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

3

4 **M. Broom¹, R.N. Hughes², M.T. Burrows³ and G.D. Ruxton⁴**

5

- 6 1. Centre for Mathematical Science, City University London, Northampton
7 Square, London EC1V 0HB, UK
8 2. School of Biological Sciences, University of Wales, Bangor, Deiniol Road,
9 Bangor, Gwynedd, LL57 2UW, UK
10 3. Scottish Marine Institute Oban, Argyll, PA37 1QA, UK
11 4. College of Medical, Veterinary and Life Sciences, University of Glasgow,
12 Glasgow G12 8QQ, UK
13

14 **Abstract**

15 Factors influencing allocation of resources to male and female offspring continue to
16 be of great interest to evolutionary biologists. A simultaneous hermaphrodite is
17 capable of functioning in both male and female mode at the same time, and such a
18 life-history strategy is adopted by most flowering plants and by many sessile aquatic
19 animals. In this paper, we focus on hermaphrodites that nourish post-zygotic stages,
20 e.g. flowering plants and internally fertilizing invertebrates, and consider how their
21 sex allocation should respond to an environmental stress that reduces prospects of
22 survival but does not affect all individuals equally, rather acting only on a subset of
23 the population. Whereas dissemination of pollen and sperm can begin at sexual
24 maturation, release of seeds and larvae is delayed by embryonic development. We
25 find that the evolutionarily stable strategy for allocation between male and female
26 functions will be critically dependent on the effect of stress on the trade-off between
27 the costs of male and female reproduction, i.e. of sperm and embryos. Thus, we
28 identify evaluation of this factor as an important challenge to empiricists interested in
29 the effects of stress on sex allocation. When only a small fraction of the population is

30 stressed, we predict that stressed individuals will allocate their resources entirely to
31 male function and unstressed individuals will increase their allocation to female
32 function. Conversely, when the fraction of stress-affected individuals is high, stressed
33 individuals should respond to this stressor by increasing investment in sperm and
34 unstressed individuals should invest solely in embryos. A further prediction of the
35 model is that we would not expect to find populations in the natural world where both
36 stressed and unstressed individuals are both hermaphrodite.

37

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

40

41 **1. Introduction**

42 The factors influencing allocation of resources to male and female offspring continue
43 to be of great interest to evolutionary biologists [1]. Sex allocation will be influenced
44 by the breeding system of a particular species. Breeding systems can be categorised as
45 dioecious, in which individuals are either male or female for their entire lifetime or
46 hermaphroditic, in which the same individual can produce both male and female
47 gametes. Hermaphrodites can be either sequential or simultaneous. Sequential
48 hermaphrodites, or sex changers, function as one sex early in their life, and then
49 switch to the other. Simultaneous hermaphrodites are capable of both male and female
50 reproduction at the same time, representing a prevalent life-history strategy among
51 sessile organisms, notably flowering plants and modular colonial animals [2].

52 Allocation is often strongly influenced by environmental conditions [1,3] and here we
53 consider how hermaphrodites cope with an environmental stress that acts only on a
54 subset of the population simultaneously.

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

79

80 **2. Model definition**

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

89

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

96

97 $f_n \leq f_s \leq 0$, and

98 $f_n \leq \frac{1}{b_n}, f_s \leq \frac{1}{b_s}$

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

101

102 These restrictions simply mean that if all resources are spent on sperm then there can
103 be no investment in embryos, whereas if there is no investment in sperm, then all

104 resources can be channelled into embryos. If total resource allocation to male function
105 yields volume 1 of sperm for each type of individual, total allocation to female
106 function gives sperm-volumes of $1/b_n$ and $1/b_s$ to unstressed and stressed individuals
107 respectively. We note that allowing total allocation to yield different volumes of
108 sperm in stressed and non-stressed individuals makes no difference to the results, as
109 only the relative costs of embryos to sperm are important.

