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1 **Sex roles and the evolution of parental care specialisation**

2

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14

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17 **Abstract**

18

19 Males and females are defined by the relative size of their gametes (anisogamy), but  
20 secondary sexual dimorphism in fertilisation, parental investment, and mating competition is  
21 widespread and often remarkably stable over evolutionary timescales. Recent theory has  
22 clarified the causal connections between anisogamy and the most prevalent differences  
23 between the sexes, but deviations from these patterns remain poorly understood. Here we  
24 study how sex differences in parental investment and mating competition coevolve with  
25 parental care specialisation. Parental investment often consists of two or more distinct  
26 activities (e.g. provisioning and defence) and parents may care more efficiently by  
27 specialising in a subset of these activities. Our model predicts that efficient care  
28 specialisation broadens the conditions under which biparental investment can evolve in  
29 lineages that historically had uniparental care. Major transitions in sex roles (e.g. from  
30 female-biased care with strong male mating competition to male-biased care with strong  
31 female competition) can arise following ecologically induced changes in the costs or benefits  
32 of different care types, or in the sex ratio at maturation. Our model provides a clear  
33 evolutionary mechanism for sex-role transitions, but also predicts that such transitions should  
34 be rare. It consequently contributes towards explaining widespread phylogenetic inertia in  
35 parenting and mating systems.

36 Recent theory has tightened the logical links between anisogamy (i.e. sexual dimorphism in  
37 gamete size) and widely observed sex differences in gamete production, fertilisation, parental  
38 investment, and mating competition [1-8]. This work has provided plausible evolutionary  
39 accounts of the most widespread and consistent sex differences, which include larger total  
40 gamete investment by females [2,8,9] and stronger competition for mates in males [2,5,6]. In  
41 contrast, little progress has been made in explaining deviations from these general patterns,  
42 even though such deviations are surprisingly widespread [10-13] (see below).

43

44 Much theory predicts that sex differences in parental investment and mating competition are  
45 reinforced by a positive feedback loop [2,5,6,14-16]. In particular, if the less-caring sex  
46 experiences stronger sexual selection, then any trade-off between parental effort and mating  
47 competition will affect this sex more strongly, increasing the costs of parental care for the  
48 less-caring sex [6,14,17]. When this feedback loop acts strongly, the sex that initially invests  
49 more in offspring is selected to maintain that investment, while the initially less caring sex  
50 instead directs resources towards mating competition (note that the claim that selection on  
51 mating competition and parental care strongly favours egalitarian care [18] has not withstood  
52 additional theoretical scrutiny [6]). These selective pressures maintain the ancestral sex  
53 asymmetry due to anisogamy, potentially explaining why the archetype of caring females and  
54 competitive males is so prevalent in the natural world [19-22]. However, the strength of this  
55 feedback loop is mediated by ecological and demographic factors such as certainty of  
56 parentage, mortality rates, population density, encounter rates, and sex ratios [4,6,14,15,22].  
57 In addition, the feedback loop can be weakened or broken if cooperative care is highly  
58 beneficial, leading to a more even distribution of parental investment [6,23,24]. Despite these  
59 additional factors, however, the sex making the largest initial investment in offspring is  
60 usually predicted to remain the dominant provider, and consequently to experience less

61 competition for mates. These theoretical predictions are consistent with patterns of parental  
62 investment and mating competition across a wide range of animal taxa [19-22].

63

64 Despite the successful generalisation that anisogamy tends to predict sex differences in  
65 parental investment, exceptions to this generalisation occur and are not well explained by  
66 existing theory. Male parental investment and female mating competition occur across a  
67 surprisingly wide array of organisms, and in many cases even exceed female investment and  
68 male mating competition (e.g. in species of pipefish [25,26]; waders [27-29]; coucals [30,31];  
69 katydids [32,33]; honeylocust beetles [34,35]; dance-flies [36,37]; reviewed in [10,11]). In  
70 such species, males' greater investment in offspring leads to lower potential reproductive  
71 rates in males than in females, which is expected to result in competition among females for  
72 mates (e.g. vigorous courtship [35], sexually selected ornamentation [38,39], or, in rare cases,  
73 physical fights over mates [28,29]). Many of these species additionally show high degrees of  
74 sex-specific specialisation in parental care, with males and females performing  
75 complementary parental activities [40-42] (see below). This suggests that parental care  
76 specialisation may play a role in facilitating the evolution of elaborate male care and female  
77 mating competition. While some theory has been developed in relation to such systems, we  
78 lack a framework that explains both how these systems evolve in the first place and why they  
79 are so rare [12].

80

81 Across species, costly mating traits in one sex almost invariably co-occur with substantial  
82 parental investment (or, in some cases, nuptial gifts) by the other sex, an observation that has  
83 long drawn the attention of theorists [17,43,44]. Surprisingly, however, most formal models  
84 of sexual selection treat parenting patterns as fixed (e.g. via fixed sex-specific 'time-outs' for  
85 reproduction) [7,44-48]. On the other hand, theory on parental investment often neglects

