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# 1 Individual variation in parental care drives divergence of sex roles

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## 7 Abstract

8 In many animal species, parents provide care for their offspring, but the parental roles of the two  
9 sexes differ considerably between and within species. Here, we use an individual-based simulation  
10 approach to investigate the evolutionary emergence and stability of parental roles. Our conclusions  
11 are in striking contrast to the results of analytical models. In the absence of initial differences between  
12 the sexes, our simulations do not predict the evolution of egalitarian care, but either female-biased or  
13 male-biased care. When the sexes differ in their pre-mating investment, the sex with the highest  
14 investment tends to evolve a higher level of parental care; this outcome does not depend on non-  
15 random mating or uncertainty of paternity. If parental investment evolves jointly with sexual selection  
16 strategies, evolution results in either the combination of female-biased care and female choosiness or  
17 in male-biased care and the absence of female preferences. The simulations suggest that the parental  
18 care pattern drives sexual selection, and not *vice versa*. Finally, our model reveals that a population  
19 can rapidly switch from one type of equilibrium to another one, suggesting that parental sex roles are  
20 evolutionarily labile. By combining simulation results with fitness calculations, we argue that all these  
21 results are caused by the emergence of individual variation in parental care strategies, a factor that  
22 was hitherto largely neglected in sex-role evolution theory.

23

## 24 Introduction

25 In the animal kingdom, species differ remarkably in the way and degree female and male parents are  
26 involved in parental care<sup>1,2</sup>. In virtually all mammals, most of the care is provided by females<sup>1,3</sup>, while  
27 in birds biparental care (with a certain bias towards females) is the most prevalent pattern<sup>1,4</sup>. Teleost  
28 fishes exhibit a broad variety of care patterns, with male-biased care being the rule rather than the  
29 exception<sup>1,5</sup>. Even within species, parental care patterns can be highly diverse<sup>6</sup>. For example, in  
30 Eurasian penduline tits (*Remiz pendulinus*) female-only care and male-only care co-occur in the same  
31 population<sup>7</sup>, while in Chinese penduline tits (*Remiz consobrinus*) female-only care, male-only care, and  
32 biparental care all coexist<sup>8</sup>. Moreover, phylogenetic studies suggest that parental care patterns are  
33 highly dynamic in that transitions between patterns occur frequently<sup>9,10,11</sup>.

34 The explanations that have been proposed for sex differences in parental roles often initiated heated  
35 debates in the literature. One debate centres around the role of anisogamy (the difference in gamete  
36 size between males and females). Robert Trivers<sup>12</sup> argued that anisogamy explains the fact that in  
37 many taxa females tend to invest more in post-zygotic parental care than males. According to Trivers,  
38 the female parent has a strategic disadvantage with respect to the male parent: because the mother  
39 has made a large initial investment in the ovum, she has more to lose when deserting the clutch than  
40 the father. Some authors pointed out a flaw in Trivers' argument: optimal decision-making should not  
41 be based on past investments, but rather on future costs and benefits<sup>13</sup>. While agreeing with this  
42 critique, other authors pointed out that Trivers' prediction can be revived when taking other factors  
43 into account, such as female choosiness or uncertainty of paternity<sup>14,15</sup>. This viewpoint is, in turn, hotly  
44 debated<sup>16-19</sup>. Another debate in the literature is on whether and how the relative abundance of males  
45 and females drives parental sex roles<sup>20</sup>. A popular theory predicts that the 'operational sex ratio' (the  
46 ratio of males to females among those individuals participating in mating) should play a decisive role,  
47 because the sex that is overrepresented on the mating market (and hence has fewer mating  
48 opportunities) should be predestined for taking on the parental care tasks<sup>21</sup>. More recently, attention  
49 has shifted to the 'adult sex ratio' (the ratio of males to females in the overall adult population) as a  
50 predictor of sex differences in parental sex roles<sup>22,23</sup>. Last, but not least, there is debate in the literature  
51 on the role of sexual selection in determining parental sex roles<sup>12,14,24</sup>. All these debates are intricate  
52 in themselves; moreover, they are interwoven, because initial investments, sex ratios, and sexual  
53 selection are mutually dependent<sup>12</sup>.

54 In a situation like this, where the outcome of evolution is determined by the intricate interplay of  
55 mutually dependent factors, verbal theories can easily lead astray. As a major step forward, Kokko  
56 and Jennions<sup>25</sup> developed a comprehensive modelling framework, allowing to disentangle the role of  
57 the various factors involved in the evolution of parental sex roles. In a first step, male and female  
58 fitness functions are calculated, based on a scheme describing the interactions of the sexes in a  
59 population. These functions are then analysed mathematically (see Methods), allowing to predict how  
60 sex differences in life history parameters, biased sex ratios, multiple mating, and sexual selection  
61 affect the evolution of parental sex roles. However, this analytical approach has its limitations. First,  
62 the calculations are not trivial and error-prone. Indeed, Fromhage and Jennions<sup>26</sup> pointed out mistakes  
63 and erroneous conclusions in the study of Kokko and Jennions<sup>25</sup>. Second, to keep the model  
64 analytically tractable, the factors involved have to be stripped to their bare-bone essentials. For  
65 example, the dynamic process of sexual selection is reduced to a set of fixed parameters that cannot  
66 coevolve with the parental strategies. Third, the analytical approach focuses on the evolution of  
67 population means and thereby neglects intra-population variation around the mean. In other words,  
68 populations are considered monomorphic, while it has recently become clear that in natural  
69 populations individuals differ systematically in all kinds of behavioural tendencies<sup>27,28,29</sup>, including  
70 parental behaviour<sup>30,31,32</sup>. Various studies have shown that such variation is often shaped by  
71 diversifying selection<sup>33,34</sup>, and that it can have important evolutionary implications<sup>35,36</sup>.

