of induced offspring resistance against parasitism (e.g. Mitchell & Read, 2005; Ben-Ami *et al.*, 2010; Stjernman & Little, 2011). Although two of these studies also assessed whether high- and low-resource mothers produced offspring of a different size (Ben-Ami *et al.*, 2010; Stjernman & Little, 2011), they did not investigate whether high- and low-resource mothers differ in their offspring size plasticity when responding to perceived offspring risk.

Our model suggests a number of possible directions for future work. One important aspect that has hardly been considered in this and other analyses of offspring size plasticity (e.g. Parker & Begon, 1986; McGinley *et al.*, 1987; Fischer *et al.*, 2011) is the presence and impact of parent-offspring conflict (but see Hendry *et al.*, 2001). Our results show that higher-resource mothers are selectively favoured to adjust offspring size less in response to a risky local environment, implying that this maximizes the fitness of the maternal brood as a whole. However, from the point of view of individual offspring that end up in a high-risk environment, a relatively small size may be highly detrimental. Consequently, parent-offspring conflict may be relatively

stronger in high-resource mothers (who on average produce smaller offspring sizes) relative to low-resource mothers, potentially leading to state-dependent arms races between parents and offspring. Moreover, recent studies have highlighted that even in the absence of resource variation, limited dispersal affects the level of parental investment (Lion & Van Baalen, 2007) and the extent of parent–offspring conflict over investment (Kuijper & Johnstone, 2012). First, parents may be selected to increase the level of care to random offspring in viscous populations, because limited dispersal increases the probability that parents care for related as opposed to unrelated offspring (Lion & Van Baalen, 2007). However, population viscosity also increases the level of local competition among siblings, so that individual offspring favour a disproportionately larger share of total parental investment at the expense of their siblings, when compared to well-mixed populations. As a result, parent–offspring conflict is likely to be enhanced in viscous populations (Kuijper & Johnstone, 2012). Future studies should assess how these insights regarding parental care and parent–offspring conflict in viscous populations are affected by the degree of environmental or resource variation.

Another issue that has received little attention here or elsewhere is the transgenerational impact of offspring size. Several empirical studies have shown that the size of an offspring can be correlated (either positively or negatively) with its fecundity as an adult (e.g. Falconer, 1965; Naguib & Gil, 2005; Gilbert *et al.*, 2012). A model by Mangel *et al.* (1994), which focused on transgenerational effects of offspring size in an environment characterized by temporal fluctuations in density dependence, suggested that optimal offspring size decisions will depend on the amount of density dependence that these offspring themselves are likely to encounter during their adult reproductive lifespan: mothers should produce small offspring that have low fecundity whenever density dependence in the offspring's generation is relatively strong, whereas mothers should produce highly fecund, large offspring whenever density dependence in the offspring's generation is relatively small. No predictions exist, however, on how maternal offspring size decisions are affected by perceived levels of offspring risk, which not only affect offspring survival, but also density dependence during their adult lifespan. In general, the transgenerational consequences of parental investment are currently poorly understood.

Another interesting extension would be to allow for an influence of offspring size on dispersal probability, which has been particularly well documented in the context of plant seed mass (e.g. Westoby *et al.*, 1996; Jansen *et al.*, 2004; Muller-Landau *et al.*, 2008). Dependent on the mode of dispersal (e.g. wind vs. animal-based seed dispersal), larger seeds may either be more or less likely to disperse than smaller ones,

which in turn feeds back on the degree of local competition that each juvenile plant experiences and also affects whether the juvenile's environment is correlated with the maternal environment. Although formal modelling is necessary to investigate the interaction between offspring size and dispersal, we would tentatively predict that differences in plasticity between high- and low-resource mothers are likely to be exacerbated when offspring dispersal decreases with size (as is the case in wind-dispersed plants, Westoby *et al.*, 1996). Low-resource mothers are more responsive to local risk and therefore produce – on average – larger offspring. If this entails a reduction in dispersal capability, then such mothers will become even more reliant on the success of philopatric young and so even more responsive to local risk. By contrast, high-resource mothers will (regardless of size-dependent dispersal) still be rapidly limited by the local number of breeding positions, so high-resource mothers are selectively favoured to decrease offspring size to boost dispersal. Consequently, we would predict that high-resource mothers thus become even less responsive to local levels of risk, relative to low-resource mothers. In general, surprisingly few general predictions exist about the coevolution of social traits (such as offspring size: Van Cleve *et al.*, 2010; Kuijper & Johnstone, 2012) with characters that influence dispersal probability (Ronce, 2007). Because offspring size is a crucial component in the evolution of maternal effects (Bernardo, 1996a; Fox & Czesak, 2000), our model shows that the complicated relationship between parental investment, local competition and dispersal is far from understood.