110 We also assume that the derivatives of both functions are always negative.

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

$$119 \quad f_n = \frac{1 - m_n}{b_n}, \quad f_s = \frac{1 - m_s}{b_s}$$

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

127

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

137

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

145

$$146 \quad R(m; m^*) = \frac{m}{m^*} + \frac{1-m}{1-m^*}.$$

147

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

152

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

154

$$155 \quad R(m_n, m_s; m_n^*, m_s^*) = \frac{(-s \overline{m}_n + sm_s p_m)}{(-s \overline{m}_n^* + sm_s^* p_m)} + \frac{(-s \overline{f}_n(m_n) + sf_s(m_s) p_f)}{(-s \overline{f}_n(m_n^*) + sf_s(m_s^*) p_f)}. \quad (1)$$

156

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

158 we define

159

$$160 \quad \alpha = \frac{sp_m}{1-s}$$

161 and

$$162 \quad \beta = \frac{sp_f}{1-s}.$$

163

164 From our arguments above about the relative values of p_m and p_f , we would expect α

165 to be greater than β in the overwhelming majority of ecological circumstances. We

166 will also simplify the notation for embryos, using simply f_n and f_s to denote $f_n(m_n)$ and

167 $f_s(m_s)$; and f_n^* and f_s^* to denote $f_n(m_n^*)$ and $f_s(m_s^*)$. We will also use ' to denote the

168 derivative of these functions. So that $f_s^{* \prime}$ is the derivative of f_s evaluated at m_s^* .

169

170 Using these notational simplifications, we can simplify our expression (1) for the pay-

171 off to a mutant to the expression below:

172

$$173 \quad R(m_n, m_s; m_n^*, m_s^*) = \frac{m_n + \alpha m_s}{m_n^* + \alpha m_s^*} + \frac{f_n + \beta f_s}{f_n^* + \beta f_s^*}. \quad (2)$$

174

175 A strategy $\{m_n^*, m_s^*\}$ is an ESS if and only if within a population where almost all
 176 individuals play this strategy, and a small fraction ε play an alternative strategy
 177 $\{m_n, m_s\}$, the payoff to an individual playing $\{m_n, m_s\}$ would be less than the payoff to
 178 an individual playing $\{m_n^*, m_s^*\}$, i.e.

179

$$180 \quad R(m_n^*, m_s^*; (1-\varepsilon)m_n^* + \varepsilon m_n, (1-\varepsilon)m_s^* + \varepsilon m_s) > R(m_n, m_s; (1-\varepsilon)m_n^* + \varepsilon m_n, (1-\varepsilon)m_s^* + \varepsilon m_s)$$

181

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

183

$$184 \quad R(m_n^*, m_s^*; m_n^*, m_s^*) > R(m_n, m_s; m_n^*, m_s^*) \quad (3)$$

185

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

191

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

$$195 \quad \frac{\partial R}{\partial m_n} = 0$$

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

$$197 \quad \frac{\partial^2 R}{\partial m_n^2} < 0$$

198 at $m_n = m_n^*$.

199 If $m_n^* = 1$ we require

$$200 \quad \frac{\partial R}{\partial m_n} > 0$$

201 at $m_n = 1$.

202 If $m_n^* = 0$ we require

$$203 \quad \frac{\partial R}{\partial m_n} < 0$$

204 at $m_n = 0$.

205 These conditions ensure that a population cannot be invaded by individuals playing

206 $\{m_n, m_s^*\}$ where m_n is sufficiently close to m_n^* .

207 Similar conditions are required for m_s .

208 These necessary conditions are also sufficient for $\{m_n^*, m_s^*\}$ to be an ESS whenever

209 at most one of $0 < m_n^* < 1$, $0 < m_s^* < 1$ holds, and there are no extra cases where R has

210 zero derivative, other than when the population strategy is $\{m_n^*, m_s^*\}$.

