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Sexual allocation by both stressed and unstressed hermaphrodites within the same population

M. Broom[1], R.N. Hughes[2], M.T. Burrows[3] and G.D. Ruxton[4]

1. Centre for Mathematical Science, City University London, Northampton Square, London EC1V 0HB, UK
2. School of Biological Sciences, University of Wales, Bangor, Deiniol Road, Bangor, Gwynedd, LL57 2UW, UK
3. Scottish Marine Institute Oban, Argyll, PA37 1QA, UK
4. College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK

Abstract

Factors influencing allocation of resources to male and female offspring continue to be of great interest to evolutionary biologists. A simultaneous hermaphrodite is capable of functioning in both male and female mode at the same time, and such a life-history strategy is adopted by most flowering plants and by many sessile aquatic animals. In this paper, we focus on hermaphrodites that nourish post-zygotic stages, e.g. flowering plants and internally fertilizing invertebrates, and consider how their sex allocation should respond to an environmental stress that reduces prospects of survival but does not affect all individuals equally, rather acting only on a subset of the population. Whereas dissemination of pollen and sperm can begin at sexual maturation, release of seeds and larvae is delayed by embryonic development. We find that the evolutionarily stable strategy for allocation between male and female functions will be critically dependent on the effect of stress on the trade-off between the costs of male and female reproduction, i.e. of sperm and embryos. Thus, we identify evaluation of this factor as an important challenge to empiricists interested in the effects of stress on sex allocation. When only a small fraction of the population is stressed, we predict that stressed individuals will allocate their resources entirely to male function and unstressed individuals will increase their allocation to female function. Conversely, when the fraction of stress-affected individuals is high, stressed individuals should respond to this stressor by increasing investment in sperm and unstressed individuals should invest solely in embryos. A further prediction of the model is that we would not expect to find populations in the natural world where both stressed and unstressed individuals are both hermaphrodite.

keywords: sex allocation, hermaphroditic, dioecious, simultaneous hermaphrodite, stress, evolutionarily stable strategy

1. Introduction

The factors influencing allocation of resources to male and female offspring continue to be of great interest to evolutionary biologists [1]. Sex allocation will be influenced by the breeding system of a particular species. Breeding systems can be categorised as dioecious, in which individuals are either male or female for their entire lifetime or hermaphroditic, in which the same individual can produce both male and female gametes. Hermaphrodites can be either sequential or simultaneous. Sequential hermaphrodites, or sex changers, function as one sex early in their life, and then switch to the other. Simultaneous hermaphrodites are capable of both male and female reproduction at the same time, representing a prevalent life-history strategy among sessile organisms, notably flowering plants and modular colonial animals [2]. Allocation is often strongly influenced by environmental conditions [1,3] and here we consider how hermaphrodites cope with an environmental stress that acts only on a subset of the population simultaneously.

It has been demonstrated in hermaphroditic plants and animals that environmental stress promotes increased allocation to male rather than female function [4,5]. During the time required to produce a seed or larva, a hermaphroditic plant or animal can potentially release many pollen grains or sperm and so fitness through male function can begin to accrue immediately after sexual maturation whereas fitness through female function is delayed. Hence a plausible explanation for stress-induced allocation to male function is that the stressed organism is less likely to die before reproducing successfully as a male than as a female. Here we present a mathematical model that allows the quantitative consequences of this differential survivorship to be evaluated. Specifically, we assume that under many ecological circumstances, some (but not all) of a population will be subject to stress. For a population of flowering plants or sessile aquatic invertebrates, such patchy stresses might include localised grazing, overgrowth by larger individuals, or localised damage by wind or water currents [5]. We further assume that individuals can control their allocation to both male and female function in response to environmental cues that signal whether or not that individual will be subject to the stressor. Under these assumptions, we produce predictions for evolutionarily stable strategies (ESS) in terms of the division of resources to male and female reproduction not just for stressed individuals but also for unstressed individuals within the same population. Although generally ignored by previous treatments, there is no reason to expect that the changed allocation by stressed individuals will not induce a change in unstressed individuals within the same inter-breeding population. We will particularly focus on quantifying how the evolutionarily stable strategies of both stressed and unstressed individuals are affected by the fraction of the population that is stressed.