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References

- Allen, R.M., Buckley, Y.M. & Marshall, D.J. 2008. Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *Am. Nat.* **171**: 225–237.
- Bashey, F. 2006. Cross-generational environmental effects and the evolution of offspring size in the Trinidadian guppy *Poecilia reticulata*. *Evolution* **60**: 348–361.
- Ben-Ami, F., Ebert, D. & Regoes, R.R. 2010. Pathogen dose infectivity curves as a method to analyze the distribution of host susceptibility: a quantitative assessment of maternal effects after food stress and pathogen exposure. *Am. Nat.* **175**: 106–115.

- Berg, O.K., Hendry, A.P., Svendsen, B., Bech, C., Arnekleiv, J.V. & Lohrmann, A. *et al.*, 2001. Maternal provisioning of offspring and the use of those resources during ontogeny: variation within and between Atlantic salmon families. *Funct. Ecol.* **15**: 13–23.
- Bernardo, J. 1996a. Maternal effects in animal ecology. *Am. Zool.* **36**: 83–105.
- Bernardo, J. 1996b. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am. Zool.* **36**: 216–236.
- Carrière, Y. & Roff, D.A. 1995. The evolution of offspring size and number: a test of the Smith-Fretwell model in three species of crickets. *Oecologia* **102**: 389–396.
- Dingemanse, N.J., Kazem, A.J., Réale, D. & Wright, J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.* **25**: 81–89.
- Einum, S. & Fleming, I.A. 2002. Does within-population variation in fish egg size reflect maternal influences on optimal values? *Am. Nat.* **160**: 756–765.
- Falconer, D. 1965. Maternal effects and selection response. In: *Genetics Today, Proceeding of the XI International Congress on Genetics* (S.J. Geerts, ed.), pp. 763–774. Pergamon, Oxford.
- Fischer, B., Taborsky, B. & Kokko, H. 2011. How to balance the offspring quality-quantity tradeoff when environmental cues are unreliable. *Oikos* **120**: 258–270.
- Fox, C.W. & Czesak, M.E. 2000. Evolutionary ecology of progeny size in arthropods. *Ann. Rev. Entomol.* **45**: 341–369.
- Gardner, A. & West, S.A., 2006. Demography, altruism, and the benefits of budding. *J. Evol. Biol.* **19**: 1707–1716.
- Giesing, E.R., Suski, C.D., Warner, R.E. & Bell, A.M. 2011. Female sticklebacks transfer information via eggs: effects of maternal experience with predators on offspring. *Proc. R. Soc. Lond. B Biol. Sci.* **278**: 1753–1759.
- Gilbert, L., Williamson, K.A. & Graves, J.A. 2012. Male attractiveness regulates daughter fecundity non-genetically via maternal investment. *Proc. R. Soc. Lond. B Biol. Sci.* **279**: 523–528.
- Gotthard, K., Berger, D. & Walters, R. 2007. What keeps insects small? Time limitation during oviposition reduces the fecundity benefit of female size in a butterfly. *Am. Nat.* **169**: 768–779.
- Hendry, A.P., Day, T. & Cooper, A.B. 2001. Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. *Am. Nat.* **157**: 387–407.
- Jansen, P.A., Bongers, F. & Hemerik, L. 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatterhoarding rodent. *Ecol. Monogr.* **74**: 569–589.
- Johnstone, R.A. & Cant, M.A. 2008. Sex differences in dispersal and the evolution of helping and harming. *Am. Nat.* **172**: 318–330.
- Krist, M. 2011. Egg size and offspring quality: a meta-analysis in birds. *Biol. Rev.* **86**: 692–716.
- Kuijper, B. & Johnstone, R.A. 2012. How dispersal influences parent-offspring conflict over investment. *Behav. Ecol.* **23**: 898–906.
- Leips, J., Richardson, J.M.L., Rodd, F.H. & Travis, J. 2009. Adaptive maternal adjustments of offspring size in response to conspecific density in two populations of the Least Killifish, *Heterandria formosa*. *Evolution* **63**: 1341–1347.