86 sexual selection entirely, or models its strength via fixed parameters [4,14,16,18,23,24]. In  
87 other words, most models ignore the potential feedback between parental care and sexual  
88 selection as care patterns, sexually selected traits, and preferences evolve [49]. However, a  
89 small but growing body of literature has begun to correct this omission by explicitly  
90 modelling the coevolution of care and competition in males and females [5,6,15,50].  
91  
92 Here we expand the recent model of Fromhage and Jennions [6] to study how care  
93 specialisation coevolves with sex roles (i.e. sex-specific behavioural patterns) in mating  
94 competition and parental investment. In many species, parental investment consists of two or  
95 more distinct activities (e.g. egg provisioning, brooding or oxygenation of eggs, defence  
96 against predators, or offspring provisioning [43]). Due to time and resource constraints, a  
97 single individual may not provide multiple types of care as effectively as an individual  
98 specialised in a subset of care types [40-42]. We show that such inefficiencies can lead to sex  
99 specialisation in parental investment, with males and females adopting distinct roles. Care  
100 specialisation broadens the conditions under which biparental investment can evolve in  
101 lineages that historically had uniparental care [24]. Ecological changes in the costs or benefits  
102 of different care types, or in the sex ratio at maturation, can then select for partial or full  
103 reversals of sex roles in mating and parenting. Our model provides a plausible evolutionary  
104 route from the ancestral condition of female-only care to systems with male-biased care and  
105 strong female mating competition. In line with the empirical evidence, however, it also  
106 predicts that such transitions should be rare.

107

## 108 **Model**

109

110 Our model is closely based on the ‘two-trait’ model of Fromhage and Jennions [6], which  
111 corrected and extended the influential model of Kokko and Jennions [18]. We model the  
112 coevolution of three continuous traits: the duration of parental investment ( $T$  for females and  
113  $\tilde{T}$  for males); the proportion of parental investment allocated to each of two care types ( $q$  and  
114  $1 - q$  for females,  $\tilde{q}$  and  $1 - \tilde{q}$  for males); and a ‘mating trait’ ( $x$  and  $\tilde{x}$ ) that increases an  
115 individual’s mating rate but at the cost of higher mortality (see Table S1 in electronic  
116 supplementary material for a summary of parameters and variables). Note that our ‘care  
117 types’ may include parental investment of any kind and are not limited to post-zygotic or  
118 post-hatching care.

119

120 Our model assumes that all processes (e.g. mating, mortality) occur continuously in time and  
121 that generations are overlapping. Individuals alternate between two possible states: searching  
122 or competing for mates (‘time-in’) and providing or recovering from parental investment  
123 (‘time-out’). During time-in, individuals mate at instantaneous rates of  $a$  (for females) or  $\tilde{a}$   
124 (for males), which depend on the values of their mating traits. After mating, individuals enter  
125 time-out for a duration of  $T$  or  $\tilde{T}$ . If still alive, they then return to time-in. During both  
126 time-in and time-out, individuals experience mortality at an instantaneous rate of  $\mu$  or  $\tilde{\mu}$ . To  
127 vary the mean relatedness between carers and offspring, we suppose that each breeding event  
128 involves  $n$  females and  $\tilde{n}$  males (e.g. all offspring sired by a single pair if  $n = \tilde{n} = 1$ , mixed  
129 paternity if  $\tilde{n} > 1$ , or mixed maternity if  $n > 1$ ). Parental investment is shared among all  
130 offspring produced in a given breeding event. We focus mainly on the case where both males  
131 and females have full parentage of all offspring they invest in ( $n = \tilde{n} = 1$ ), as this is the most

132 common mating system in which substantial male care and female mating competition evolve  
133 (but see electronic supplementary material for results with mixed parentage).

134

### 135 *Mating rates and mortality*

136 Mortality rates during both time-in and time-out increase with an individual's mating trait,  
137 according to:

$$\mu(x) = \mu_{\min}(1 + x^{1.5}) \quad [1]$$

138 The equation for males is analogous. The parameter  $\mu_{\min}$  determines the minimum mortality  
139 rate, which applies to individuals that do not invest in the mating trait. Note that sex-specific  
140 mortality rates are the same whether an individual is in time-in or time-out. Our model  
141 consequently assumes that the costs of bearing a large mating trait 'carry over' into time-out  
142 [7]. The term  $(1 + x^{1.5})$  was chosen so that the mortality rate is an accelerating function of  
143 mating trait investment; similarly-shaped functions give similar results.

144

145 Mating traits are also under sexual selection due to their effects on individual mating rates.

146 Mating rates are given by  $a = Mx\tilde{x}nr_o^{1/2}$  for females and  $\tilde{a} = Mx\tilde{x}\tilde{n}r_o^{-1/2}$  for males [6,18],

147 where  $r_o$  is the operational sex ratio (i.e. the ratio of males to females in time-in). The

148 operational sex ratio depends on both the sex ratio at maturity (MSR) and sex-specific

149 mortalities (see electronic supplementary material). The parameter  $M$  accounts for species-  
150 specific factors like population density and movement capacity.

151

### 152 *Parental investment and offspring survival*

153 Offspring require two types of parental investment to survive (e.g. egg production and

154 post-hatching care, or provisioning and defence). We assume that offspring survive to reach

155 maturity (i.e. their first time-in) with probability:



$$S = \exp\left(-\frac{\alpha_1}{\tau_{1 \text{ all}}}\right) \exp\left(-\frac{\alpha_2}{\tau_{2 \text{ all}}}\right) \quad [2]$$

156 Here  $\tau_{1 \text{ all}}$  represents the total expected parental investment into care of type 1 that a brood  
 157 receives, summed across all contributing parents; similarly,  $\tau_{2 \text{ all}}$  represents the total expected  
 158 investment into type-2 care (see below). Each factor  $\exp(-\alpha_i/\tau_{i \text{ all}})$  is a sigmoidal function  
 159 of expected parental investment, showing diminishing returns as investment increases. The  
 160 parameters  $\alpha_1$  and  $\alpha_2$  determine the amount of parental investment needed to achieve a given  
 161 offspring survival probability (larger  $\alpha_i$  means greater investment is needed).