2. Model definition

The strategy of an individual is defined by the pair $\{m_n,m_s\}$, this being the investment in male sexual function (hereafter "sperm") by an individual experiencing either normal (n) or stressed (s) conditions ($m_n, m_s \in [0,1]$). An individual playing $\{m_n,m_s\}$ will produce a fraction $m_n(m_s)$ of the sperm in the unstressed (stressed) condition that it would produce if it chose to invest entirely in sperm: $m_n=1(m_s=1)$. Thus we explicitly assume that individuals have a flexible strategy for investment between male and female functions, and change strategy according to whether they perceive themselves as stressed or not.

In order to capture the assumption that male and female functions compete for resources, we assume that female sexual function (hereafter termed "embryos") can be found for either of these two cases from relations $f_n(m_n)$ and $f_s(m_s)$. That is, once investment in sperm is specified, these functions can be used to calculate the consequence of this investment for investment in embryos. These two functions may be different from each other, but have the following properties:

$f_n(1) = f_s(1) = 0$, and

$$f_n(0) = \frac{1}{b_n},\ f_s(0) = \frac{1}{b_s}$$

where the relative cost of embryos to sperm in unstressed (stressed) individuals is b_n (b_s).

These restrictions simply mean that if all resources are spent on sperm then there can be no investment in embryos, whereas if there is no investment in sperm, then all resources can be channelled into embryos. If total resource allocation to male function yields volume 1 of sperm for each type of individual, total allocation to female function gives sperm-volumes of $1/b_n$ and $1/b_s$ to unstressed and stressed individuals respectively. We note that allowing total allocation to yield different volumes of sperm in stressed and non-stressed individuals makes no difference to the results, as only the relative costs of embryos to sperm are important.

We also assume that the derivatives of both functions are always negative. Biologically this assumption means that increasing investment in sperm can only be achieved at the cost of reduced production of embryos. An individual playing $\{m_n,m_s\}$ will thus produce a fraction $f_n\ (m_n)(f_s\ (m_s))$ of the embryos in the unstressed (stressed) condition that it would produce if it chose to invest entirely in eggs: $m_n=0(m_s=0)$. We use the general functions $f_n\ (m_n)$ and $f_s\ (m_s)$ to allow for different levels of cost to be available for intermediate levels of resource allocation. If volume of embryos is just proportional to resources allocated we get the simple linear resource functions used later in this section

$$f_n = \frac{1-m_n}{b_n},\ \ f_s = \frac{1-m_s}{b_s}$$

so that if half of the resources are allocated to embryos and half to sperm, half the maximum volume of each are produced, $f_n\ (0.5)=0.5/\ b_n$, for unstressed individuals. It is possible to envisage situations where production is either more (or less) efficient when divided, so that if sufficient resource was allocated to produce half of the maximum sperm volume then more (or less) than half of the maximum volume of embryos would be produced i.e. $f_n\ (0.5)>0.5/\ b_n$ ($f_n\ (0.5)<0.5/\ b_n$), for unstressed individuals.

To find the ESSs, we consider a mutant individual that plays $\{m_n,m_s\}$ in a population of other individuals that play the resident strategy $\{m_n^*,m_s^*\}$. We assume that each individual has (independent) probability s of being stressed. If an individual is stressed, then there is a probability that the individual will die before resources allocated to sperm can be released as functioning gametes. This is represented as a probability p_m that resources allocated to male function lead to successful production of viable gametes. There is a similar probability for investment in female function p_f. As discussed in the introduction, the overwhelming empirical evidence is for p_m to be greater than p_f.