- Lion, S. & Gandon, S. 2009. Habitat saturation and the spatial evolutionary ecology of altruism. *J. Evol. Biol.* **22**: 1487–1502.
- Lion, S. & Van Baalen, M. 2007. From infanticide to parental care: why spatial structure can help adults be good parents. *Am. Nat.* **170**: E26–E46.
- Lion, S., Jansen, V.A. & Day, T. 2011. Evolution in structured populations: beyond the kin versus group debate. *Trends Ecol. Evol.* **26**: 193–201.
- Lloyd, D.G. 1987. Selection of offspring size at independence and other size-versus-number strategies. *Am. Nat.* **129**: 800–817.
- Mangel, M., Rosenheim, J.A. & Adler, F.R. 1994. Clutch size, offspring performance, and intergenerational fitness. *Behav. Ecol.* **5**: 412–417.
- Marshall, D.J. & Keough, M.J. 2007. The evolutionary ecology of offspring size in marine invertebrates. In: *Advances in Marine Biology* (D.W. Sims, ed.), vol. 53, pp. 1–60. Academic Press, New York.
- Marshall, D.J., Heppell, S.S., Munch, S.B. & Warner, R.R. 2010. The relationship between maternal phenotype and offspring quality: do older mothers really produce the best offspring? *Ecology* **91**: 2862–2873.
- McGinley, M.A., Temme, D.H. & Geber, M.A. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. *Am. Nat.* **130**: 370–398.
- Meffe, G.K. 1987. Embryo size variation in mosquitofish: optimality vs plasticity in propagule size. *Copeia* **1987**: 762–768.
- Mitchell, S.E. & Read, A.F. 2005. Poor maternal environment enhances offspring disease resistance in an invertebrate. *Proc. R. Soc. Lond. B Biol. Sci.* **272**: 2601–2607.
- Morris, D.W. 1998. State-dependent optimization of litter size. *Oikos* **83**: 518–528.
- Muller-Landau, H.C., Wright, S.J., Calderón, O., Condit, R. & Hubbell, S.P. 2008. Interspecific variation in primary seed dispersal in a tropical forest. *J. Ecol.* **96**: 653–667.
- Naguib, M. & Gil, D. 2005. Transgenerational body size effects caused by early developmental stress in zebra finches. *Biol. Lett.* **1**: 95–97.
- Nasution, S., Roberts, D., Farnsworth, K., Parker, G.A. & Elwood, R.W. 2010. Maternal effects on offspring size and packaging constraints in the whelk. *J. Zool.* **281**: 112–117.
- Nussey, D.H., Wilson, A.J. & Brommer, J.E., 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol.* **20**: 831–844.
- Parker, G.A. & Begon, M. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. *Am. Nat.* **128**: 573–592.
- Parker, G.A. & Macnair, M.R. 1978. Models of parent-offspring conflict. I. Monogamy. *Anim. Behav.* **26**: 97–110.
- Quinn, T.P., Hendry, A.P. & Wetzel, L.A. 1995. The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). *Oikos* **74**: 425–438.
- Räsänen, K., Söderman, F., Laurila, A. & Merilä, J. 2008. Geographic variation in maternal investment: acidity affects egg size and fecundity in *Rana arvalis*. *Ecology* **89**: 2553–2562.
- Rodrigues, A.M.M. & Gardner, A. 2012. Evolution of helping and harming in heterogeneous populations. *Evolution* **66**: 2065–2079.
- Roff, D. 2002. *Life History Evolution*. Sinauer, Sunderland.
- Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Evol. Syst.* **38**: 231–253.

Rousset, F. 2004. *Genetic Structure in Subdivided Populations*. Princeton University Press, Princeton.

Segers, F.H. & Taborsky, B. 2011. Egg size and food abundance interactively affect juvenile growth and behaviour. *Func. Ecol.* **25**: 166–176.

Segers, F.H.I.D. & Taborsky, B. 2012. Juvenile exposure to predator cues induces a larger egg size in fish. *Proc. R. Soc. Lond. B Biol. Sci.* **279**: 1241–1248.