211

212 Thus to find ESSs we must consider the signs of the derivatives of the function R , and

213 we obtain the following expressions:

214

$$215 \quad \frac{\partial R}{\partial m_n} > < 0 \Leftrightarrow f_n^* + m_n^* f_n' + \beta f_s + \alpha m_s^* f_n' > < 0 \quad (4)$$

216 and

$$217 \quad \frac{\partial R}{\partial m_s} > < 0 \Leftrightarrow \alpha f_n^* + \beta m_n^* f_s' + \alpha \beta m_s^* f_s'^* + \alpha \beta f_s > < 0. \quad (5)$$

218

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

220

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

223

$$224 \quad \alpha m_n + \beta f_s. \quad (6)$$

225

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

229

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

234

$$235 \quad f_n = \frac{1 - m_n}{b_n}$$

236 and

$$237 \quad f_s = \frac{1 - m_s}{b_s}.$$

238

239 Thus, the values given to the two parameters b_n and b_s describe the relationship
240 between female and male functionality for the two cases (stressed and unstressed). A
241 value of one for either of these parameters suggests an equal cost of sperm and
242 embryos. A value higher than one implies a larger cost (in terms of investment
243 required to produce one gamete) to egg production than sperm production. The

244 overwhelming empirical evidence is that, per gamete, sperm are cheaper and quicker
 245 to produce than embryos. Thus we would expect b_n and b_s to both be greater than one.

246

247 Let us further define the following composite parameters:

248

249
$$b = \frac{b_n}{b_s},$$

250
$$c_1 = \frac{1}{1+b\beta} \text{ and}$$

251
$$c_2 = 1 - c_1 = \frac{b\beta}{1+b\beta}.$$

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

258

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

261

262
$$\left(\frac{m_n + \alpha n_s}{b_n b_s} \right) \left(\frac{f_n + \beta f_s}{c_1 + \beta b_n - b_s m_n - \beta b_n m_s} \right). \quad (7)$$

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

265

266 $S(m_n, m_s) = (m_n + \alpha m_s) - c_1 m_n - c_2 m_s$. (8)

267

268 The derivatives of S are easily obtained:

269

270 $\frac{\partial S}{\partial m_n} = 1 - 2c_1 m_n - (\alpha c_1 + c_2) m_s$ (9)

271 and

272 $\frac{\partial S}{\partial m_s} = \alpha \left(1 - 2c_2 m_s - \left(c_1 + \frac{c_2}{\alpha} \right) m_n \right)$. (10)

273

274 3. Possible ESS forms

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

279

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

285

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

288

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

290

291
$$\frac{\partial S}{\partial m_n} = \frac{\partial S}{\partial m_s} = 0.$$

292

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

294

295
$$b\beta = \alpha.$$

296

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

304

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

307

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

310

311
$$\frac{\partial S}{\partial m_n} < 0, \quad \frac{\partial S}{\partial m_s} > 0.$$

312

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

314

315 $\alpha > 1, \beta b < 1.$

316

317 **Case 2) Unstressed individuals invest only in embryos, but stressed individuals**

318 **divide resources between both embryos and sperm: $\{m_n, m_s\} = \{0, 0 < m_s < 1\}$**

319

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

321

322 $\frac{\partial S}{\partial m_n} < 0, \quad \frac{\partial S}{\partial m_s} = 0.$

323

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

325

326 $\alpha > \beta b, \quad \beta b > 1$

327

328 and give the equilibrium strategy for stressed individuals below:

329

330 $m_s = \frac{1 + \beta b}{2\beta b}.$

331

332 For this to be an ESS we also need to verify stability against changes in the value of

333 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

334 population mixture, this means that R is constant for all m_s . As stated earlier in the

335 text following condition (3), this is enough to prevent invasion by an individual

336 playing an alternative value of m_s , and we thus have stability.