162

163 Consider a female that provides parental investment for a maximum duration of  $T$ . At the  
 164 beginning of any given time-out, the probability that she survives the full interval  $T$  is given  
 165 by  $p_0 = e^{-\mu T}$ . The probability density function for her dying at some earlier time  
 166  $t \in [0, T]$  is  $\mu e^{-\mu t}$ . Her expected duration of parental investment, including care of both  
 167 types, is consequently:

$$\tau_{\text{total}} = p_0 T + \int_0^T \mu e^{-\mu t} t dt = \frac{1 - e^{-\mu T}}{\mu} \quad [3]$$

168 Females allocate a proportion  $q$  of their parental investment to type-1 care and the remainder  
 169  $1 - q$  to type-2 care. We assume that it is inefficient for the same individual to provide both  
 170 types of care, so that all parental investment is discounted by a factor of  $d = 1 - \gamma q(1 - q)$ .  
 171 The parameter  $\gamma$  represents the efficiency benefit of specialising in a single type of care. If  
 172  $\gamma = 0$  then offspring survival is identical when cared for by two unspecialised parents or by  
 173 two specialised parents, provided the overall duration of parental investment in each care  
 174 type is the same. Larger values of  $\gamma$  correspond to more-efficient care by parents that  
 175 specialise in a single care type. For a female playing  $T$  and  $q$ , her *effective* contributions to  
 176 each care type are then  $\tau_1 = q d \tau_{\text{total}}$  and  $\tau_2 = (1 - q) d \tau_{\text{total}}$  (and analogously for males).  
 177 We assume that  $0 \leq \gamma < 3$ , which ensures that  $\tau_1$  and  $\tau_2$  are strictly increasing functions of  $q$

178 and  $1 - q$  respectively (proof in electronic supplementary material). The effective parental  
179 investment that a brood receives from all contributing parents combined is  $\tau_{1 \text{ all}} = n\tau_1 + \tilde{n}\tilde{\tau}_1$   
180 for type-1 care and  $\tau_{2 \text{ all}} = n\tau_2 + \tilde{n}\tilde{\tau}_2$  for type-2 care.

181

### 182 *Fitness and selection trajectories*

183 We calculated evolutionary trajectories using a standard adaptive dynamics framework. Trait  
184 values are assumed to change in proportion to selection gradients on mutant trait values,  
185 calculated against a background population in which all other individuals play the same  
186 sex-specific strategies (see electronic supplementary material for derivations of fitness  
187 functions and selection gradients). In particular, this assumes weak selection, as well as  
188 similar rates of mutational input and no genetic correlations among traits [51].

189

190 In some cases, we found local equilibria that were not stable to large-effect mutations in care  
191 specialisation. For instance, populations with unspecialised female-only care (i.e. with  $\tilde{T} = 0$   
192 and  $q = 1/2$ ) could sometimes be invaded by caring males, but only if the males were highly  
193 specialised in one care type (e.g.  $\tilde{q} = 0$ ). In such cases, we first allowed the population to  
194 evolve gradually towards the local equilibrium, then introduced the mutation of large effect,  
195 and allowed gradual evolution towards a final, globally stable equilibrium (see e.g. Figure  
196 1e,f). This approach is consistent with the assumption that mutations of large effect are rare.  
197 Our qualitative results are, however, unaffected by the numerical details of this approach.

198

## 199 **Results**

200

201 Our model predicts three possible types of stable equilibria: female-only care, male-only care  
202 and biparental care. When there is no inefficiency in providing both types of care (Figure

203 1a,b), only uniparental care is stable. The sex that initially provided more care ends up caring  
204 alone, while the non-caring sex competes more strongly for mates. When the need for  
205 specialisation is moderate (Figure 1c,d), either uniparental or biparental care can evolve,  
206 depending on the initial conditions. When the need for specialisation is high (Figure 1e,f),  
207 only biparental care is stable. The evolution of sex roles is predicted to be highly  
208 conservative, in that each of three equilibria is generally highly stable once it has evolved.

209

210 *Sole carers are generalists, joint carers are specialists*

211 Under biparental care, each sex fully specialises in one care type as long as there is *any*  
212 inefficiency in providing both types of care. In other words, at biparental equilibria we  
213 always have either  $(q, \tilde{q}) = (0,1)$  or  $(q, \tilde{q}) = (1,0)$  whenever the need for specialisation  
214  $\gamma > 0$  (see red circles in Figure 1c-f, which indicate full specialisation). If there is no  
215 inefficiency in providing both care types (i.e.  $\gamma = 0$ ), then biparental care is unstable  
216 (Figure 1a,b). The relative amount of care provided by each sex depends on the sex ratio at  
217 maturity (Figure 2) and the relative need for each type of care ( $\alpha_1$  and  $\alpha_2$ : Figure 3) (see  
218 below).