Shine, R. & Downes, S.J. 1999. Can pregnant lizards adjust their offspring phenotypes to environmental conditions? *Oecologia* **119**, 1–8.

Smith, C.C. & Fretwell, S.D. 1974. The optimal balance between size and number of offspring. *Am. Nat.* **108**: 499–506.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull. Mar. Sci.* **60**: 1129–1157.

Stjernman, M. & Little, T.J. 2011. Genetic variation for maternal effects on parasite susceptibility. *J. Evol. Biol.* **24**: 2357–2363.

Taborsky, B., Skubic, E. & Bruintjes, R. 2007. Mothers adjust egg size to helper number in a cooperatively breeding cichlid. *Behav. Ecol.* **18**: 652–657.

Taylor, P.D. 1992. Altruism in viscous populations: an inclusive fitness model. *Evol. Ecol.* **6**: 352–356.

Taylor, P.D. & Frank, S.A. 1996. How to make a kin selection model. *J. Theor. Biol.* **180**: 27–37.

Tollrian, R. 1995. Predator-induced morphological defenses: costs, life history shifts, and maternal effects in *Daphnia pulex*. *Ecology* **76**: 1691–1705.

Van Cleve, J., Feldman, M.W. & Lehmann, L. 2010. How demography, life history, and kinship shape the evolution of genomic imprinting. *Am. Nat.* **176**: 440–455.

Westoby, M., Leishman, M., Lord, J., Poorter, H. & Schoen, D.J. 1996. Comparative ecology of seed size and dispersal [and discussion]. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **351**: 1309–1318.

Appendix: Model description

Production of breeding offspring by a focal female

We are interested in the evolution of the offspring size traits m_{ki} , summarized in the vector $\mathbf{m} = [m_{hg}, m_{hb}, m_{lg}, m_{lb}]$. Let $q(n_h)$ describe the distribution of the number of female breeders n_h in a patch who receive a high amount of reproductive resources ($0 \leq n_h \leq n$). When resource variation occurs among mothers occupying the same patch (within-patch variation), the number of high-resource breeders per patch is given by the binomial distribution

$$q_h(n_h) = \binom{n}{n_h} p_h^{n_h} (1 - p_h)^{n - n_h},$$

where p_h is the probability that a mother acquires a large amount of resources. Alternatively, when resource variation occurs between different patches (between-patch variation), the distribution of n_h is given by

$$q_h(n_h) = \begin{cases} n & \text{with probability } p_h \\ 0 & \text{with probability } 1 - p_h \end{cases}.$$

We now derive the expected number $w_{i,i \rightarrow j}$ of juveniles of one sex (identical for both female and male young) produced by a focal mutant female in a type i environment that successfully compete for a breeding position in a type j environment:

$$w_{i,i \rightarrow j} = \delta_{i=j} (1 - d) \sum_{n_h=0}^n q_h(n_h) \frac{\frac{n_h}{n} (x_h/m_{hi}) f_j(m_{hi}) + \frac{n-n_h}{n} (x_\ell/m_{\ell i}) f_j(m_{\ell i})}{C_j(n_h, \hat{\mathbf{m}}^f, \bar{\mathbf{m}})} + dq_j \sum_{n_h=0}^n q_h(n_h) \sum_{\tilde{n}_h=0}^n q(\tilde{n}_h) \frac{\frac{n_h}{n} (x_h/m_{hi}) f_j(m_{hi}) + \frac{n-n_h}{n} (x_\ell/m_{\ell i}) f_j(m_{\ell i})}{C_j(\tilde{n}_h, \bar{\mathbf{m}}, \bar{\mathbf{m}})} \tag{A1}$$

The first line of $w_{i,i \rightarrow j}$ reflects offspring that remain in their natal environment with probability $1-d$. Here,

