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Disparate Maturation Adaptations to Size-dependent Mortality

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Disparate maturation adaptations to size-dependent mortality

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Disparate maturation adaptations to size-dependent mortality

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SUMMARY

Body size is an important determinant of resource use, fecundity, and mortality risk. Evolution of maturation size in response to size-dependent selection is thus a fundamental part of life-history theory. Increased mortality among small individuals has previously been predicted to cause larger maturation size, whereas increased mortality among large individuals is expected to have the opposite effect. Here we use a continuously size-structured model to demonstrate that, contrary to these widespread expectations, increased mortality among small individuals can have three alternative effects: maturation size may increase, decrease, or become evolutionarily bistable. We show that such complex responses must be reckoned with whenever mortality is size-dependent, growth is indeterminate, reproduction impairs growth, and fecundity increases with size. Predicting adaptive responses to altered size-dependent mortality is thus inherently difficult, since, as demonstrated here, such mortality can not only reverse the direction of adaptation, but also cause abrupt shifts in evolutionarily stable maturation sizes.

INTRODUCTION

An individual's body size typically influences its fecundity, mortality, and intra- and interspecific interactions. Adaptation of traits affecting body size in response to size-dependent selection pressures is thus a central topic in life-history theory (Roff 1992). It is also of practical importance, since size-dependent mortality occurs in many species, either naturally (Werner & Gilliam 1984) or induced by human exploitation (Law 2000). A key trait affecting body size is maturation size. Few evolutionary studies, however, have addressed maturation size directly, and fewer, still, have examined its response to size-dependent mortality (Roff 1992). Most theoretical analyses have instead focussed on reproductive effort (Law 1979; Michod 1979) or energy allocation patterns (DeAngelis *et al.* 1985), or have analyzed the effects of age- or stage-structured mortality, rather than of size-structured mortality (Schaffer & Rosenzweig 1977; Law 1979; Michod 1979; Roff 1981; Day *et al.* 2002). Existing evolutionary models of maturation size assessing size-dependent mortality predict that mortality among large individuals causes maturation size to decrease (Taylor & Gabriel 1992; Ernande *et al.* 2004), whereas mortality among small individuals is predicted to induce delayed maturation, at larger sizes (Taylor & Gabriel 1992). Both predictions have received empirical support (Edley & Law 1988; Reznick *et al.* 1990; Haugen & Vollestad 1991; Wellborn 1994; Johnson & Belk 2001). Thus, the effect of size-dependent mortality on the evolution of maturation size seemed clear-cut. In particular, when maturation size is the only evolving trait, its evolutionary response to size-dependent mortality appeared to be uniquely determined.

In contrast, we show that mortality among small individuals has disparate effects on maturation size whenever mortality is size-dependent, growth is indeterminate, reproduction impairs growth, and fecundity increases with size. We investigate a size-structured evolutionary model and show that the effect of mortality among small individuals on maturation size depends on how mortality varies with size, because the latter alters the trade-offs underlying maturation. Our results expose that predicting adaptive responses to size-dependent mortality, urgently needed, *e.g.*, in fisheries (Law 2000), requires detailed knowledge of both natural mortality patterns and induced mortality. Such refined predictions are important, since, as shown here, gradual changes in selection pressure can alter the direction of adaptation and cause abrupt shifts in evolutionarily stable maturation size.

MODEL

We consider an organism in which somatic growth is indeterminate and piecewise linear (*e.g.*, some fish; Jørgensen 1992), reproduction reduces body growth, and all mature individuals reproduce. Size s is continuous and measured as body length. Individual growth rate $g(s)$ in length s is then

$$g(s) = \begin{cases} g_i & s_0 < s \le s_m \\ g_m & s > s_m \end{cases}, \tag{1a}$$

where s_0 is size at birth, s_m is size at maturation, and g_i and g_m are the growth rates of immatures and matures, respectively. Owing to eq. 1a, size at maturation, s_m, and age at maturation, s_m / g_i, are strictly correlated traits, just representing two sides of the same coin.

Effective fecundity at size s is assumed to be proportional to weight, and thus to volume,

$$f(s) = bs^3, \tag{1b}$$

with scaling constant b. Notice that effective fecundity measures the number of *viable* offspring, such that effects of parental size on, for example, offspring survival soon after birth are accounted for.

We assume that mortality changes at threshold sizes s_l and s_T, such that

$$m(s) = \begin{cases} m_l & s_0 < s \le s_l \\ m_1 & s_l < s \le s_T \\ m_2 & s > s_T \end{cases}. \tag{1c}$$

That is, small (large) individuals experience an (instantaneous) mortality m_1 (m_2). Since our focus is on size-dependent mortality, we avoid confounding its evolutionary effects by density-dependent mortality, by assuming that density regulation occurs through the mortality m_l of individuals ('larvae') too small ($s \le s_l$) ever to reproduce.