72 For these reasons, we here consider an extended version of the modelling framework of Kokko and  
73 Jennions<sup>25</sup>, and we study the evolution of parental roles by means of individual-based simulations<sup>37</sup>.

74 This approach has the advantage that more natural assumptions can be made concerning the inclusion  
75 of sexual selection or factors such as sex differences in pre-mating investment. Moreover, individual  
76 variation emerges in a natural way, making it possible to study its evolutionary implications<sup>37</sup>.

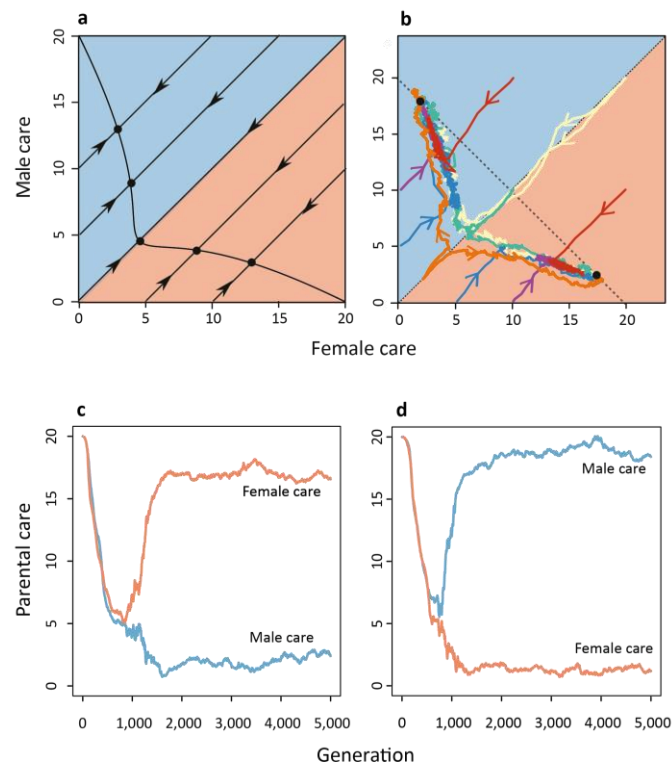
77 In a nutshell, our model (see Methods) follows individual males and females from birth to death. After  
78 maturation, adult individuals can be in one of two states: the mating state and the caring state.  
79 Individuals seek mating opportunities in the mating state; once mated both members of the mated  
80 pair switch to the caring state. Each individual provides care for a time period corresponding to its  
81 inherited sex-specific parental care strategy and switches back to the mating state afterwards. The  
82 total amount of care provided by both parents determines the survival probability of the offspring in  
83 the clutch. The offspring inherit the care strategies from their parents (according to Mendelian  
84 inheritance and subject to rare mutations of small effect size). Parental care strategies have to strike  
85 a balance between caring as efficiently as possible and mating as often as possible. Both caring and  
86 mating are costly, since individuals can die in any state, with a mortality rate that depends on their  
87 state and sex. Strategies that perform well are transmitted to a large number of offspring, thereby  
88 increasing in relative frequency in the population. Over the generations, an evolutionary equilibrium  
89 emerges during the simulation; fitness calculations are not required for this. As explained below, the  
90 model can easily be extended to include sexual selection and sex-differences in pre-mating investment.

91 Although the model is very similar in spirit to the analytical models mentioned above, we show that  
92 the evolutionary outcome is remarkably different from that reported in the earlier studies of parental  
93 sex-role evolution.

## 94 **Results**

95 **Sex-biased care evolves in the absence of sex differences.** First, we consider the baseline scenario  
96 where mating is at random and the sexes do not differ in their mortality rates or other life-history  
97 parameters (Fig. 1). Based on their analytical model, Kokko and Jennions<sup>25</sup> predicted the evolution of  
98 egalitarian biparental care for this scenario. Correcting a mistake in the fitness calculations, Fromhage  
99 and Jennions<sup>26</sup> showed that instead the analytical model predicts convergence to a line of equilibria.  
100 If we apply the selection gradient method of refs 25 and 26 (see Supplementary Fig. 5 - 7) to our  
101 slightly modified model, we arrive at the same conclusion (Fig. 1a): the care effort of females and  
102 males converges to an equilibrium; there is a continuum of equilibria, which are located on a curve  
103 that includes a broad spectrum of parental care patterns. In other words, depending on the initial  
104 conditions all types of care strategy, from female-only care via egalitarian biparental care to male-only  
105 care, can evolve.