$\delta_{i=j}$ is Kronecker’s delta, which is 1 when $i = j$ and otherwise 0, because a philopatric juvenile always competes for breeding positions in the same environment as its mother (note that the environment of a particular patch only changes after juveniles have established themselves as adult breeders). With probability $q_h(n_h)$, the focal mutant mother resides on a patch that contains n_h high-resource mothers. Hence, to calculate the expected number of successful juveniles, we need to average over the probability distribution $q_h(n_h)$ of the number of high-resource mothers residing in the focal’s patch. For each value of n_h , the probability that the focal mother is one of the high-resource mothers is given by n_h/n . She then receives x_h resources, and her corresponding fecundity is given by x_h/m_{hi} . Upon reproduction, her philopatric offspring will survive with a probability of $f_j(m_{hi})$. Alternatively, the focal mutant mother is one of the $n - n_h$ low-resource mothers with corresponding fecundity $x_\ell/m_{\ell i}$, leading to a size-dependent juvenile survival probability $f_j(m_{\ell i})$. The total number of philopatric and immigrant juveniles who compete for breeding positions in the focal’s patch is given by $C_j(n_h, \hat{\mathbf{m}}^f, \bar{\mathbf{m}})$, hence the probability that the focal mother’s offspring successfully obtains a breeding position is proportional to $1/C_j(n_h, \hat{\mathbf{m}}^f, \bar{\mathbf{m}})$. Here, $\hat{\mathbf{m}}^f = [\hat{m}_{hg}^f, \hat{m}_{lg}^f, \hat{m}_{hb}^f, \hat{m}_{lb}^f]$ is the vector of offspring size traits averaged over all local breeding females (including the focal mutant mother), and $\bar{\mathbf{m}}$ is the analogous vector of offspring size traits averaged over the whole population.

The total number of competing juveniles $C_j(n_h, \hat{\mathbf{m}}^f, \bar{\mathbf{m}})$ is given by

$$C_j(n_h, \hat{\mathbf{m}}^f, \bar{\mathbf{m}}) = n_h(x_h/\hat{m}_{hi}^f)f_j(\hat{m}_{hi}^f) + (n - n_h)(x_\ell/\hat{m}_{\ell i}^f)f_j(\hat{m}_{\ell i}^f) + D_j(\bar{\mathbf{m}}), \tag{A2}$$

where the first part reflects all local offspring that compete for breeding positions, born from either the n_h high-resource mothers or the $n - n_h$ low-resource mothers. The last part, $D_j(\bar{\mathbf{m}})$, reflects the number of immigrant juveniles from any remote patch that have arrived on the focal patch:

$$D_j(\bar{\mathbf{m}}) = d \sum_{k=\{g,b\}} q_k \sum_{n_h=0}^n q(n_h)[n_h(x_h/\bar{m}_{hk})f_j(\bar{m}_{hk}) + (n - n_\ell)(x_\ell/\bar{m}_{\ell k})f_j(\bar{m}_{\ell k})], \tag{A3}$$

which is the number of dispersing offspring averaged over each of the different natal environments $k = \{g, b\}$ (encountered with probability similar to the asymptotic frequency of environment k , $q_k = s_{i \rightarrow k}/(s_{k \rightarrow i} + s_{i \rightarrow k})$) and the distribution of high-resource mothers n_h living in the patch of origin. Note that the average offspring size strategy in any remote environment k is given by $(\bar{m}_{hk}, \bar{m}_{\ell k})$.

Lastly, the second line in eq. (A1) reflects the probability that offspring from a focal mutant female disperse elsewhere (with probability d) and successfully compete for a breeding position in a remote patch. With probability $q_j = s_{i \rightarrow j}/(s_{j \rightarrow i} + s_{i \rightarrow j})$, a juvenile arrives on a patch having environmental quality j , whereas $q(\tilde{n}_h)$ is the probability of arriving on a patch that contains \tilde{n}_h high-resource parents, so that a total of $C_j(\tilde{n}_h, \mathbf{m}, \bar{\mathbf{m}})$ juveniles compete for breeding positions on that patch.

Production of breeding offspring by a focal male

Analogous to the previous expression $w_{i,i \rightarrow j}$ in eq. (A1), the expected number of juveniles of one sex sired by a father living in a type i environment that establish themselves in a type j environment is given by:

$$w_{m,i \rightarrow j} = \delta_{i=j}(1 - d) \sum_{n_h=0}^n q_h(n_h) \frac{n_h(x_h/\hat{m}_{hi}^m)f_j(\hat{m}_{hi}^m) + \frac{n-n_h}{n}(x_\ell/\hat{m}_{\ell i}^m)f_j(\hat{m}_{\ell i}^m)}{C_j(n_h, \hat{\mathbf{m}}^f, \bar{\mathbf{m}})} + dq_j \sum_{n_h=0}^n q_h(n_h) \sum_{\tilde{n}_h=0}^n q(\tilde{n}_h) \frac{n_h(x_h/\hat{m}_{hi}^m)f_j(\hat{m}_{hi}^m) + \frac{n-n_h}{n}(x_\ell/\hat{m}_{\ell i}^m)f_j(\hat{m}_{\ell i}^m)}{C_j(\tilde{n}_h, \bar{\mathbf{m}}, \bar{\mathbf{m}})}, \tag{A4}$$