The dynamics of the density of individuals with size $s > s_0$ at time t are given by (Metz & Diekmann 1986)

$$\frac{\partial n(s,t)}{\partial t} = -\frac{\partial g(s)n(s,t)}{\partial s} - d(s)n(s,t) \tag{2a}$$

and the boundary condition

$$n(s_0,t) = g(s_0)^{-1}\int_{s_m}^{\infty} f(s)n(s,t)ds\,. \tag{2b}$$

We find evolutionarily stable and attainable equilibrium value(s) of maturation size, s_m^*, through evolutionary invasion analysis. When a variant with maturation size s_m' appears in a monomorphic resident population with maturation size s_m, the variant's fate is determined by its invasion fitness, *i.e.*, by its exponential growth rate when rare in the resident population (Metz *et al.* 1992; Geritz *et al.* 1998). The invasion fitness is therefore given by the dominant Lyapunov exponent of the rare variant's (linear) dynamics. As Lyapunov exponents are difficult to calculate for infinite-dimensional dynamics arising in continuously structured populations we use the sign-equivalent proxy I of invasion fitness, based on the variant's lifetime reproductive success R_0,

$$I(s_m', s_m) = R_0 - 1 = p_l(s_m)\, p_i(s_m')\int_{s_m'}^{\infty} p_m(s_m', s)\, f(s)\, g_m^{-1} ds - 1\,, \tag{3}$$

where $p_l(s_m)$, $p_i(s_m')$, and $p_m(s_m', s)$ denote, respectively, the variant's probabilities of surviving the larval stage, the immature stage, and from maturation to size s (see Appendix). Since $R_0 = 1$, and thus $I = 0$, always holds for the resident population at equilibrium,

$s'_m = s_m$, it is evident that advantageous (deleterious) variants s'_m are characterized by $I > 0$ ($I < 0$).

RESULTS

Figure 1 shows that size-dependent mortality can have four different effects on maturation size. Mortality among small individuals can (1) increase maturation size, (2) decrease it, or (3) cause two alternative stable maturation sizes to emerge (evolutionary bistability), whereas (4) mortality among large individuals always decreases maturation size.

We now develop a mechanistic understanding of these findings. Disparate effects on maturation of mortality among small individuals occur because of three trade-offs, presented below, which emerge from three empirically well-justified assumptions: (i) somatic growth is reduced when reproducing, (ii) fecundity increases with size, and (iii) mortality can be size-dependent:

- **Trade-off 1**: When mortality is size-independent ($m_1 = m_2$), there is only one trade-off: whenever reproduction impairs growth and fecundity increases with size, this trade-off occurs between fecundity and the probability to survive until maturation. Individuals maturing at small sizes have lower fecundity than those maturing at larger sizes, but are more likely to survive until maturation (p_i decreases with s'_m, eq. A2b). Because growth is slower after maturation, any difference in fecundity at age between early- and late-maturing individuals will persist throughout life. Increased size-independent mortality thus decreases maturation size (fig. 1, compare thick curves at dashed vertical lines across panels).

When mortality depends on size, an additional trade-off emerges, the nature of which is determined by *how* mortality changes with size. There are two alternative options for this second trade-off:

- **Trade-off 2**: If mortality increases with size ($m_1 < m_2$), the second trade-off occurs between fecundity and instantaneous mortality. Both the probabilities p_i and p_m to survive until and after maturation, respectively, then decrease with maturation size (p_i more so than when $m_1 = m_2$; eqs. A2b). When this effect is strong, *i.e.*, when small individuals experience much less mortality than larger individuals, maturation size is much decreased. Thus, as mortality among small individuals increases at low levels, maturation size increases (fig. 1, lower thick curves on the far left in all panels), before trade-off 1, above, takes over and decreases s_m^*. If overall mortality is sufficiently small, late maturation may be as beneficial as early maturation, and evolutionary bistability occurs, resulting in two alternative s_m^* (fig. 1a, d, upper and lower thick curves in left part) separated by an unstable equilibrium (thin curves). This means that a population will evolve towards either smaller or larger s_m^*, depending on whether the initial maturation size lies below or above the unstable equilibrium. Notice that, without the addition of extra frequency dependence (see Appendix), the alternative s_m^* are mutually exclusive, and evolutionary bistability thus cannot result in dimorphism.

- **Trade-off 3**: When mortality decreases with size ($m_1 > m_2$) there is a 'refuge' from mortality at large body sizes ($s > s_T$), and an alternative second trade-off emerges, now operating between survival until (p_i) and after maturation (p_m) for individuals maturing at small sizes (eqs. A2b,c). These individuals have high p_i, but, as reproduction impairs growth, they will take longer to grow to refuge size s_T beyond which mortality decreases (*i.e.*, p_m is low). There are two solutions to this trade-off: individuals may either postpone reproduction until s_T (fig. 1, upper thick curves in right part), or mature smaller than s_T (lower thick curves; this bistability occurs also in fig. 1 f, i, outside the illustrated range of m_1). When mortality among small individuals increases, maturation below the size refuge becomes more beneficial, because the probability p_T to survive to the size refuge decreases (eq. A3). Thus, and also because of trade-off 1, the evolutionarily stable maturation size below the size refuge decreases (fig. 1, lower thick curves in right part).