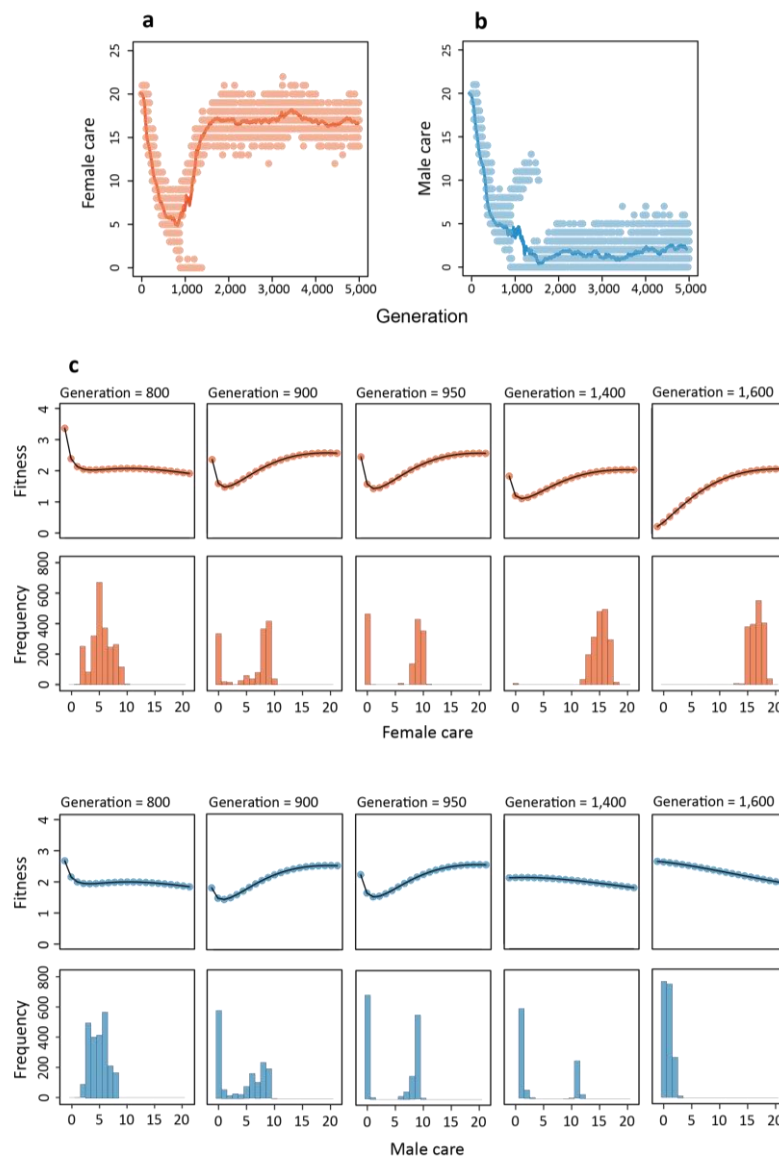
106 In contrast to these analytical predictions, our individual-based simulations never resulted in  
107 egalitarian care or a line (or curve) of equilibria. Instead, all our simulations (>5,000, for different  
108 parameter values and different initial conditions) converged to one of two stable equilibria  
109 corresponding to either strongly female-biased care or strongly male-biased care. Initial conditions  
110 with sex-biased care tended to converge to the corresponding sex-biased equilibrium, while initial  
111 conditions without sex-bias converged to each of the two equilibria with equal probability (Fig. 1b).  
112 Fig. 1c and 1d show the time trajectories of two replicate simulations starting at a high level of  
113 egalitarian care. In a first phase, both populations follow the analytical prediction and converge to a



**Fig. 1 | Evolution of sex-biased parental roles in the absence of sexual selection.** The graphs depict evolutionary trajectories when mating is at random and males and females do not differ in mortality rates or other life-history parameters. **(a)** For this scenario, the selection gradient method predicts convergence to a curve of equilibria (solid black line). **(b)** In contrast, individual-based simulations converge in a characteristic manner to one of two equilibria (black dots) corresponding to either strongly female-biased care or strongly male-biased care. Replicate simulations starting with egalitarian care levels will converge, with equal probability, to **(c)** the female-care equilibrium or **(d)** the male-care equilibrium. Differently coloured lines in (b) indicate different initial conditions. The red and blue lines in (c) and (d) depict the average levels of female care and male care in the evolving population. The dotted line in (b) corresponds to those care levels where the sum of female and male care is equal to  $D = 20$ , the value of total care maximizing the marginal benefits of care in our model (see Methods). Population sizes fluctuated around 2,000 females and 2,000 males.

114 low level of egalitarian care. Then strongly sex-biased care evolves, along the curve of equilibria of the  
115 analytical model. Both stable equilibria have the property that the total care provided by the two  
116 parents equals  $D = 20$ , the value maximizing the marginal benefit of care in our model (see Methods).