which can be derived in a similar fashion as eq. (1), remembering that offspring size is under maternal control, so that the size of young sired by the focal male is a function of the average allelic values for offspring size among females in the local patch, \hat{m}_{hi}^m (for offspring produced by a high-resource mother) and $\hat{m}_{\ell i}^m$ (for offspring produced by a low-resource mother). The superscript m indicates that the focal offspring size allele resides in male.

Environmental change

We assume that patches potentially change their environmental state $i = \{g, b\}$ after offspring establish themselves as breeders but before they reproduce. Transition probabilities are given by the matrix \mathbf{S} ,

$$\mathbf{S} = \begin{bmatrix} 1 - s_{b \rightarrow g} & s_{g \rightarrow b} \\ s_{b \rightarrow g} & 1 - s_{g \rightarrow b} \end{bmatrix}, \tag{A5}$$

where both environments have stationary frequencies $q_g = s_{b \rightarrow g}/(s_{g \rightarrow b} + s_{b \rightarrow g})$ and $q_b = s_{g \rightarrow b}/(s_{g \rightarrow b} + s_{b \rightarrow g})$.

Fitness

Let \mathbf{W} be a 2×2 matrix, of which element W_{ij} describes the expected number of juveniles of both sexes produced by a parent (who might be either male or female and either resource-rich or resource-poor) in environment i that establish themselves and go on to breed in environment j . \mathbf{W} is then given by

$$\mathbf{W} = \frac{1}{2}\mathbf{SE}, \tag{A6}$$

in which the factor of 1/2 reflects the genetic share of each parent in an offspring, and \mathbf{E} is a matrix, which reflects the expected number of offspring that successfully establish themselves in each environment:

$$\mathbf{E} = \begin{bmatrix} W_{f,b \rightarrow b} + W_{m,b \rightarrow b} & W_{f,g \rightarrow b} + W_{m,g \rightarrow b} \\ W_{f,b \rightarrow g} + W_{m,b \rightarrow g} & W_{f,g \rightarrow g} + W_{m,g \rightarrow g} \end{bmatrix}. \tag{A7}$$

The fitness a focal gene copy in environment i , denoted W_i , can then be obtained by summing the number of offspring that go on to breed in both good and bad environments, weighted according to the individual reproductive values of breeders in each environment (Taylor & Frank, 1996):

$$W_i = \sum_{j=\{g,b\}} \frac{v_j}{v_i} W_{ij}. \tag{A8}$$

where v_j denotes the individual reproductive value of mothers living in environment j . These reproductive values can be obtained by calculating the left eigenvector from the matrix \mathbf{W} . The direction of natural selection acting on the offspring size trait m_{ki} is then given by eqn. (1) in the main text. We find the candidate ESS for each of these offspring size traits by numerically solving the system of

selection differentials until all selection differentials vanish.

Relatedness coefficients

Here, we derive relatedness coefficients for haploid populations. Writing Q_g and Q_b for the equilibrium probability of identity between copies of the offspring size gene sampled from two distinct, randomly chosen adult breeders (i.e. sampling without replacement) in a good (low-risk) and in a bad (high-risk) local territory, respectively, we have the following equations:

$$Q_b = \sum_{n_h=0^n} q(n_h) \left[\begin{aligned} &+ \frac{1}{4} \{ (n_h \bar{g}_{hb}^2 + (n - n_h) \bar{g}_{tb}^2) + ((n_h \bar{g}_{hb} + (n - n_h) \bar{g}_{tb})^2 - (n_h \bar{g}_{hb}^2 + (n - n_h) \bar{g}_{tb}^2)) z(Q_b, Q_g) \} \\ &+ \frac{1}{2} (n_h \bar{g}_{hb} + (n - n_h) \bar{g}_{tb})^2 z(Q_b, Q_g) \\ &+ \frac{1}{4} \left\{ (n_h \bar{g}_{hb} + (n - n_h) \bar{g}_{tb})^2 \left(\frac{1}{n} + \left(1 - \frac{1}{n} \right) z(Q_b, Q_g) \right) \right\} \end{aligned} \right] \tag{A9a}$$