Mortality among large individuals decreases both the probability p_m to survive until maturation (for individuals maturing at sizes larger than s_T; eq. A2b) and overall life expectancy. It therefore increases the benefits of early maturation, and s_m^* decreases (fig. 1, thick curves, across panels from left to right). Maturation size always decreases with increasing g_m / g_i (fig. 1), because the growth cost of reproduction decreases. Notice that the effect of m_1 does not qualitatively depend on these costs: m_1 can increase, decrease, and cause evolutionary bistability of maturation size for any g_m / g_i.

These results are robust to variation in both parameters and type of size-dependent mortality. Our model has only three evolutionarily relevant parameters (see Appendix), all varied in fig. 1, which thus characterizes the model's evolutionary behaviour exhaustively. Numerical analysis (see Appendix) confirms that our conclusions extend to models in which the assumed discontinuity in size-dependent mortality (at $s = s_T$) is smoothed (fig. 2a-d, fig. 3), and even to models without any threshold size for mortality (fig. 2e-h, fig. 4).

Disparate maturation effects are most pronounced when mortality changes steeply with size (fig. 2). When mortality changes more gradually with size (large w in fig. 2a-d or large s_T in fig. 2e-h), m_1 affects not only mortality at small sizes, but at most sizes (fig. 2a,e). The parameter ranges for which m_1 increases s_m^* or causes evolutionarily bistable maturation sizes are then much smaller (fig. 2d, f-h) than when m_1 predominantly affects mortality at small sizes (fig. 1, fig. 2b-c). This is as expected: when m_1 increases mortality at both small and large sizes, the probability to survive until maturation becomes very low for individuals postponing maturation until large sizes. As a result, bistability is then less frequent, and larger s_m^* disappear with increasing m_1.

DISCUSSION

Previous life-history theory predicted that increased mortality among small individuals selects for delayed maturation (*e.g.*, Taylor & Gabriel 1992), manifested either as an increased age or increased size at maturation. Here we have shown that, by contrast, such mortality can also decrease maturation size or cause evolutionary bistability, depending on how mortality changes with size. In fact, mortality among small individuals can only increase maturation size if mortality increases with size. Our results are original in a second regard: previous predictions of evolutionary bistability of maturation (Schaffer & Rosenzweig 1977; DeAngelis *et al.* 1985; Taborsky *et al.* 2003) all involved at least two evolving traits. By contrast, here we report evolutionary bistability when maturation size is the only evolving trait.

Disparate maturation responses to mortality among small individuals are expected in species with indeterminate growth and density-regulation early in life whenever (1) mortality depends on size, (2) reproduction reduces body growth, and (3) fecundity increases with size – conditions that are widespread in nature (Roff 1992) and particularly common in fish (Wootton 1990). While the effect of mortality among large individuals in our model accords with earlier life-history theory (Taylor & Gabriel 1992; Ernande *et al.* 2004) and with empirical evidence (Edley & Law 1988; Wellborn 1994; Johnson & Belk 2001), previous models did not find disparate maturation responses to mortality among small individuals since either (a) one of the conditions (1) to (3) was lacking, as in models where mortality is age- or stage-dependent rather than size-dependent (Law 1979; Michod 1979; Roff 1981; Day *et al.* 2002), or (b) disparate responses may have been overlooked (Taylor & Gabriel 1992; Takada & Caswell 1997; Nakaoka 1998). For example, evolutionary bistability is undetectable when optimal maturation size is assessed separately for maturation sizes smaller and larger than a size refuge from mortality, as in Takada & Caswell (1997). Alternatively, a focus on evolutionary effects other than those caused by variation in size-dependent mortality may have obscured the occurrence of the disparate responses documented here. For example, careful inspection of predicted maturation sizes in Table 2 of Nakaoka (1998) reveals consistency with our findings (Nakaoka's analysis concentrated on the evolutionary effects of, in our notation, changes in s_T and m_2, and only investigated the case $m_1 > m_2$).

Disparate responses of maturation size to mortality among small individuals are most pronounced when there is a size threshold to mortality (fig. 1, fig. 2a-b) as, *e.g.*, in species that can escape predation by outgrowing a vulnerable size range (Werner & Gilliam 1984).

Nevertheless, disparate changes in maturation size are predicted also when mortality changes more gradually with size (fig. 2c-d, fig. 3). Even in complete absence of size thresholds, such as when mortality is an exponential function of size (fig. 2e), mortality among small individuals can both elevate and depress maturation size, as well as induce evolutionarily bistable maturation sizes (fig. 2f-h, fig. 4; Taborsky *et al.* 2003). Thus, the disparate maturation responses highlighted here are predicted to occur for several general types of size-dependent mortality.