117 **The evolution of sex-biased parental roles is driven by individual variation.** Fig. 2 shows in more  
118 detail how sex-biased care evolves from egalitarian care. In the simulation shown, the population was  
119 initialized at the same care level (20) for males and females. Hence, initially the sum of the parental  
120 care levels exceeds the value  $D = 20$  that, for the parameters chosen, maximizes the marginal benefits  
121 of care. Accordingly, there is strong selection in both sexes to reduce the level of care. In the first 800  
122 generations, the care level in males and females rapidly declines until a value of 5 is reached in both  
123 sexes (Fig. 2a,b), in line with the predictions of the selection gradient approach (see Fig. 1a). At this  
124 care level, the mortality of offspring is very high and additional care would provide a considerable



**Fig. 2 | Sex role divergence driven by individual variation in parental roles.** Evolution of **(a)** female and **(b)** male care for the simulation in Fig. 1c. Lines show the average care level of females (red) and males (blue) in the population, while dots represent individual care levels. **(c)** For five different generations, the histograms show the distribution of care levels in females (red) and males (blue). The fitness profiles above the histograms indicate in each case the expected lifetime reproductive success of females and males with care strategies ranging from 0 to 20 in the corresponding population.

125 benefit. Yet, the parents are caught in a cooperation dilemma: both are interested in the survival of  
 126 their offspring, but each parent is better off if most of the care is provided by the other parent<sup>12,38,39</sup>

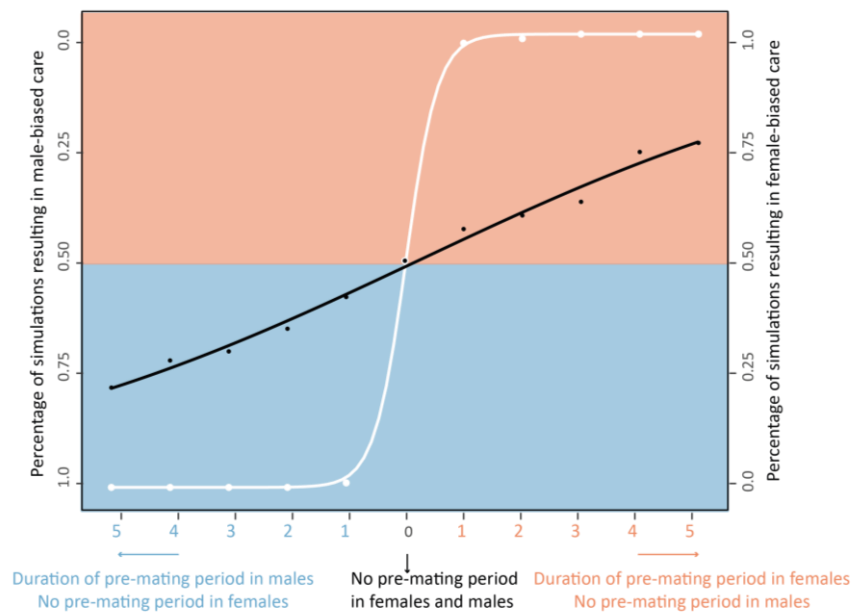
127 To understand the further course of evolution, we first considered the simplified version of the model  
 128 where parental care is constrained to be egalitarian (i.e., individuals cannot determine their care  
 129 duration dependent on their sex). In this egalitarian model, a care level of 5 for both parents  
 130 corresponds to an ‘evolutionary branching point’<sup>40</sup> (see Supplementary Fig. 2): at such a point,

131 directional selection changes into disruptive selection, where extreme strategies have the highest  
132 fitness. This is confirmed by the U-shaped fitness profile and the emerging bimodal distribution of care  
133 levels in both sexes in generation 900 (see Fig. 2c). The process continues, and in generation 950 there  
134 are two types of females and two types of males: one type not caring at all and the other type caring  
135 at a level around 10. In the egalitarian version of the model, the process would continue until part of  
136 the population would not care at all while the other part would care at level  $D = 20$ . Such a population  
137 is not very efficient, because many matings would result in either no care at all or a very high care  
138 level of 40. When individuals can make their care strategy dependent on their sex (or any other  
139 phenotypic marker), there is an escape route<sup>41</sup>: one of the two ‘branches’ becomes associated with  
140 the female sex, while the other becomes associated with the male sex. In the simulation in Fig. 2, the  
141 high-care strategy becomes associated with the female sex and the no-care strategy becomes  
142 associated with the male (the opposite happened in 50% of the simulations): in generation 1400, the  
143 no-care strategy has almost disappeared in females and selection is directional in males (in favour of  
144 the no-care strategy). In the end (generation 1600), directional selection keeps the care level low in  
145 males, while stabilizing selection keeps the care level just below 20 in females. Without exception, the  
146 same sequence of events (with similar timing) was observed in hundreds of simulations starting with  
147 similar care levels in the two sexes.