If we make the simple Fisherian assumption that both male and female gain functions are linear (effectively that all females will have the same number of offspring on average, and each male is equally likely to be the father of any given offspring), then we can apply the classical fitness function for the sex-ratio game [5,6]. For a mutant parent which has a fixed expected number of children irrespective of their sex and has male children with probability m in a population where males are in proportion m^* this fitness function is given by

$$R(m;m^*)=\frac{m}{m^*}+\frac{1-m}{1-m^*}.$$

Here the unique evolutionarily stable solution is for the population to invest in both sexes in equal proportion $m^*=0.5$. We shall see that the situation is more complex in our case, as there are potentially different costs applied to two distinct types of individuals.

Using the above equation we can express the pay-off to the mutant as

$$R(m_n, m_s; m_n^*, m_s^*) = \frac{(1-s)m_n + s m_s p_m}{(1-s)m_n^* + s m_s^* p_m} + \frac{(1-s)f_n(m_n) + s f_s(m_s) p_f}{(1-s)f_n(m_n^*) + s f_s(m_s^*) p_f}. \quad (1)$$

We can simplify this expression by defining some composite constants. Specifically, we define

$$\alpha = \frac{s p_m}{1-s}$$

and

$$\beta = \frac{s p_f}{1-s}.$$

From our arguments above about the relative values of p_m and p_f, we would expect α to be greater than β in the overwhelming majority of ecological circumstances. We will also simplify the notation for embryos, using simply f_n and f_s to denote $f_n(m_n)$ and $f_s(m_s)$; and f_n^* and f_s^* to denote $f_n(m_n^*)$ and $f_s(m_s^*)$. We will also use $'$ to denote the derivative of these functions. So that $f_s^{*\prime}$ is the derivative of f_s evaluated at m_s^*.

Using these notational simplifications, we can simplify our expression (1) for the pay-off to a mutant to the expression below:

$$R(m_n, m_s; m_n^*, m_s^*) = \frac{m_n + \alpha m_s}{m_n^* + \alpha m_s^*} + \frac{f_n + \beta f_s}{f_n^* + \beta f_s^*}. \qquad (2)$$

A strategy {m_n*,m_s*} is an ESS if and only if within a population where almost all individuals play this strategy, and a small fraction ε play an alternative strategy {m_n,m_s}, the payoff to an individual playing {m_n,m_s} would be less than the payoff to an individual playing {m_n*,m_s*}, i.e.

$$R\left(m_n{}^*,m_s{}^*;(1-\varepsilon)m_n{}^*+\varepsilon m_n,(1-\varepsilon)m_s{}^*+\varepsilon m_s)\right) > R\left(m_n,m_s;(1-\varepsilon)m_n{}^*+\varepsilon m_n,(1-\varepsilon)m_s{}^*+\varepsilon m_s)\right)$$

It is clear that a necessary condition for this to hold for arbitrarily small ε is

$$R\left(m_n{}^*,m_s{}^*;m_n{}^*,m_s{}^*\right) \geq R\left(m_n,m_s;m_n{}^*,m_s{}^*\right) \qquad (3)$$

for all alternative {m_n,m_s}. We note because of the form of the payoff function in equation (2), condition (3) is a sufficient condition as well, since whenever an invading group uses a larger (smaller) male investment, this increases (decreases) the number of males in the population, which decreases (increases) the payoff to males compared to females.

For general functions *R* it is not possible to give more specific conditions which are equivalent to condition (3), but we can give some necessary conditions. For normal individuals, if 0< m_n*<1 we require (at ε=0) that

$$\frac{\partial R}{\partial m_n} = 0$$

and either *R* is constant in a population of {m_n*,m_s*} individuals or

$$\frac{\partial^2 R}{\partial m_n{}^2} < 0$$

at $m_n = m_n^*$.

If $m_n^*=1$ we require

$$\frac{\partial R}{\partial m_n} > 0$$

at $m_n=1$.

If $m_n^*=0$ we require

$$\frac{\partial R}{\partial m_n} < 0$$

at $m_n=0$.

These conditions ensure that a population cannot be invaded by individuals playing $\{m_n, m_s^*\}$ where m_n is sufficiently close to m_n^*.

Similar conditions are required for m_s.