219

220 In contrast, uniparental carers always provide both types of care, as otherwise their offspring  
221 would not survive. For these parents, the optimal allocation of parental effort depends on  
222 both the relative importance of each care type and the need for specialisation. If the two care  
223 types are equally important ( $\alpha_1 = \alpha_2$ ) and the need for specialisation is not too great ( $\gamma \leq 2$ ),  
224 then sole carers provide both care types equally ( $q = \frac{1}{2}$ : see blue circles in Figure 1a-d, which  
225 indicate no specialisation). If one type of care is more necessary than the other, sole carers  
226 unsurprisingly invest more in that type of care (e.g.  $q > 1/2$  when  $\alpha_1 > \alpha_2$ : data not shown).  
227 In the interesting case where  $\gamma > 2$ , the inefficiency of providing both care types is so severe

228 that sole carers always evolve partial specialisation, even when both types of care are equally  
229 important (small purple circles in Figure 1e,f). However, uniparental care is unstable in this  
230 case: the non-caring sex is under selection to start providing the more neglected type of care  
231 (Figure 1e,f).

232

233 *Biased sex ratios at maturation (MSR) select for both greater care and more competition in*  
234 *the more common sex, unless the care system becomes unstable*

235 Under biparental care, biases in the sex ratio at maturation select for both greater parental  
236 investment and greater competition (i.e. larger mating trait values) by the more common sex  
237 (lighter-coloured regions in Figure 2c,d). Similarly, under uniparental care, individuals of the  
238 caring sex provide greater parental investment, in absolute terms, when they outnumber the  
239 non-caring sex at maturation (data not shown). This increase in parental investment is  
240 accompanied by an increase in mating competition in the caring sex, although the non-caring  
241 sex remains the more competitive of the two (Figure 2b,f).

242

243 This simple pattern, which applies within care systems, is complicated by transitions among  
244 systems. Biparental care can transition to uniparental care when the MSR is highly biased and  
245 the need for specialisation is low (lower corners of Figure 2c,d). This results in an abrupt  
246 change in sex roles. In the biparental system, the more common sex both cares and competes  
247 slightly more than the less common sex (i.e. both  $T$  and  $x$  are larger in the more common  
248 sex). In contrast, under uniparental care, the more common sex provides all the care, while  
249 competition is much stronger in the less common sex. The reverse transition from uniparental  
250 to biparental care can occur if the MSR is biased in the direction of the non-caring sex and  
251 the need for specialisation is high (upper left corners of Figure 2a,b; upper right corners of  
252 Figure 2e,f). Even more extreme transitions – from female-only care directly to male-only

253 care or vice versa – can occur if the need for specialisation is low and the MSR is extremely  
254 biased towards the non-caring sex (bottom left corners of Figure 2a,b; bottom right corners of  
255 Figure 2e,f).

256

### 257 *Relative importance of the two care types*

258 Biparental care is stable to changes in the relative importance of the two care types (i.e. the  
259 magnitudes of  $\alpha_1$  and  $\alpha_2$ : Figure 3c,d). The sex specialising in the more important care type  
260 provides more care, all else being equal, while the other sex competes more strongly (note  
261 that we assume without loss of generality that males are initially specialised in type-1 care).  
262 This can result in strong sex biases in care even under biparental care. Uniparental care can  
263 be invaded by biparental care if the benefits of specialisation are high enough (upper regions  
264 of Figure 3a,b,e,f). In this case, the initially caring sex specialises in the more important care  
265 type, while continuing to provide more care and compete less. Existing sex roles are  
266 consequently preserved, although in a less pronounced form, after the transition to biparental  
267 care. For any given benefits of specialisation  $\gamma$ , biparental care invades more easily when the  
268 two care types differ in importance (Figure 3a,b,e,f). This is because partial specialisation by  
269 the caring sex creates an opportunity for the non-caring sex to specialise in the  
270 complementary care type.

271

### 272 *Major transitions in sex-roles*

273 Gradual shifts in sex roles, with respect to both parental care and mating competition, can  
274 occur in our model when the initial care system is biparental. These shifts in roles can be  
275 driven by changes in the MSR or in the relative importance of the two care types (Figures  
276 2c,d and 3c,d). Large differences in the needs for each care type can lead to large sex biases  
277 in the amount of care provided. A full transition from female-only to male-only care is also

278 possible, with an accompanying reversal of mating competition. For instance, biparental care  
279 might first evolve from female care via increased benefits of specialised care (higher  $\gamma$ :  
280 Figures 2e,f and 3e,f). Male-only care could then be favoured by a subsequent reduction in  
281 the benefits of specialisation, along with a male-biased MSR (Figure 2c,d). Notably, this  
282 scenario requires only two large ecological shifts to precipitate the transitions from  
283 uniparental care to biparental care and from biparental care to uniparental care by the other  
284 sex. A less likely outcome, which our model predicts should be possible but rare, is a direct  
285 transition from female-only care to male-only care, or vice versa. Such a transition requires a  
286 low benefit of specialisation and a large bias in the MSR (Figure 2e,f), although it is unclear  
287 how such an extreme MSR would arise.