148 **Anisogamy affects the evolution of parental sex roles even in the absence of sexual selection.** In  
149 most taxa females tend to invest more in post-zygotic parental care than males<sup>1-4</sup>. Since females are,  
150 by definition, the sex producing larger gametes, it is plausible to assume that anisogamy plays an  
151 important role in the evolution of parental sex roles<sup>18,26</sup>. Trivers’ argument that the sex with the  
152 highest pre-mating investment is predestined to invest more in post-zygotic care because it has ‘more  
153 to lose’ is generally considered to be flawed<sup>13</sup>, but various authors pointed out other causal links from  
154 anisogamy to female-biased care, via secondary effects of anisogamy, such as higher competition  
155 among males or a lower certainty of parentage in males<sup>14,15</sup>. To investigate the role of pre-mating  
156 investment, we extended our model by introducing a pre-mating period for one of the sexes. After  
157 any parental care period, an individual of that sex has to spend a fixed number of days with other  
158 activities (like growing a new clutch of eggs in females or building a new nest in males) before entering  
159 the mating phase again. Mating is still assumed to be at random, and there are no other differences  
160 between the sexes.

161 Fig. 3 shows, for two mortality levels in the pre-mating period, that the sex with the higher pre-mating  
162 investment tends to evolve a higher degree of post-zygotic parental care. This trend is very  
163 pronounced (white curve) if the mortality in the pre-mating period is five times as high as in the mating  
164 period, but it is also noticeable when the pre-mating period does not involve direct fitness costs,  
165 because the mortality level is zero (black curve). Hence, we clearly observe a ‘Trivers effect’ in the  
166 absence of sexual selection and multiple matings. We think that this outcome results from the  
167 interplay of two factors. First, a longer pre-mating period leads to a shorter life expectancy, which  
168 shifts the balance between current and future reproduction toward a higher investment in the current  
169 clutch<sup>42,43</sup>. Second, the sex with the shorter pre-mating period has a higher variance in mating success,



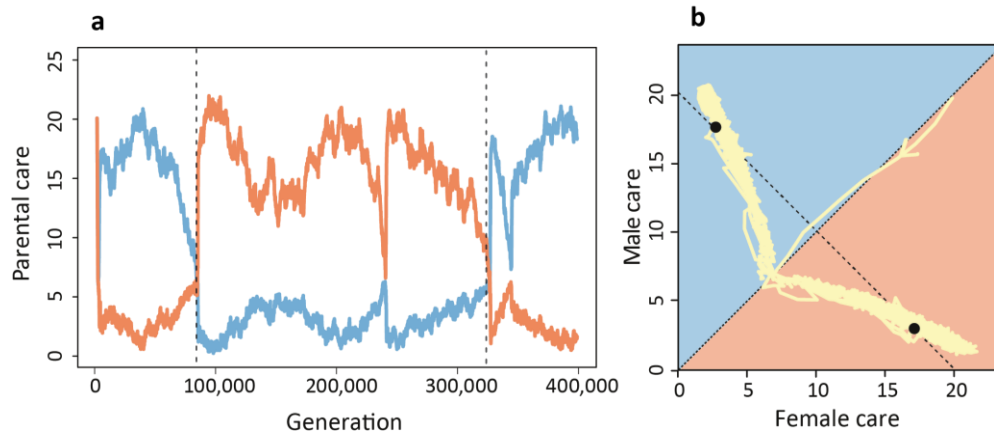


**Fig. 3 | A pre-mating investment bias selects for parental sex roles.** Percentage of simulations resulting in male-biased care (left axis) or female-based care (right axis) depending on the duration of the pre-mating period in either males (blue) or females (red). Mortality in the pre-mating period was either zero (black dots and black line fitted by logistic model) or five times as high as in the mating phase (white dots and white line fitted by logistic model). 100 replicate simulations were run per setting, all starting from egalitarian care. All of these 2,200 simulations resulted either in female-biased care or male-biased care. In case of a female pre-mating period, female-biased care was the more likely outcome, while male-biased care evolved more often when males had a pre-mating period.

170 which selects for higher mating effort and reduced parental care<sup>44</sup>. The first factor does not play a role  
171 when there is no mortality in the pre-mating period (because in that case life expectancy is not  
172 affected). Fig. 3 (black dots and line) demonstrates that even in that case the second factor, which was  
173 first predicted by Sutherland<sup>44</sup>, has a noticeable effect on the evolutionary outcome. In other words,  
174 Trivers was right, but for different reasons than he envisaged. Additional implications of anisogamy,  
175 such as paternity uncertainty or intrinsically more intense competition among males are not required  
176 but will most probably enhance the Trivers effect.

177 **Parental sex roles can be evolutionarily labile.** Up to now, all simulations converged to one of two  
178 alternative equilibria that correspond to either male-biased or female-biased care. As shown in Fig. 4,  
179 rapid switches from one equilibrium to the other were regularly observed on a long-term perspective.  
180 In fact, such switches *always* occurred in situations with alternative stable equilibria, provided that  
181 the simulations were run for a sufficiently long time period. Accordingly, our simulations suggest that  
182 parental roles can be evolutionarily labile. This is in line with phylogenetic studies, which also conclude  
183 that parental care patterns are highly dynamic and that, on a long-term perspective, transitions  
184 between different care patterns have occurred frequently in many animal taxa<sup>9,10,11</sup>.