These necessary conditions are also sufficient for $\{m_n^*, m_s^*\}$ to be an ESS whenever at most one of $0< m_n^*<1$, $0< m_s^*<1$ holds, and there are no extra cases where R has zero derivative, other than when the population strategy is $\{m_n^*, m_s^*\}$.

Thus to find ESSs we must consider the signs of the derivatives of the function R, and we obtain the following expressions:

$$\frac{\partial R}{\partial m_n} >=< 0 \Leftrightarrow f_n^* + m_n^* f_n' + \beta f_s + \alpha m_s^* f_n' >=< 0 \tag{4}$$

and

$$\frac{\partial R}{\partial m_s} >=< 0 \Leftrightarrow \alpha f_n^* + \beta m_n^* f_s' + \alpha\beta m_s^* f_s^{*}{}' + \alpha\beta f_s >=< 0\,. \tag{5}$$

To find ESSs, we must substitute $m_n = m_n^*$ and $m_s = m_s^*$ into (4) and (5).

The expressions in (4) & (5) can also be derived by differentiating the simpler function

$$(m_n + \alpha m_s)(f_n + \beta f_s). \tag{6}$$

Thus we shall consider the derivatives of (6), which is equivalent to considering those of our original (but more complex) expression, since only the signs of those derivatives are important.

To make further progress we must explicitly specify the trade-off between male and female functions for both stressed and unstressed members of the interbreeding population. As discussed above, we will assume the following simple linear resource allocation functions:

$$f_n = \frac{1 - m_n}{b_n}$$

and

$$f_s = \frac{1 - m_s}{b_s}.$$

Thus, the values given to the two parameters b_n and b_s describe the relationship between female and male functionality for the two cases (stressed and unstressed). A value of one for either of these parameters suggests an equal cost of sperm and embryos. A value higher than one implies a larger cost (in terms of investment required to produce one gamete) to egg production than sperm production. The overwhelming empirical evidence is that, per gamete, sperm are cheaper and quicker to produce than embryos. Thus we would expect b_n and b_s to both be greater than one.

Let us further define the following composite parameters:

$$b = \frac{b_n}{b_s},$$

$$c_1 = \frac{1}{1 + b\beta} \text{ and}$$

$$c_2 = 1 - c_1 = \frac{b\beta}{1 + b\beta}.$$

Thus b describes the effect of stress on the trade-off between sperm and embryos. If b is equal to one then stress has no effect on this trade-off. If b is greater than 1, then sperm is more expensive (relative to embryos) for stressed individuals compared to unstressed individuals. Conversely, if b is less than one then sperm is less expensive for stressed individuals. As we shall see, the separate values of b_n and b_s do not affect our results, although their ratio b does.

Let us return to considering expression (6), which (utilising our newly-introduced composite parameters) is given by the following expression:

$$(m_n + \alpha n_s)(f_n + \beta f_s) = \left(\frac{m_n + \alpha n_s}{b_n b_s} \right)(b_s + \beta b_n - b_s m_n - \beta b_n m_s). \qquad (7)$$

After re-arrangement and dropping simple constant multipliers, one can demonstrate that (7) varies as the simpler expression:

$$S(m_n, m_s) = (m_n + \alpha m_s)(1 - c_1 m_n - c_2 m_s). \qquad (8)$$

The derivatives of *S* are easily obtained:

$$\frac{\partial S}{\partial m_n} = 1 - 2c_1 m_n - (\alpha c_1 + c_2) m_s \qquad (9)$$

and

$$\frac{\partial S}{\partial m_s} = \alpha\left(1 - 2c_2 m_s - \left(c_1 + \frac{c_2}{\alpha}\right) m_n\right). \qquad (10)$$

3. Possible ESS forms

We need to consider nine different possibilities for the form of an ESS: m_n could be zero, or one, or a value between zero and one. That is, normal individuals could invest entirely in embryos, or entirely in sperm or in a combination of the two. The same is true for stressed individuals.