288

## 289 **Discussion**

290

291 Here, we model how care specialisation shapes the evolution of parental investment and  
292 mating competition, and investigate the circumstances under which sex-role transitions in  
293 these traits are likely to arise. Our model predicts that a given set of parameter values can  
294 lead to more than one type of care system (male-only, female-only, or biparental), depending  
295 on the initial strategies for each sex (in fact, all seven possible combinations of stable  
296 equilibria occur in some parameter regions: Figure S1). The conditions that allow a transition  
297 from one parental care system to another are usually much stricter than the conditions for  
298 maintaining a given system once it has evolved (Figures 2,3). For instance, the parameter  
299 regions where biparental care is stable once evolved (light-coloured regions in Figure 2c and  
300 3c) are much larger than the parameter regions where biparental care can arise from  
301 uniparental care (lighter-coloured regions in Figure 2a,e and 3a,e). The model consequently  
302 predicts that transitions among the three types of equilibrium will be uncommon. These

303 alternative stable states arise because strong mating competition selects for large mating traits  
304 in the less caring sex, which indirectly trade off against parental care. The positive feedback  
305 cycle acting on sex roles is consequently relaxed but not eliminated in our model [52].

306

307 Our model predicts that males and females should specialise in complementary care types  
308 when it is inefficient for a single parent to provide multiple types of care. Care specialisation  
309 allows for greater evolutionary lability of sex roles than predicted by most previous theory  
310 [2,5,6,14-16]. In particular, (1) increases in the efficiency of care specialisation can select for  
311 transitions from uniparental to biparental care; (2) under biparental care, if the relative  
312 importance of one care type increases, then the sex providing that care type evolves to care  
313 more and compete less; and (3) biases in the sex ratio at maturity select for greater care by  
314 the more common sex, although the effect on mating competition is more complicated.

315 Together, these factors enable the evolution of varied sex roles, including transitions between  
316 female-only, male-only and biparental care.

317

318 Although parental care specialisation occurs in many taxa [43], the efficiency of  
319 specialisation has to our knowledge never been measured empirically (but see refs [40,42] for  
320 interesting related work). Efficiency benefits may result if, for example, some important care  
321 activities are both demanding and exclusive of other activities. In convict cichlids, for  
322 instance, females spend most of their time tending offspring, leaving them little time to  
323 defend the territory or chase intruders, tasks that consequently fall to the male [39]. Our  
324 model is formulated in terms of the benefit to offspring of parental specialisation, but  
325 equivalent predictions apply if specialisation reduces the costs of care to parents. Any  
326 efficiency gains could be quantified most easily in systems where specialisation is facultative,  
327 e.g. when individuals switch from specialised to unspecialised caring strategies upon the

328 death or desertion of a partner [40,42]. For instance, offspring and parental outcomes could  
329 be compared between one joint brood cared for by both parents and two half-sized broods  
330 each cared for by one parent. We note, however, that differences in parental effort may also  
331 affect the results of such manipulations [53].

332

333 Our model assumes that changes in the parameter values are ecological in origin, or at least  
334 not directly caused by shifts in parental or mating behaviour. Optimal parental investment in  
335 care activities – e.g. provisioning, defence, brooding, or oxygenation – may be particularly  
336 sensitive to ecological factors. For instance, the need to oxygenate broods depends on  
337 temperature and dissolved oxygen levels, while the benefits of offspring defence depend on  
338 the density of potential predators [54-56]. Temporal or spatial variation in these factors  
339 should consequently affect the relative need for different care types (e.g.  $\alpha_1$  and  $\alpha_2$  in our  
340 model), leading to sex-role variation within or among biparental species where males and  
341 females specialise in different care types. Similarly, changes in how strongly offspring  
342 depend on their parents (e.g. the evolution of precocial vs altricial young in birds) may affect  
343 the benefits of care specialisation ( $\gamma$ ) [56-58].

344

345 The sex ratio at maturation (MSR) likely depends on complex interactions between  
346 ecological and evolutionary factors, which we do not model here explicitly. Biases in the  
347 MSR may result either from skewed sex ratios at conception (i.e. primary sex ratios) or from  
348 sex-biased mortality during early development or juvenile stages [59]. For instance,  
349 population-level bias in the primary sex ratio can occur when the relationship between  
350 parental investment and offspring fitness differs between male and female offspring. Such  
351 differences can favour overproduction of the competitive sex by carers that are in good  
352 condition (i.e. the Trivers-Willard hypothesis: [60]). Similarly, selection for costly mating



353 traits in the competing sex (e.g. due to size advantage in contests) may favour riskier juvenile  
354 growth trajectories that generate larger mating traits when successful [61]. Such factors could  
355 lead to feedback effects of mating competition on the MSR that are not accounted for in our  
356 model. Feedback is perhaps more likely when mating success is an accelerating function of  
357 investment in sexually selected traits (in contrast to our model, where the relationship is  
358 assumed linear).

359

360 Sex differences in juvenile mortality may also result from factors that are at least partly  
361 independent of parental investment or mating competition, including sex-biased dispersal  
362 [62], sex differences in ecological niche [63,64], or sex differences in susceptibility to  
363 disease, parasites or genetic abnormalities. Major transitions in sex roles may consequently  
364 be precipitated by changes in the mortality risk due to such external factors. Interestingly,  
365 Eberhart-Phillips and colleagues [65] found that variation in the adult sex ratio in plovers was  
366 largely driven by sex differences in juvenile survival, and that parental cooperation was most  
367 common in populations with more equal sex ratios. In a more extreme example, Jiggins and  
368 colleagues [66] observed female lekking behaviour in populations of *Acraea* butterflies in  
369 which the male-killing parasite *Wolbachia* had led to heavily female-biased sex ratios; we  
370 note, however, that there is no male parental care in this species.