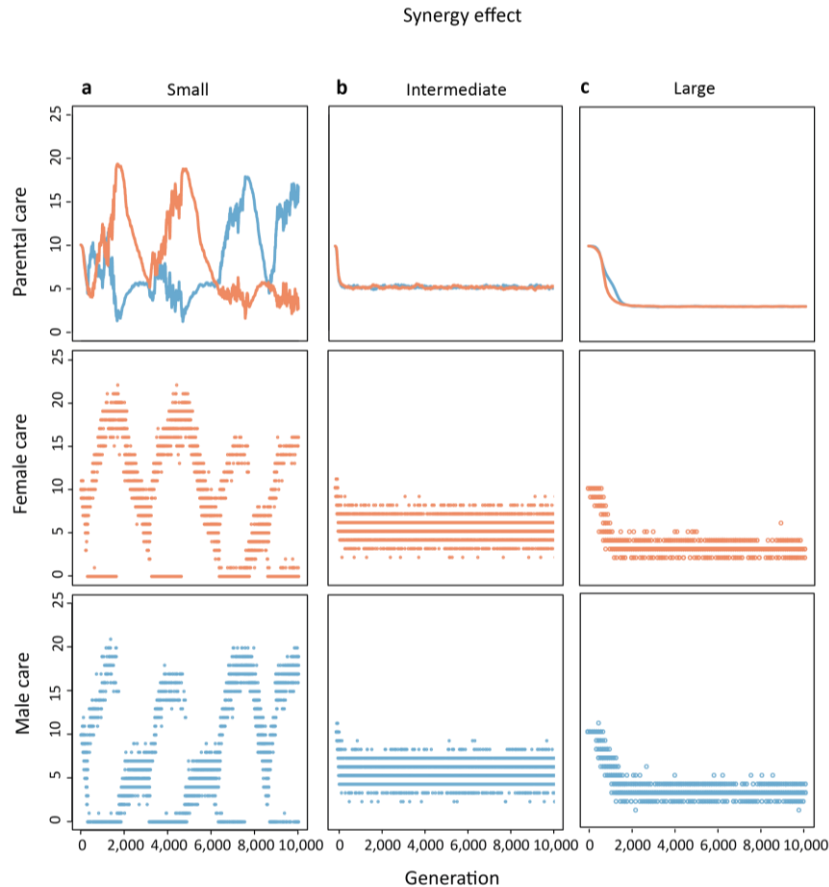


**Figure 4 | Evolutionary lability of parental sex roles.** Whenever simulations were run for extended periods of time, transitions occurred between the two stable equilibria. In other words, long periods of male- or female-biased care were followed by rapid switches to a situation where most of the care was provided by the other sex. Here, this is shown for a long-term simulation of the random-mating scenario in Fig. 1, but with a one-day pre-mating period in both sexes.

185 In a stochastic dynamical system with alternative stable states, spontaneous transitions from one state  
186 to the other are not really surprising<sup>45</sup>. They occur, for example, in ecological systems<sup>46,47</sup>, in the  
187 climate system<sup>48</sup>, and in physical systems<sup>49</sup> (think of the spontaneous reversal of polarity in magnets<sup>50</sup>).  
188 The average time between switches depends on the degree of stochasticity and the strength of  
189 attraction, which in our case corresponds to population size and the steepness of the selection  
190 gradients. Decreasing the population size by relaxing density dependence did indeed lead to much  
191 faster transitions between states (see Supplementary Fig. 3). The same happened when we weakened  
192 selection by prolonging the pre-mating period in one or both sexes (as in Fig. 4).

193 **Biparental synergy can lead to fluctuating polymorphism or inefficient biparental care.** In contrast  
194 to the simulations reported above, egalitarian biparental care occurs in many bird and fish species,  
195 and in other animal taxa<sup>1-4</sup>. A potential reason is that in natural populations the parents complement  
196 each other, thereby providing more benefits to their offspring than the sum of their individual  
197 contributions<sup>51</sup>. Division of labour or other sources of synergy among the parents could reduce sexual  
198 conflict about who should do the caring and strongly select for biparental care<sup>52,53</sup>. Here we introduce  
199 parental synergy in our model in line with earlier modelling studies<sup>26,52</sup>: we assume that the care levels  
200  $T_f$  and  $T_m$  of the two parents provide a benefit  $T_f + T_m + \sigma T_f T_m$  to their offspring, where the degree of  
201 synergy  $\sigma$  is a positive parameter (In the additive model considered until now,  $\sigma=0$ ). In the  
202 analytical model of Fromhage and Jennions<sup>26</sup>, the introduction of a small degree of synergy  
203 transformed their curve of equilibria (Supplementary Fig. 5) into a single stable equilibrium  
204 corresponding to egalitarian biparental care.