The ubiquity of size-dependent mortality and the occurrence of size refuges from mortality (Werner & Gilliam 1984) suggest that disparate responses to mortality among small individuals may be a common phenomenon. Yet, empirical evidence of evolutionary responses available to date only confirms that such mortality can increase maturation size (Edley & Law 1988; Reznick *et al.* 1990; Haugen & Vollestad 2001). According to our results, this is expected when mortality increases with size, with the opposite response predicted when mortality decreases with size. In their experiments, Edley & Law (1988) and Reznick *et al.* (1990) compared two different selection regimes, but when applying high mortality among small individuals they simultaneously changed mortality from being positively to negatively size-dependent, which can either increase or decrease maturation size depending on relative mortalities in each selection regime (fig. 1). In contrast, Haugen & Vollestad (2001) studied the selection pressure from harvesting of grayling, which changed over time but remained positively size-dependent. The increased maturation size they found thus accords with our predictions, whereas we are unaware of any experiment appropriate for testing our predicted adaptations to mortality among small individuals when mortality decreases with size.

The non-monotonic dependence of maturation size on mortality among small individuals reported here makes adaptive responses to increased mortality highly unpredictable in natural populations, for three reasons. First, gradual changes in mortality can abruptly increase stable maturation size whenever evolutionary bistability is lost (fig. 1). Second, whenever alternative stable equilibria exist, adaptive responses to mortality changes depend on initial life histories (fig. 1). Third, even in the absence of evolutionary bistability, a slight increase in mortality among small individuals can alter the direction of the adaptive response from gradually increasing to decreasing maturation size (fig. 1). Acknowledging this complexity in adaptive responses to size-dependent mortality is crucial for improving the match between life-history theory and natural observations.

A case in point is evolutionary responses to fishing (Law 2000; Hutchings 2004). Fisheries may induce genetic changes in maturation (Olsen *et al*. 2004), with detrimental consequences for yield, stability, and recovery potential of exploited stocks (Hutchings 2004). The extent of and remedies for such evolutionary changes are still uncertain. Our results show that suggested remedies, such as targeting only small individuals to reverse evolutionary changes induced by fishing (Conover & Munch 2002) may cause undesired effects by decreasing instead of increasing maturation size. According to our results, successful management of evolutionary responses by altering mortality among small individuals requires consideration of both pre-selection mortality patterns and the magnitude of mortality changes, in reflection of the complex evolutionary responses size-dependent mortality induces.

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APPENDIX

Resident equilibrium structure

Below we explain results for $s_m < s_T$; the opposite case is treated analogously. We obtain the equilibrium density distribution $n^*(a)$ of resident individuals at age a from eqs. 1 and 2. The resultant distribution is converted to the resident's equilibrium density distribution of sizes, $n^*(s) = n^*(a)(\partial s(a)/\partial a)^{-1}$, using eq. 1a. Dividing $n^*(s)$ by the total equilibrium population density N^*, we obtain the resident's equilibrium frequency distribution $P^*(s)$ of sizes s,

$$P^*(s) = \begin{cases} g_i^{-1}\int_{s_m}^{\infty} f(\tilde{s})P^*(\tilde{s})d\tilde{s}\exp(-m_l^* g_i^{-1}(s_l - s_0)) & s = s_l \\ P^*(s_l)\exp(-m_1 g_i^{-1}(s - s_l)) & s_l < s \le s_m \\ P^*(s_m)g_i g_m^{-1}\exp(-m_1 g_m^{-1}(s - s_m)) & s_m < s \le s_T \\ P^*(s_T)\exp(-m_2 g_m^{-1}(s - s_T)) & s > s_T \end{cases}, \tag{A1}$$

where m_l^* is the density-dependent equilibrium mortality among individuals ('larvae') too small to ever reproduce; other parameters are as described in the main text. Relaxing the assumption that m_l acts uniformly throughout the larval stage does not alter the results qualitatively or quantitatively; neither does explicit modelling of growth between birth and s_l, or varying s_l as such. In specific systems, the smallest possible maturation size s_l might be given by allometric constraints on, *e.g.*, body cavity size. The only unknown remaining in eq. A1, the resident's equilibrium probability of surviving the larval stage, is obtained from the first line of eq. A1, $p_l(s_m) = \exp(-m_l^* g_i^{-1}(s_l - s_0)) = g_i P^*(s_l) / \int_{s_m}^{\infty} f(s)P^*(s)ds$. This expression is further resolved in three steps by (i) using the third and fourth lines of eq. A1 in the integral, (ii) using the second and third lines of eq. A1 to replace $P^*(s_m)$ and $P^*(s_T)$ with expressions only involving $P^*(s_l)$, and (iii) cancelling $P^*(s_l)$, which yields

$$\begin{aligned} p_l^{-1}(s_m) = bg_m^{-1} \exp(-m_1 g_i^{-1}(s_m - s_l))[\int_{s_m}^{s_T} s^3 \exp(-m_1 g_m^{-1}(s - s_m))ds \\ + \exp(-m_1 g_m^{-1}(s_T - s_m))\int_{s_T}^{\infty} s^3 \exp(-m_2 g_m^{-1}(s - s_T))ds] \end{aligned} . \qquad \text{(A2a)}$$

Variant survival probabilities

The variant's probability to survive the larval stage equals that of the resident (eq. A2a). The variant's probability to survive the immature stage is

$$p_i(s_m') = \begin{cases} \exp(-m_1 g_i^{-1}(s_m' - s_l)) & s_m' < s_T \\ \exp(-m_1 g_i^{-1}(s_T - s_l) - m_2 g_i^{-1}(s_m' - s_T)) & s_m' \geq s_T \end{cases} . \qquad \text{(A2b)}$$