Two of the nine combinations, *S*(0,0) and *S*(1,1), can be immediately discounted, since for them S= 0 which yields minimum reward. Thus neither {0,0} nor {1,1} can ever be an ESS. This clearly makes sense, as it would never be beneficial for the whole population of stressed and unstressed individuals to all invest only in embryos or all invest only in sperm.

Let us now consider the case where both stressed and unstressed individuals adopt a hermaphrodite strategy of investing in both embryos and sperm: i.e. $0 < m_n, m_s < 1$.

For this to occur, the following is a necessary condition:

$$\frac{\partial S}{\partial m_n} = \frac{\partial S}{\partial m_s} = 0 .$$

It is straightforward to show that this leads to the condition below:

$$b\beta = \alpha .$$

This expression leads to our first general conclusion, only in very unlikely circumstances, where parameter values are carefully tuned, could we get an ESS where both stressed and unstressed individuals are hermaphrodite. In almost all circumstances, we would expect one or both of them to specialise and invest all their resources in either embryos or sperm. We will now consider the remaining six cases where at least one party (the stressed or the unstressed individuals within the population) specialises in only one sexual role.

Case 1) Unstressed individuals invest only in embryos, stressed individuals only in sperm: {m_n,m_s} = {0,1}.

For this to be an ESS necessary and sufficient conditions are that at {0,1} the following to expressions are satisfied:

$$\frac{\partial S}{\partial m_n} < 0, \quad \frac{\partial S}{\partial m_s} > 0 .$$

From (9) and (10), this simplifies to the conditions

$$\alpha > 1, \quad \beta b < 1.$$

Case 2) Unstressed individuals invest only in embryos, but stressed individuals devide resources between both embryos and sperm: $\{m_n, m_s\} = \{0, 0 < m_s < 1\}$

For this to be an ESS, necessary conditions are that at $\{0, m_s\}$:

$$\frac{\partial S}{\partial m_n} < 0, \quad \frac{\partial S}{\partial m_s} = 0.$$

From (9) and (10), this simplifies to the conditions below:

$$\alpha > \beta b, \quad \beta b > 1$$

and give the equilibrium strategy for stressed individuals below:

$$m_s = \frac{1 + \beta b}{2\beta b}.$$

For this to be an ESS we also need to verify stability against changes in the value of m_s. The derivative of S, and so R, is zero at $m_s = m_s{}^*$. Since R is linear in m_s, given the population mixture, this means that R is constant for all m_s. As stated earlier in the text following condition (3), this is enough to prevent invasion by an individual playing an alternative value of m_s, and we thus have stability.

Case 3) Unstressed individuals invest only in sperm; stressed individuals only in embryos: {m_n,m_s} = {1,0}.

For this to be an ESS, necessary and sufficient conditions are that at {1,0}

$$\frac{\partial S}{\partial m_n} > 0, \quad \frac{\partial S}{\partial m_s} < 0 .$$

This simplifies to the conditions below:

$$\alpha < 1, \quad \beta b > 1 .$$

Case 4) Unstressed individuals divide investment between both sperm and embryos, whereas stressed individuals invest only in embryos: {m_n,m_s} = {0<m_n<1,0}.

For this to be an ESS, necessary conditions are that at {m_n,0}

$$\frac{\partial S}{\partial m_s} < 0, \quad \frac{\partial S}{\partial m_n} = 0 .$$

This simplifies to the conditions below:

$$\alpha < \beta b, \quad \beta b < 1,$$

and give the equilibrium for division of resources for unstressed individuals as below:

$$m_n = \frac{1+\beta b}{2}.$$

This is shown to be an ESS in the same way as in Case 2.

Case 5) Unstressed individuals divide investment between both sperm and embryos; stressed individuals invest only in sperm: {m_n,m_s} = {0<m_n<1,1}.