205 Fig. 5 shows that this prediction is only partly confirmed by individual-based simulations. When  
206 synergy is weak ( $\sigma=0.05$ , Fig. 5a), the population does not converge to an equilibrium. Instead, the  
207 average care level in both sexes (top panel of Fig. 5a) exhibits large fluctuations, corresponding to

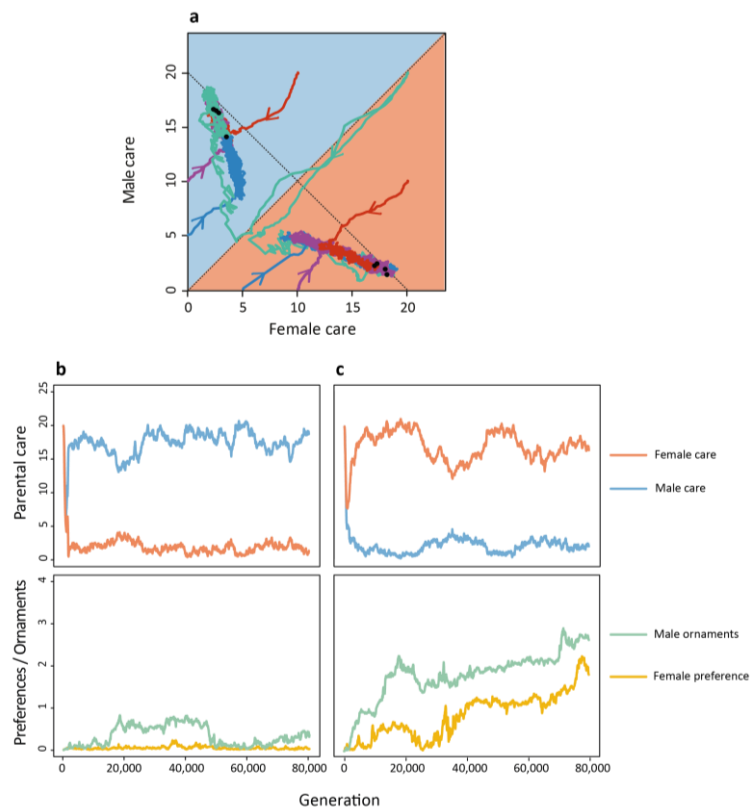


**Figure 5 | Evolution of parental roles when biparental care has a synergistic effect.** Representative simulations for the case that the effects of the parents on offspring survival are not additive but synergistic. **(a)** In case of weak synergy ( $\sigma=0.05$ ), evolution leads to a rapid succession of male- and female-biased care. For long periods of time, one or both sexes are highly polymorphic, with a no-care strategy coexisting with a high-care strategy. **(b)** In case of intermediate synergy ( $\sigma=0.20$ ), evolution leads to egalitarian care equilibrium. However, diverse care strategies coexist in both sexes. Total care  $T_f + T_m + \sigma T_f T_m$  is considerably smaller than  $D=20$ , the value maximizing the marginal benefit of care in our model. **(c)** In case of strong synergy ( $\sigma=2.0$ ), the evolving egalitarian-care equilibrium exhibits relatively little variation and total care now matches  $D=20$ .

208 rapid transitions between female-biased and male-biased care. Moreover, both sexes are polymorphic  
 209 most of the time: a considerable fraction of individuals does not care at all, while others provide a high  
 210 level of care. In case of an intermediate degree of synergy ( $\sigma=0.20$ , Fig. 5b), the population  
 211 converges to egalitarian care, although both the male and the female population remain highly  
 212 polymorphic. Notice that the average care level (top panel of Fig. 5b) in both sexes is about  $T_f = T_m = 5$   
 213 and, hence, very low. Taking synergy into account, this investment results in a total care level of about  
 214  $5+5+0.2 \cdot 25=15$ . This is considerably less than in the additive model without synergy (Fig. 1b),  
 215 where in both non-egalitarian equilibria the total care level is equal to  $D=20$ , the value maximizing  
 216 the marginal benefits of parental care. Apparently, the introduction of synergism does not allow the  
 217 parents to escape from the cooperation dilemma by the evolution of either male-biased or female-  
 218 biased care. Instead, the conflict between the sexes continues, resulting in a broad spectrum of care  
 219 strategies and an outcome that is, regarding offspring survival, quite inefficient. This conclusion only

220 changes for a high degree of synergy ( $\sigma = 2.0$ , Fig. 5c): now the population converges to an egalitarian  
221 care level satisfying  $T_f + T_m + \sigma T_f T_m = D$ .

222 **Joint evolution of mating and parental strategies.** Mating and parental care strategies are closely  
223 interrelated, but the causal relationships between the two types of strategy are difficult to disentangle.  
224 Mathematical models incorporating both factors tend to be analytically intractable and can only be  
225 solved by iteration methods<sup>52</sup>. Many models on the evolution of parental roles therefore represent  
226 mating patterns by a parameter that cannot change in time<sup>25,26</sup>. It is a clear advantage of individual-  
227 based simulation models that various scenarios for the joint evolution of mating and parental care  
228 strategies can be implemented in a natural way. To demonstrate this, we extended the baseline  
229 version of the model by allowing female preferences and male ornaments to evolve alongside with  
230 the parental strategies. We restrict ourselves to a simple model of sexual selection, leaving the analysis  
231 of more complicated scenarios (e.g., mutual mate choice, differences in parental ability, condition-  
232 dependent mating and parental strategies) to a future attempt. In our Fisherian model<sup>54</sup>, female  
233 preferences and male ornaments are characterized by heritable parameters  $p$  and  $s$ , respectively.  
234 When female preferences are zero, all males have the same probability of being chosen and mating



**Figure 6 | Joint evolution of mating and parental strategies. (a)** If parental care strategies evolve alongside with the evolution of female preferences for a costly male ornament, all simulations result in one of two alternative equilibria. **(b)** One equilibrium is characterized by male-biased care, the absence of female preferences, and a small degree of male ornamentation. **(c)** The other equilibrium is characterized by female-biased care, strong female preferences, and a high degree of male ornamentation. In this simulation, there was no pre-mating period and no parental synergy.