371

372 Several limitations of the model should be kept in mind. First, we model mating competition  
373 via a hypothetical ‘mating trait’ that is assumed *a priori* to increase an individual’s mating  
374 rate. We consequently do not model whether opposite-sex individuals should prefer mates  
375 with higher mating trait values (i.e. this is not a preference-trait model: see [45,46,67]). The  
376 assumptions of our model are most plausible when the mating trait is interpreted as mate  
377 search effort [5,7,68], an armament used in mating competition [69], or an ornament that

378 exploits perceptual biases [70,71], rather than an ornament that coevolves with active mate  
379 choice [45,46,67].

380

381 Second, our model assumes that the benefits of a given care type are not synergistic between  
382 the sexes, in the sense that the value of a female investing  $x$  and her partner investing  $y$  is  
383 identical to one parent investing  $x + y$ . In biparental systems, this assumption selects for  
384 males and females to specialise fully in complementary care types. In reality, there may be  
385 synergistic benefits when both parents participate in the same care type (e.g. offspring  
386 provisioning or nest defence may be considerably more effective when both parents  
387 participate) [6,23,72]. This situation might favour the evolution of incomplete specialisation  
388 by males and females, an outcome that does not occur in our model. Further, the evolution of  
389 biparental care from uniparental ancestors is driven by care specialisation in our model, with  
390 the consequence that specialisation and biparental care evolve in tandem. An alternative  
391 scenario would be for unspecialised biparental care to evolve first (e.g. due to synergy),  
392 followed by care specialisation whenever the latter is efficient. Under either scenario, sex  
393 roles in parental care and mating competition would be sensitive to ecological factors  
394 influencing the costs and benefits of sex-limited care types once care specialisation has  
395 evolved (see above).

396

397 Third, our model permits the evolution of exclusively male parental investment, with no  
398 investment at all by females. In nature, however, female investment in offspring is apparently  
399 never negligible, possibly because in most organisms only females have evolved to provision  
400 the zygote directly. The evolution of parenting roles may consequently be more constrained  
401 than predicted by our model. More generally, coevolution between care effort and the ability

402 to care (e.g. lactation in female mammals) may constrain sex-role evolution because the lack  
403 of co-adaptations for caring creates an entry barrier for the non-caring sex [16,73].

404

405 Lastly, our model assumes that important mating system parameters like the operational sex  
406 ratio are constant over time. In many species, however, such parameters change dynamically  
407 due to factors like the seasonality of breeding conditions or sex-biased mortality [74-76].

408 These fluctuations can lead to sex-role variation within a single population over time. In the  
409 two-spotted goby (*Gobiusculus flavescens*), for instance, the operational sex ratio shifts  
410 dramatically over the course of a breeding season due to male-biased mortality. Male  
411 courtship and mating competition is consequently replaced by female courtship and  
412 competition as the season progresses [75,76].

413

414 One important prediction of our model is that a given regime of parental investment and  
415 mating competition, once it evolves, remains relatively stable under a broad range of  
416 conditions. Empirical evidence suggests that the evolution of mating and parenting systems is  
417 characterised by strong phylogenetic inertia, such that clades of closely related species,  
418 despite sometimes varying greatly in ecology, often share similar sex-role patterns [77,78].

419 Our model sheds light on the origins of such conservatism: transitions in sex-roles are  
420 predicted to occur only under restrictive conditions, whereas the conditions for maintaining a  
421 particular sex-role pattern may be broad. We expect, however, that our model does not  
422 describe the only mechanism of sex-role transitions. Rather, the considerable taxonomic and  
423 life-history diversity of species with unusual sex roles suggests that multiple mechanisms are  
424 at play. Considerable scope remains for theory on how exceptions to the dominant sex-role  
425 patterns arise, and why they arise so rarely.