For this to be an ESS, necessary conditions are that at {m_n,1}

$$\frac{\partial S}{\partial m_s} > 0, \quad \frac{\partial S}{\partial m_n} = 0.$$

This simplifies to the conditions below

$$\alpha < 1, \quad \beta b < \alpha,$$

and gives the equilibrium value of investment for unstressed individuals:

$$m_n = \frac{1-\alpha c_1 - c_2}{2c_1} = \frac{1-\alpha}{2}.$$

This is shown to be an ESS in the same way as in Case 2.

Case 6) Unstressed individuals invest only in sperm; stressed individuals divide investment between both embryos and sperm: $\{m_n,m_s\} = \{1,0<m_s<1\}$.

For this to be an ESS, necessary conditions are that at $\{1,m_s\}$

$$\frac{\partial S}{\partial m_n} > 0, \quad \frac{\partial S}{\partial m_s} = 0 .$$

This simplifies to the conditions that

$$\alpha < \beta b, \quad \alpha > 1,$$

and also give the equilibrium value defining investment by stressed individuals:

$$m_s = \frac{1 - c_1 - \dfrac{c_2}{\alpha}}{2c_2} = \frac{\alpha - 1}{2\alpha} .$$

This is again shown to be an ESS in the same way as in Case 2.

4. Discussion

Combining all of these cases, it is easy to see that we always have a unique ESS. For any combination of parameter values, we can find the ESS strategies for both stressed and unstressed individuals. These are summarised in Figure 1.

When there are no stressed individuals, then $s \rightarrow 0$, and so $\alpha \rightarrow 0$ and $\beta \rightarrow 0$, and thus the ESS strategy is for individuals to divide their investment equally between embryos and sperm ($m_n = 0.5$). This equal investment in embryos and sperm is a consequence of us making the simple Fisherian assumption that both male and female gain functions (change in fitness as a function of allocation) are linear. How allocation is predicted to change as a small number of individuals become stressed depends on parameter values. In particular it depends on whether $b\beta > \alpha$, which can be re-expressed as the condition:

$$\frac{b_n}{b_s} > \frac{p_m}{p_f} . \qquad (11)$$

If condition (11) is satisfied, then stressed individuals should invest fully in embryos ($m_s = 0$) and unstressed individuals should increase their investment in sperm above 50% ($m_n > 0.5$). As the fraction of the individuals that are stressed increases (but remains relatively modest), the investment of unstressed individuals in sperm should increase. If (11) is not satisfied, then stressed individuals should invest fully in sperm ($m_s = 1$) and unstressed individuals should increase their investment in embryos above 50% ($m_n < 0.5$). As the fraction of the individuals that are stressed increases (but is still relatively modest), investment of unstressed individuals in embryos should increase.

We must now interpret condition (11) biologically. It is more likely to be satisfied if $p_f > p_m$, and we argue in the introduction that we expect this to be very unlikely. It is also more likely to be satisfied if the trade-offs between embryos and sperm differ in stressed and unstressed individuals such that embryos are more expensive (relative to sperm) for unstressed individuals. Thus, another general conclusion that we draw from investigation of our model is that the evolutionarily stable strategy for allocation between male and female functions will be critically dependent on the effect of stress on the trade-off between the costs of sperm and embryos (the parameter b in our model). If b is equal to one then stress has no effect on this trade-off. If b is greater than 1, then sperm are more expensive (relative to embryos) for stressed individuals compared to unstressed individuals. Conversely, if b is less than one then sperm is less expensive for stressed individuals. Thus, we identify evaluation of this factor as an important challenge to empiricists interested in the effect of stress on sex allocation.

In the absence of any clear reason to think otherwise, if we assume that the relative physiological costs of embryos and sperm are unaffected by stress, then b will equal one and we would expect (11) not to be satisfied and so stressed individuals to allocate entirely to male function and unstressed individuals to increase their allocation to female function. However, this prediction holds only when the fraction of the population that is stressed is relatively small.

Within this region where only a small fraction of the population is stressed at any one time (the bottom left quadrant of Figure 1), the evolutionarily stable strategy for the unstressed individuals varies smoothly as parameter values are varied smoothly, whereas the ESS for stressed individuals undergoes dramatic change from complete specialisation in embryos on one side of the dividing line to complete specialisation in sperm on the other side. However, unless the dividing line given by expression (11) is crossed, the specialist strategy of stressed individuals is insensitive to changes in parameter values.