337

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

340

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

342

343
$$\frac{\partial S}{\partial m_n} > 0, \quad \frac{\partial S}{\partial m_s} < 0.$$

344

345 This simplifies to the conditions below:

346

347
$$\alpha < 1, \quad \beta b > 1.$$

348

349 **Case 4) Unstressed individuals divide investment between both sperm and**
350 **embryos, whereas stressed individuals invest only in embryos: $\{m_n, m_s\} =$**

351 **$\{0 < m_n < 1, 0\}$.**

352

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

354

355
$$\frac{\partial S}{\partial m_s} < 0, \quad \frac{\partial S}{\partial m_n} = 0.$$

356

357 This simplifies to the conditions below:

358

359
$$\alpha < \beta b, \quad \beta b < 1,$$

360

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

362

363
$$m_n = \frac{1 + \beta b}{2}.$$

364

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

366

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

369

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

371

372
$$\frac{\partial S}{\partial m_s} > 0, \quad \frac{\partial S}{\partial m_n} = 0.$$

373

374 This simplifies to the conditions below

375

376
$$\alpha < 1, \quad \beta b < \alpha,$$

377

378 and gives the equilibrium value of investment for unstressed individuals:

379

380
$$m_n = \frac{1 - \alpha c_1 - c_2}{2c_1} = \frac{1 - \alpha}{2}.$$

381

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

383

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

386

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

388

389 $\frac{\partial S}{\partial m_n} > 0, \quad \frac{\partial S}{\partial m_s} = 0.$

390

391 This simplifies to the conditions that

392

393 $\alpha < \beta b, \quad \alpha > 1,$

394

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

396

397
$$m_s = \frac{1 - c_1 - \frac{c_2}{\alpha}}{2c_2} = \frac{\alpha - 1}{2\alpha}.$$

398

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

400

401 **4. Discussion**

402 Combining all of these cases, it is easy to see that we always have a unique ESS.

403 For any combination of parameter values, we can find the ESS strategies for both

404 stressed and unstressed individuals. These are summarised in Figure 1.

405

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

$$414 \quad \frac{b_n}{b_s} > \frac{p_m}{p_f}. \quad (11)$$

415
416 If condition (11) is satisfied, then stressed individuals should invest fully in embryos
417 ($m_s = 0$) and unstressed individuals should increase their investment in sperm above
418 50% ($m_n > 0.5$). As the fraction of the individuals that are stressed increases (but
419 remains relatively modest), the investment of unstressed individuals in sperm should
420 increase. If (11) is not satisfied, then stressed individuals should invest fully in sperm
421 ($m_s = 1$) and unstressed individuals should increase their investment in embryos above
422 50% ($m_n < 0.5$). As the fraction of the individuals that are stressed increases (but is
423 still relatively modest), investment of unstressed individuals in embryos should
424 increase.

425
426 We must now interpret condition (11) biologically. It is more likely to be satisfied if p_f
427 $> p_m$, and we argue in the introduction that we expect this to be very unlikely. It is
428 also more likely to be satisfied if the trade-offs between embryos and sperm differ in
429 stressed and unstressed individuals such that embryos are more expensive (relative to

430 sperm) for unstressed individuals. Thus, another general conclusion that we draw
431 from investigation of our model is that the evolutionarily stable strategy for allocation
432 between male and female functions will be critically dependent on the effect of stress
433 on the trade-off between the costs of sperm and embryos (the parameter b in our
434 model). If b is equal to one then stress has no effect on this trade-off. If b is greater
435 than 1, then sperm are more expensive (relative to embryos) for stressed individuals
436 compared to unstressed individuals. Conversely, if b is less than one then sperm is
437 less expensive for stressed individuals. Thus, we identify evaluation of this factor as
438 an important challenge to empiricists interested in the effect of stress on sex
439 allocation.

440

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

447

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

454 crossed, the specialist strategy of stressed individuals is insensitive to changes in
455 parameter values.