$$Q_g = \sum_{n_h=0^n} q(n_h) \left[\begin{aligned} &+ \frac{1}{4} \{ (n_h \bar{g}_{hg}^2 + (n - n_h) \bar{g}_{tg}^2) + ((n_h \bar{g}_{hg} + (n - n_h) \bar{g}_{tg})^2 - (n_h \bar{g}_{hg}^2 + (n - n_h) \bar{g}_{tg}^2)) z(Q_g, Q_b) \} \\ &+ \frac{1}{2} (n_h \bar{g}_{hg} + (n - n_h) \bar{g}_{tg})^2 z(Q_g, Q_b) \\ &+ \frac{1}{4} \left\{ (n_h \bar{g}_{hg} + (n - n_h) \bar{g}_{tg})^2 \left(\frac{1}{n} + \left(1 - \frac{1}{n} \right) z(Q_g, Q_b) \right) \right\} \end{aligned} \right] \tag{A9b}$$

Focusing on the right hand side of eq. (9), we average over the different possible numbers n_h of high-resource females on the focal patch in the previous generation. For any given value of n_h , the term on the second line reflects the possibility that both alleles are maternally inherited (which occurs with probability 1/4): in this case, with probability $n_h \bar{g}_{hb}^2$, they descend from the same local high-resource female who (in the previous generation) produced a fraction \bar{g}_{hb} of locally competing young, whereas with probability $(n - n_h) \bar{g}_{tb}^2$, both alleles descend from the same local low-resource female who (in the previous generation) produced a fraction \bar{g}_{tb} of locally competing young; in either case, both alleles are identical by descent. Alternatively, with probability $(n_h \bar{g}_{hb} + (n - n_h) \bar{g}_{tb})^2 - (n_h \bar{g}_{hb}^2 + (n - n_h) \bar{g}_{tb}^2)$,

both alleles descend from different local parents, in which case, the probability of identity by descent is given by the probability $z(Q_b, Q_b)$. In a similar fashion, the third line in eq. (A9) reflects the possibility that one of the two sampled alleles was inherited from a female and one from a male, whereas the fourth line reflects that the possibility that both alleles were inherited from males. Throughout, the terms \bar{g}_{hi} and \bar{g}_{ti} denote the fraction of locally competing offspring born to a high- or low-resource mother in a type i environment containing n_h high-resource female breeders and are given by

$$\bar{g}_{hi} = \frac{(1 - d)(x_h / \bar{m}_{hi}) f_i(\bar{m}_{hi})}{C_i(n_h, \bar{\mathbf{m}}, \bar{\mathbf{m}})},$$

$$\bar{g}_{ti} = \frac{(1 - d)(x_\ell / \bar{m}_{ti}) f_i(\bar{m}_{ti})}{C_i(n_h, \bar{\mathbf{m}}, \bar{\mathbf{m}})},$$

whereas the identity by descent among distinct breeders of the previous generation in a patch that is currently in environmental state i is given by

$$z(Q_i, Q_j) = \frac{q_i(1 - s_{i \rightarrow j})Q_i + q_j s_{j \rightarrow i} Q_j}{q_i(1 - s_{i \rightarrow j}) + q_j s_{j \rightarrow i}}. \tag{A10}$$

$R_{loc,i}^f$ and $R_{loc,i}^m$ are the probabilities that a randomly chosen female breeder in the same patch shares a copy of a focal gene that resides in a female or male, respectively, while the environmental state of a patch is i . We then have

$$R_{loc,i}^f = \frac{1}{n} + \frac{n - 1}{n} \hat{Q}_i, \tag{A11}$$

$$R_{loc,i}^m = \hat{Q}_i,$$

where \hat{Q}_i is the equilibrium probability of identity between copies of the offspring size gene sampled from two, distinct and randomly chosen adult breeders in the same local patch that has environmental state i , which is the solution of eqns. (A9a,b).

Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Varying the survival differences between poor (c_b) and good (c_g) environments.

Figure S2 Varying the global frequency q_h of high resource patches in the case of between-patch resource variation.

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