We can also look at the situation where stressed individuals are very common in the population. This is the top right quadrant of Figure 1. In the extreme case where almost all individuals are stressed, $s \rightarrow 1$, then stressed individuals should divide their investment equally between embryos and sperm ($m_s = 0.5$). A prediction of the model in this case is that the evolutionarily stable strategy played by individuals when everyone is stressed is the same as the strategy played by individuals when no-one is stressed.

As the number of stressed individuals declines from a high value, then again whether or not expression (11) is satisfied is key to our predictions. If expression (11) is satisfied then stressed individuals should invest less in sperm and unstressed individuals should invest entirely in sperm. However, if expression (11) is not satisfied, then in this case the model predicts that stressed individuals should increase their investment in sperm and unstressed individuals should invest solely in embryos.

It is also possible to identify combinations of parameter values such that individuals of one type (either stressed or unstressed individuals) invest entirely in embryos and those of the other type invest entirely in sperm. For example, providing $\alpha > 1$ and $b\beta < 1$ then unstressed individuals should invest entirely in embryos and stressed individuals entirely in sperm. If we make the same assumption as above that b is equal to one, then (because we expect that $\alpha > \beta$), then the above prediction will hold for an intermediate range of s values. Thus when a moderate fraction of the population is stressed, the model predicts a complete breakdown of hermaphroditism, with stressed individuals producing only sperm and unstressed individuals only embryos.

To simplify expressions, we have used linear gain functions in our model. However, the model framework could easily accommodate non-linear gain functions (as used by Charnov [3]). Although this would make manipulation of the model more cumbersome, there is no reason to expect that the addition of this complexity would have any qualitative effect on our predictions, unless this nonlinearity made intermediate strategies more profitable (e.g. if $f_n(0.5)>0.5$), in which case the predicted breakdown of hermaphroditism above would not be complete.

A further key prediction of the model is that we would not expect to find situations in the natural world where both stressed and unstressed individuals are hermaphrodite. Rather, we would expect one or both of them to specialise in embryos or sperm. If however, populations in which stressed and unstressed individuals adopt a hermaphrodite strategy are found, then one or more of the assumptions of our model does not hold for that population. One assumption that may not be met in some real populations is that individuals have complete freedom to evolve to utilise any level of differential investment in male and female function in both the stressed and unstressed cases. It may be that there are physiological constraints on how much change in investment can be achieved. It may also be that the implicit assumption of our model of free and random mixing of gametes across the mixed population of stressed and unstressed individuals is not always valid. Further, it may also be that nonlinearity acts as described above. We reiterate that a key aspect of our interpretation of the relevance of our model prediction for the natural world has been the assumption that stress does not strongly affect the relative physiological costs of sperm and embryos. Empirical investigation of this assumption would be very valuable. Moreover, although our model applies to plants and animals with at least some post-zygotic investment of resources (excluding post-partum parental care, typically absent from sessile organisms), even a slight difference in the production rate of sperm and eggs would bring externally fertilizing invertebrates such as certain corals and hydroids [9] within its remit. To our knowledge, empirical data on the relative speeds of sperm and egg production by externally fertilizing invertebrates are lacking, but experimental determination of these values would be invaluable in the present context.

We assume that individuals respond to their own state (whether they are stressed or not) and that such response is influenced by the fraction of the population that is stressed. It seems unlikely in many situations where this fraction varies unpredictably on short-timescales that individuals will be able to track such variation and respond appropriately through phenotypic plasticity. However, in many circumstances the fraction affected will either remain (at least approximately) constant over longer timescales, or vary predictably (for example seasonally, or in response to tidal cycles). Hence, our model implicitly assumes such a situation and that selection has moulded individuals to show responses to either being stressed or unstressed that are appropriate to the fraction of stressed individuals experienced in the population as a whole.