The variant's probability to survive from size s_m' to s is

$$p_m(s_m', s) = \begin{cases} \exp(-m_1 g_m^{-1}(s - s_m')) & s_m' \leq s \leq s_T \\ \exp(-m_1 g_m^{-1}(s_T - s_m') - m_2 g_m^{-1}(s - s_T)) & s_m' \leq s_T < s \\ \exp(-m_2 g_m^{-1}(s - s_m')) & s_T < s_m' \leq s \end{cases} . \qquad \text{(A2c)}$$

Inserting eqs. A2 in eq. 3 yields I . The result shows that I is independent of m_l and b and that the resident trait s_m affects R_0 only multiplicatively through $p_l(s_m)$. Accordingly, selection on s_m is only trivially frequency-dependent (Heino *et al.* 1998), which means that neither evolutionary branching nor protected polymorphisms are possible and that all evolutionarily stable maturation sizes s_m^* are evolutionarily attainable (Meszéna *et al.* 2001). Eq. A2a shows that s_l has no bearing on the evolution of s_m (other than constraining it from below), since s_l (like s_m) affects R_0 in eq. 3 only multiplicatively through $p_l(s_m)$: we thus assumed $s_l = 0$ for simplicity.

The variant's probability to survive from size s_l to s_T is

$$p_T(s'_m) = \begin{cases} \exp(-m_1 g_i^{-1}(s'_m - s_l) - m_1 g_m^{-1}(s_T - s'_m)) & s'_m \le s_T \\ \exp(-m_1 g_i^{-1}(s_T - s_l)) & s'_m \ge s_T \end{cases}. \tag{A3}$$

This extra result helps to appreciate trade-off 3, which emerges from the existence of a size refuge for $s \ge s_T$ with $m_1 > m_2$.

Dimensionless analysis

Our model features seven parameters: m_1, m_2, g_i, g_m, s_T, b, and m_l. As shown above, b and m_l do not affect I and, thus, have no bearing on the evolution of s_m. A dimensionless version of our model follows from conveniently choosing the units in which we measure size and time, as s_T and s_T / g_i, respectively, resulting in three dimensionless parameters $m_1 s_T / g_i$, $m_2 s_T / g_i$, and g_m / g_i. All of these are varied in fig. 1, which thus characterizes the model exhaustively.

Continuous mortality functions

To relax the assumption of discontinuous mortality with a sharp step at $s = s_T$, we considered the more general continuous function $m(s) = m_2 + (m_1 - m_2)(1 - \tanh((s - s_T)/w))/(1 - \tanh(-s_T/w))$, which results in a soft step around $s = s_T$ (fig. 2a) and which for $w \to 0$ converges to the discontinuous mortality function used in figure 1 (fig. 2a). Figure 3 shows the resultant effects of m_1 on s_m^*, for the same values of m_2 and g_m / g_i as used in figure 1.

As a further robustness test, we entirely relaxed the assumption of a threshold size in mortality by assuming that mortality is an exponential function of size, $m(s) = m_2 + (m_1 - m_2)\exp(-s/s_T)$, so that $\partial^2 m(s)/\partial s^2$ had the same sign for all s. Notice that here s_T no longer is a threshold parameter, but determines the size at which mortality drops to $1/e = 36.8\%$ of its value at $s = 0$. Figure 4 shows the resultant effects of m_1 on s_m^*, using the same parameter values as in figures 1 and 3.

LEGENDS

Figure 1. Evolutionarily stable maturation sizes s_m^* depend on mortality m_1 among small individuals ($s \le s_T$), mortality m_2 among large individuals ($s > s_T$), and the relative growth rates g_m / g_i of mature individuals ($s \ge s_m$) compared with immature individuals ($s < s_m$). The effect of m_1 on s_m^* (thick lines) and on evolutionarily unstable equilibria (thin lines) is shown in panels for three by three values of m_2 and g_m / g_i. The vertical dashed lines in each panel indicate size-independent mortality, $m_1 = m_2$; left of these lines we have $m_1 < m_2$, and right of these $m_1 > m_2$. Parameters: $s_T = 1$ and $g_i = 1$. Notice that parameters varied in this figure directly correspond to all three relevant dimensionless parameters of the model (see Appendix). By measuring size and time in units of s_T and s_T / g_i, respectively, parameters used in this figure can be translated to particular systems.