456

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

464

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

471

472 It is also possible to identify combinations of parameter values such that individuals
473 of one type (either stressed or unstressed individuals) invest entirely in embryos and
474 those of the other type invest entirely in sperm. For example, providing $\alpha > 1$ and $b\beta <$
475 1 then unstressed individuals should invest entirely in embryos and stressed
476 individuals entirely in sperm. If we make the same assumption as above that b is equal
477 to one, then (because we expect that $\alpha > \beta$), then the above prediction will hold for an
478 intermediate range of s values. Thus when a moderate fraction of the population is

479 stressed, the model predicts a complete breakdown of hermaphroditism, with stressed
480 individuals producing only sperm and unstressed individuals only embryos.

481

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

489

490 A further key prediction of the model is that we would not expect to find situations in
491 the natural world where both stressed and unstressed individuals are hermaphrodite.
492 Rather, we would expect one or both of them to specialise in embryos or sperm. If
493 however, populations in which stressed and unstressed individuals adopt a
494 hermaphrodite strategy are found, then one or more of the assumptions of our model
495 does not hold for that population. One assumption that may not be met in some real
496 populations is that individuals have complete freedom to evolve to utilise any level of
497 differential investment in male and female function in both the stressed and unstressed
498 cases. It may be that there are physiological constraints on how much change in
499 investment can be achieved. It may also be that the implicit assumption of our model
500 of free and random mixing of gametes across the mixed population of stressed and
501 unstressed individuals is not always valid. Further, it may also be that nonlinearity
502 acts as described above. We reiterate that a key aspect of our interpretation of the
503 relevance of our model prediction for the natural world has been the assumption that

504 stress does not strongly affect the relative physiological costs of sperm and embryos.
505 Empirical investigation of this assumption would be very valuable. Moreover,
506 although our model applies to plants and animals with at least some post-zygotic
507 investment of resources (excluding post-partum parental care, typically absent from
508 sessile organisms), even a slight difference in the production rate of sperm and eggs
509 would bring externally fertilizing invertebrates such as certain corals and hydroids [9]
510 within its remit. To our knowledge, empirical data on the relative speeds of sperm and
511 egg production by externally fertilizing invertebrates are lacking, but experimental
512 determination of these values would be invaluable in the present context.

513

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

525

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

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

545

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548

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581 **Figure caption:** Summary of model predictions. The strategy of an individual in
582 terms of its division of investment between male and female reproduction is defined
583 by the pair $\{m_n, m_s\}$, this being the investment in male sexual function (called
584 “sperm” in the text) by an individual experiencing either normal (n) or stressed (s)
585 conditions ($m_n, m_s \in [0,1]$). An individual playing $\{m_n, m_s\}$ will produce a fraction
586 $m_n(m_s)$ of the sperm in the unstressed (stressed) condition that it would produce if it
587 chose to invest entirely in sperm: $m_n=1(m_s=1)$. It is assumed that all resources not
588 invested in male function are allocated to female function. Thus we explicitly assume
589 that individuals have a flexible strategy for investment between male and female
590 functions, and change strategy according to whether they perceive themselves as
591 stressed or not. The strategy is influenced by a combination of values given to each of
592 two parameter groups, α and $b\beta$. We assume that each individual has (independent)
593 probability s of being stressed. If an individual is stressed, then there is a probability
594 that the individual will die before resources allocated to sperm can be released as
595 functioning gametes. This is represented as a probability p_m that resources allocated to
596 male function lead to successful production of viable gametes. There is a similar
597 probability for investment in female function: p_f . As discussed in the introduction, the
598 overwhelming empirical evidence is for p_m to be greater than p_f .

599
$$\alpha = \frac{sp_m}{1-s}$$

600 and

601
$$\beta = \frac{sp_f}{1-s}.$$

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

605 compared to unstressed individuals. Conversely, if b is less than one then sperm is

606 less expensive for stressed individuals.

607