426

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429

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432

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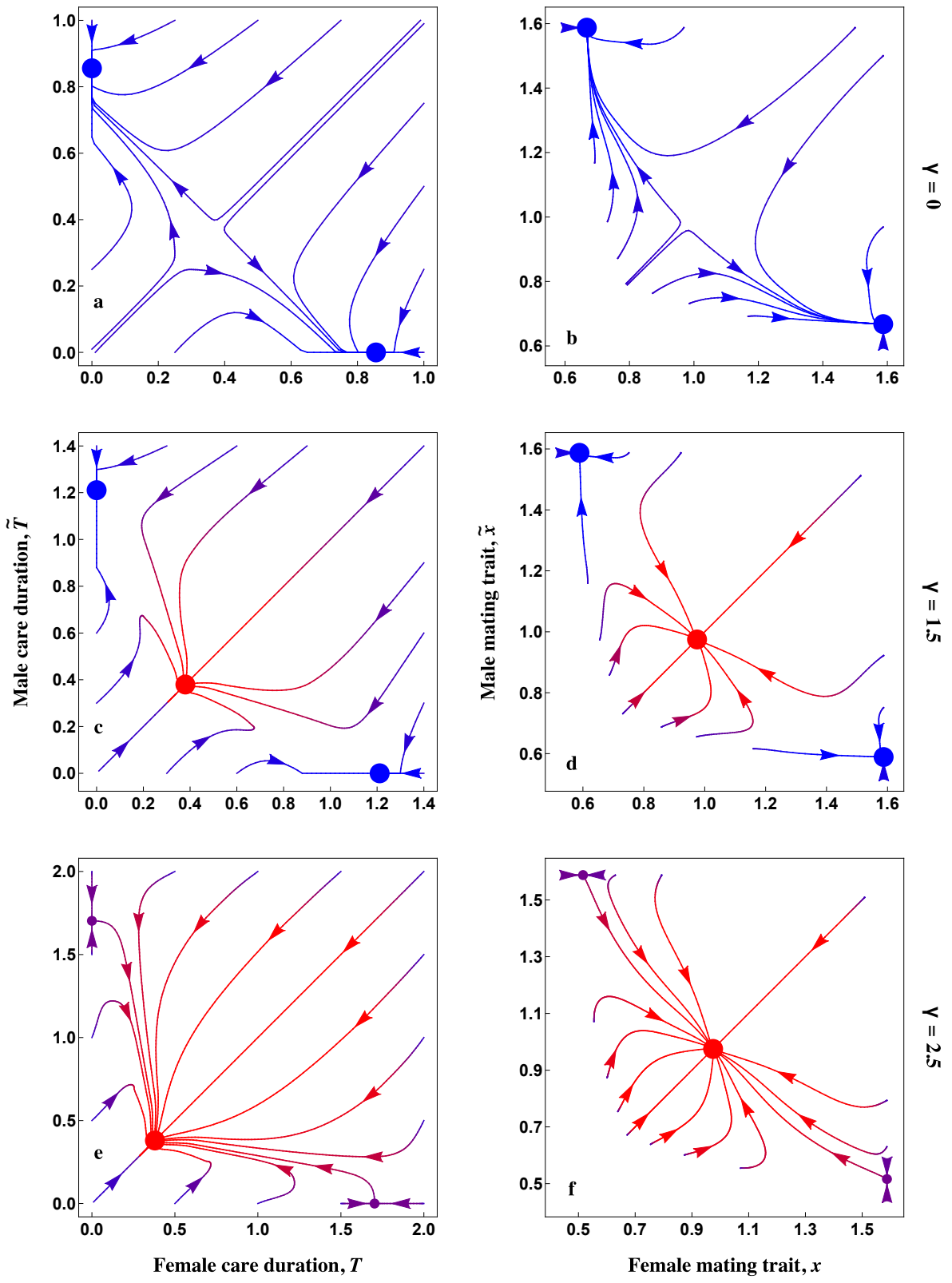
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635 **Figure legends**

636

637 **Figure 1:** The evolution of care duration ( $T$  and  $\tilde{T}$ : panels **a,c,e**), the mating trait ( $x$  and  $\tilde{x}$ :  
638 panels **b,d,f**) and the average level of care specialisation (line colouring) when the only sex  
639 asymmetry is in the initial strategies. Arrows indicate the direction of evolution. Large circles  
640 indicate globally stable equilibria; the smaller circles in panels **e** and **f** indicate locally stable  
641 equilibria that can be invaded by fully-specialised carers of the non-caring sex. We chose  
642 initial values for care duration ( $T$  and  $\tilde{T}$ ) arbitrarily as shown (panels **a,c,e**). We assumed a  
643 small initial sex asymmetry in the types of care provided ( $q = 0.4$  and  $\tilde{q} = 0.6$ ), without  
644 which specialisation cannot evolve. Initial values for the mating trait ( $x$  and  $\tilde{x}$ ) were chosen  
645 for each set of initial values ( $T, \tilde{T}, q, \tilde{q}$ ) by fixing the latter and letting the mating traits evolve  
646 to their unique local equilibrium. Line colours are based on an index  $i = 2 \frac{T|q-0.5| + \tilde{T}|\tilde{q}-0.5|}{T + \tilde{T}}$  of  
647 the average level of specialisation of caring parents, where  $i = 0$  means that all carers are  
648 completely unspecialised (shown in blue), and  $i = 1$  means that all carers are completely  
649 specialised (red). All panels are shown with  $\alpha_1 = \alpha_2 = 0.1$ ,  $\mu_{\min} = 0.01$ , and  
650  $r = n = \tilde{n} = 1$ .