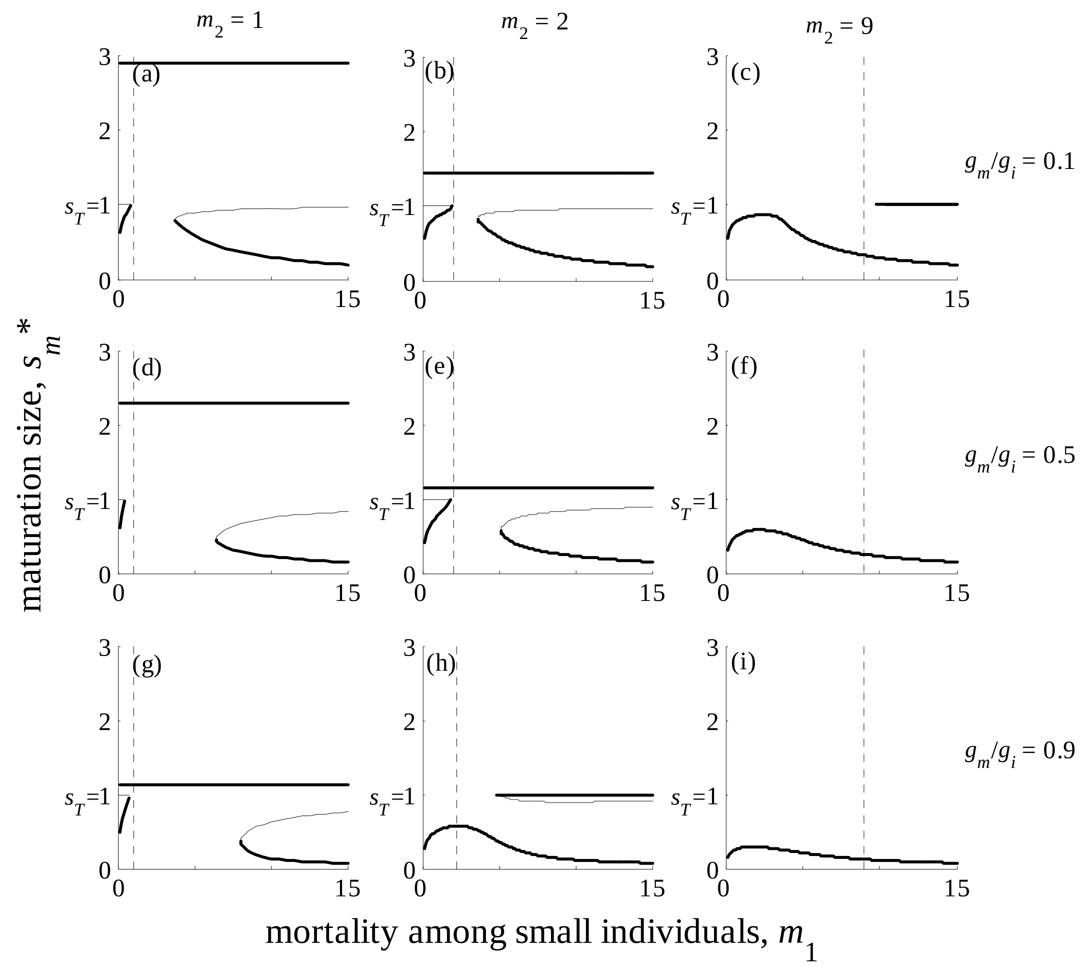
Figure 2. Disparate effects of mortality m_1 among small individuals on maturation size s_m^* occur also when mortality is a continuous function of size. Leftmost panels (a, e) show three different shapes of size-dependent mortality for (a) when there is a threshold size for mortality, $m(s) = m_2 + (m_1 - m_2)(1 - \tanh((s - s_T)/w))/(1 - \tanh(-s_T / w))$ and (e) without a threshold size, $m(s) = m_2 + (m_1 - m_2)\exp(-s / s_T)$. Panels (b-d, f-h) show the corresponding effects of m_1 on s_m^*. Each set of curves in (a, e) corresponds to a different steepness of the mortality function (determined by w in (a) and by s_T in (e)) used in panels (b-d, f-h; steepness decreases from left to right across panels). Within each set of curves in (a, e), increasing m_1 from bottom to top alters mortality from positively to negatively size-dependent. (b-d, f-h). In (g) and (h), lower lines starting at $m_1 = 6$ and $m_1 = 4$, respectively, depict a stable s_m^* and an unstable equilibrium in close proximity. Other symbols and

parameters correspond to those used in fig. 1e, with (b & black lines in a) $w = 0.1$, (c & dark grey lines in a) $w = 0.5$, (d & light grey lines in a) $w = 2$, (f & black lines in e) $s_T = 0.25$, (g & dark grey lines in e) $s_T = 0.5$, and (h & light grey lines in e) $s_T = 1$.

Figure 3. The effects of mortality m_1 among small individuals on maturation size s_m^* when mortality is a continuous function of size, $m(s) = m_2 + (m_1 - m_2)(1 - \tanh((s - s_T)/w))/(1 - \tanh(-s_T/w))$, where w determines the steepness of the change in mortality with size occurring around $s = s_T$. Notice the different scale on the vertical axis of (a). Parameters and symbols as in fig. 1, with $w = 0.5$.

Figure 4. The effects of mortality m_1 among small individuals on maturation size s_m^* when there is no threshold size for mortality, $m(s) = m_2 + (m_1 - m_2)\exp(-s/s_T)$. The lower lines in each panel depict a stable s_m^* and an unstable equilibrium in close proximity, other parameters and symbols as in fig. 1.