Two previously published ESS models capture some of the elements of the present model. Freeman et al. [4] predict increasing male allocation by hermaphroditic plants occupying patches of habitat where dryness physiologically restricts seed production.

The predicted bias toward pollen production depended on the proportion of the population occupying dry patches. Dryness would be regarded as a form of stress in our model. Day and Aarssen [8] predict greater male allocation in smaller individuals within a population of hermaphroditic plants, where survivorship increases with size. Smaller individuals are likely to die before the relatively prolonged process of seed production can be completed, yet are still likely to produce a significant quantity of pollen. If survivorship is also determined by site/patch quality independently of plant size, individuals occupying poorer sites should increase male allocation. In the above respects, therefore, Freeman et al. [4] and Day and Aarssen [8] make similar predictions to each other, and predictions that are in accord with those discussed above generated by our model. Our model contributes further to investigation of the effects of environmental stress on sexual investment by explicitly considering reciprocal dependence of optimal sex allocation in stressed and non-stressed individuals as a function of survivorship and likelihood of being stressed. We very much hope that the novel predictions generated in this regard are sufficiently clear and general to encourage empirical testing.

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References

[1] S.A. West, Sex Allocation. Princeton University Press, Princeton, NJ, 2009

[2] R.N. Hughes, Lessons in modularity: the evolutionary ecology of colonial invertebrates. Sci. Mar. 69 (2005) 169-179.

[3] E.L. Charnov, The theory of sex allocation. Princeton University Press, Princeton, 2002

[4] D.C. Freeman, Harper, K.T. & Charnov, E.L., Sex change in plants: old and new observations, and new hypotheses. Oecol. 47 (1980) 222-232.

[5] R.N. Hughes, Manríquez, P.H., Bishop, J.D.D. & Burrows, M.T., Stress promotes maleness in hermaphroditic modular animals. Proc. N. Acad. Sci. 100 (2003), 10326-10330.

[6] W.D. Hamilton, Extraordinary sex ratios. Science 156 (1967) 477-488.

[7] J. Maynard Smith, Evolution and the Theory of Games, Cambridge University Press, Cambridge, 1980

[8] T. Day, Aarssen L.W. A time commitment hypothesis for size-dependent gender allocation. Evolution 51 (1997) 988-993.

[9] R.N. Hughes, A functional biology of clonal animals. Chapman and Hall, London. 1989

Figure caption: Summary of model predictions. The strategy of an individual in terms of its division of investment between male and female reproduction is defined by the pair $\{m_n,m_s,\}$, this being the investment in male sexual function (called "sperm" in the text) by an individual experiencing either normal (*n*) or stressed (*s*) conditions (m_n, $m_s \in [0,1]$). An individual playing $\{m_n,m_s\}$ will produce a fraction $m_n(m_s)$ of the sperm in the unstressed (stressed) condition that it would produce if it chose to invest entirely in sperm: $m_n=1(m_s=1)$. It is assumed that all resources not invested in male function are allocated to female function. Thus we explicitly assume that individuals have a flexible strategy for investment between male and female functions, and change strategy according to whether they perceive themselves as stressed or not. The strategy is influenced by a combination of values given to each of two parameter groups, α and $b\beta$. We assume that each individual has (independent) probability *s* of being stressed. If an individual is stressed, then there is a probability that the individual will die before resources allocated to sperm can be released as functioning gametes. This is represented as a probability p_m that resources allocated to male function lead to successful production of viable gametes. There is a similar probability for investment in female function: p_f. As discussed in the introduction, the overwhelming empirical evidence is for p_m to be greater than p_f.

$$\alpha = \frac{sp_m}{1-s}$$

and

$$\beta = \frac{sp_f}{1-s}.$$

The parameter *b* describes the effect of stress on the trade-off between sperm and embryos. If *b* is equal to one then stress has no effect on this trade-off. If *b* is greater than 1, then sperm is more expensive (relative to embryos) for stressed individuals compared to unstressed individuals. Conversely, if b is less than one then sperm is less expensive for stressed individuals.