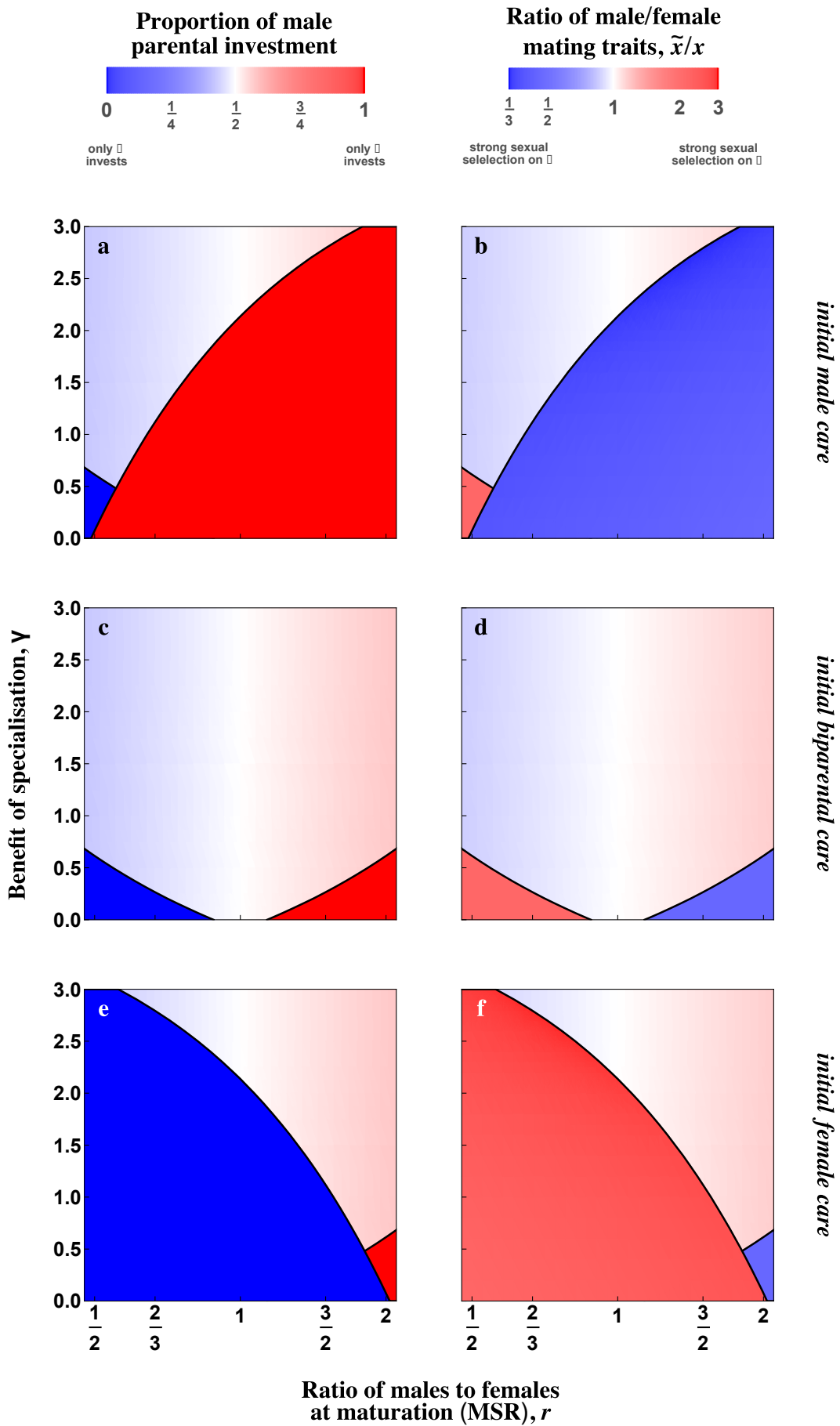
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653

654 **Figure 2:** Equilibrium proportion of male care  $\frac{\tilde{T}}{T+\tilde{T}}$  (panels **a,c,e**) and the ratio of male to  
655 female mating traits  $\frac{\tilde{x}}{x}$  (panels **b,d,f**) for populations that initially show male-only care  
656 (panels **a,b**), biparental care (panels **c,d**) and female-only care (panels **e,f**). All panels are  
657 shown with variation in the benefits of specialisation  $\gamma$  and the sex ratio at maturity  $r$ . Abrupt  
658 colour changes indicate where the initial care system is unstable, i.e. where male-only care  
659 transitions to biparental or female-only care (from bottom right corners of panels **a,b** to top  
660 left and bottom left corners respectively), biparental care transitions to female-only or  
661 male-only care (from upper parts of panels **c,d** to bottom left and bottom right corners  
662 respectively), or female-only care transitions to biparental or male-only care (from bottom  
663 left corners of panels **e,f** to top right and bottom right corners respectively). Under  
664 uniparental care, the non-caring sex competes more strongly for mates (dark blue regions in  
665 left panels correspond to dark red regions in right panels and vice versa). In contrast, under  
666 biparental care, a skewed MSR selects for both more care and stronger mating competition in  
667 the more common sex (colour transitions match between left and right panels in lighter  
668 coloured regions). All panels are shown with  $\alpha_1 = \alpha_2 = 0.1$ ,  $\mu_{\min} = 0.01$ , and  $n = \tilde{n} = 1$ .  
669



670

671

672 **Figure 3:** Equilibrium proportion of male care  $\frac{\tilde{T}}{T+\tilde{T}}$  (panels **a,c,e**) and the ratio of male to  
673 female mating traits  $\frac{\tilde{x}}{x}$  (panels **b,d,f**) for populations that initially show male-only care  
674 (panels **a,b**), biparental care (panels **c,d**) and female-only care (panels **e,f**). All panels are  
675 shown with variation in the benefits of specialisation  $\gamma$  and the importance of type-2 care  
676 relative to type-1 care,  $\alpha_2/\alpha_1$ . For the case of biparental care (panels **c,d**), we assume without  
677 loss of generality that males and females initially specialise in type-1 and type-2 care  
678 respectively. Abrupt colour changes indicate where uniparental care is unstable and  
679 transitions to biparental care (upper region of panels **a,b,e,f**). In this case, the initially caring  
680 sex ends up specialising in the more important type of care (e.g. in type-2 care when  $\alpha_2/$   
681  $\alpha_1 > 1$ ). Biparental care is always stable under the parameter values illustrated here (panels  
682 **c,d**). Under uniparental care, the non-caring sex competes more strongly for mates (dark blue  
683 regions in left panels correspond to dark red regions in right panels and vice versa). Similarly,  
684 under biparental care, the sex that cares more competes less (colour transitions in lighter  
685 coloured regions are reversed between left and right panels). All panels are shown with  $\alpha_1 =$   
686  $0.1$ ,  $\mu_{\min} = 0.01$ , and  $r = n = \tilde{n} = 1$ .

687