Figure 1



$m_2 = 1$
$m_2 = 2$
$m_2 = 9$
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
$g_m/g_i = 0.1$
$g_m/g_i = 0.5$
$g_m/g_i = 0.9$
3
2
s_T=1
0
15
maturation size, s_m^*
mortality among small individuals, m_1

Figure 2

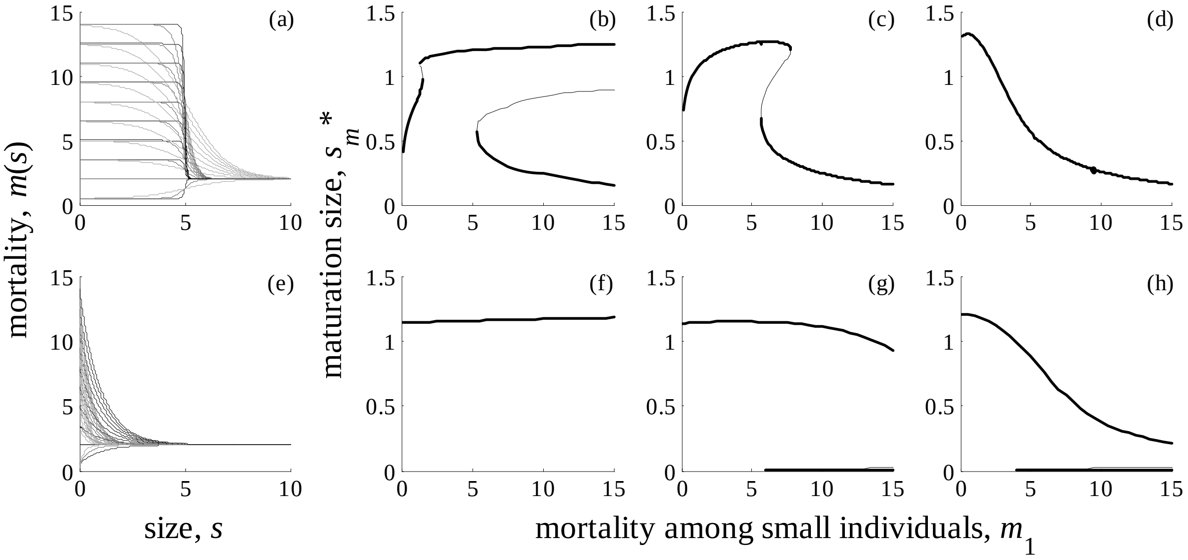
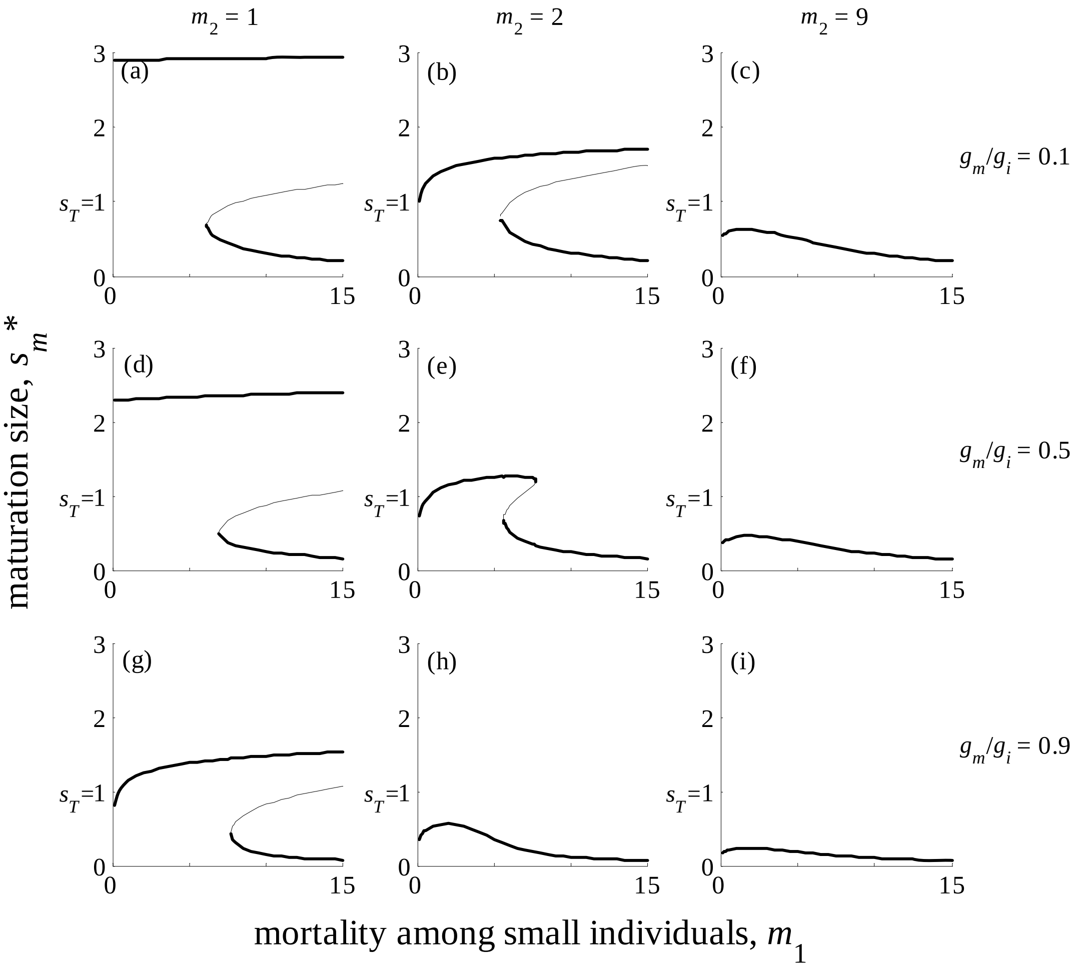
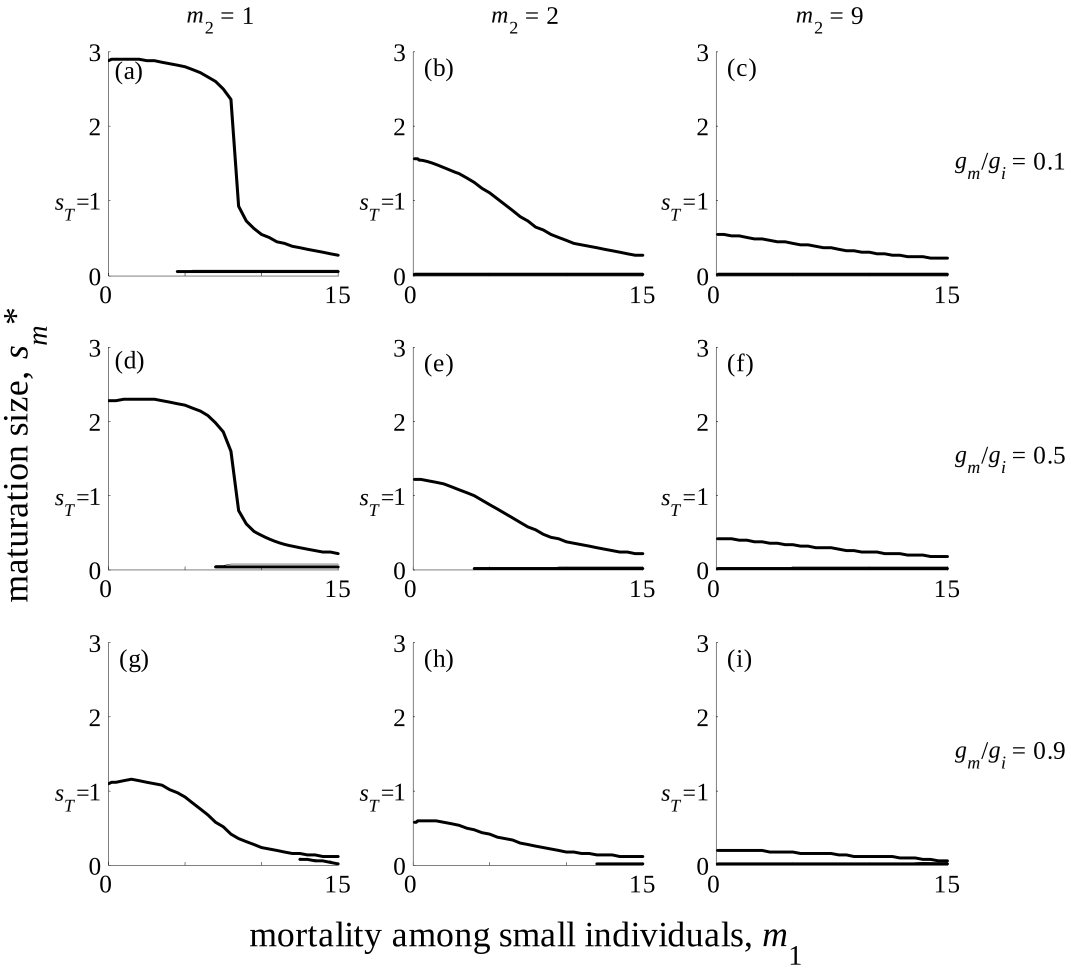

(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
mortality, $m(s)$
maturation size, s_m^*
size, s
mortality among small individuals, m_1
0
5
10
15
0.5
1
1.5

Figure 3



$m_2 = 1$
$m_2 = 2$
$m_2 = 9$
$g_m/g_i = 0.1$
$g_m/g_i = 0.5$
$g_m/g_i = 0.9$
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
3
2
s_T=1
0
0
15
maturation size, s_m^*
mortality among small individuals, m_1

Figure 4



$m_2 = 1$
$m_2 = 2$
$m_2 = 9$
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
$g_m/g_i = 0.1$
$g_m/g_i = 0.5$
$g_m/g_i = 0.9$
0
s_T=1
2
3
0
15
maturation size, s_m^*
mortality among small individuals, m_1