235 occurs at random. When female preferences are above zero, males with large ornaments are  
236 preferred. Male ornamentation is costly in that it negatively affects male survival. Female choosiness  
237 is costly, because choosy females may take a longer time before they find a mate. Fig. 6 shows some  
238 representative simulations, all starting with random mating ( $p = s = 0$ ) but with different initial levels  
239 of parental care. All simulations converge to one of two equilibria (with equal probability) that are  
240 characterized by either male-biased care or female-biased care. Whenever male-biased care evolved  
241 (Fig. 6b), female preferences stayed at a very low level, corresponding to random mating. Whenever  
242 female-biased care evolved (Fig. 6c), female preferences for male ornaments evolved as well, together  
243 with elaborate male ornamentation. In all simulations leading to female-biased care, female  
244 choosiness only got off the ground after female care levels had reached relatively high levels.

245 Also these two types of equilibrium do not persist forever. As shown in Supplementary Fig. 4, each  
246 equilibrium defines the dominant sex role pattern for long periods of time (many thousands of  
247 generations), followed by a rapid switch to the other type of equilibrium. These transitions proceed in  
248 both directions. We investigated many of these transitions, and in all cases the parental strategy  
249 changed first (either from male-biased care to female-biased care, or *vice versa*), followed by the  
250 emergence or disappearance of female choosiness and male ornamentation. From this we tacitly  
251 conclude that, at least for the mating strategies considered in our simple model, the causal  
252 relationship goes from parental sex roles to mating roles, and not the other way around.

## 253 Discussion

254 Here we investigated an individual-based simulation implementation of a modelling framework<sup>25</sup> that  
255 may be viewed as the cornerstone of sex-role evolution theory. Although we made very similar  
256 assumptions as the analytical models, we arrived at remarkably different conclusions than the earlier  
257 mathematical analyses. First, the populations in our ‘null model’ (random mating, no sex differences  
258 in life-history parameters) do not evolve to egalitarian care<sup>25</sup> or to a line (or curve) of equilibria<sup>26</sup> but  
259 rather to one of two stable equilibria corresponding to strongly male-biased or strongly female-biased  
260 care, respectively. Second, our simulations suggest that even a small sex difference in pre-mating  
261 investment (like anisogamy) can induce the ‘Trivers effect’<sup>12</sup> that the sex with the highest pre-mating  
262 investment is predestined for doing most of the post-mating parental care. This does not depend on  
263 factors as sexual selection or uncertainty of paternity, which can be expected to strengthen the Trivers  
264 effect. Third, parental synergy does not necessarily lead to egalitarian care. Even if it does, the  
265 evolutionary outcome is not necessarily efficient: in the presence of synergy the parents can be kept  
266 in a parental cooperation dilemma that in the absence of synergy is resolved by parental specialisation.  
267 Fourth, our simulations reveal that, as in the analytical models<sup>25,26</sup> sexual selection can lead to a  
268 situation where males are highly competitive on the mating market, while females provide most of  
269 the parental care. However, this is not the only outcome: there is a second equilibrium (that is equally  
270 likely) where males do most of the caring while the evolution of female choosiness is suppressed. Our  
271 simulations provide evidence that, in our model, the parental care pattern drives sexual selection and  
272 not the other way around<sup>12</sup>. Lastly, our simulations suggest that (parental and mating) sex roles are  
273 evolutionarily labile. For most of the parameters considered, the model has two stable equilibria.

274 Whenever this is the case, a simulation attains one of these equilibria for a long but limited period of  
275 time, followed by a rapid transition to the other equilibrium. Hence, male-biased care can switch to  
276 female-biased care, and *vice versa*. Similarly, a population can rapidly switch from a state of female  
277 choosiness, male competitiveness, and female-biased care to a state of male-biased care in the  
278 absence of choosiness and competitiveness. These transitions occur for the same parameter settings;  
279 in contrast to other models (e.g. ref 55) they are not necessarily induced by a change in environmental  
280 conditions.

281 Why do our simulations lead to contrasting conclusions from the earlier analyses of very similar  
282 models? We think that our results highlight three limitations of analytical approaches that are mainly  
283 based on fitness considerations. As shown by Kokko & Jennions<sup>25</sup> and Fromhage & Jennions<sup>26</sup> the  
284 analysis of selection differentials and selection gradients can be very informative: they clearly indicate  
285 the effects of strategic parameters (like parental effort) on life history parameters (like own survival  
286 and offspring survival), thus quantifying the trade-offs between fitness components. However,  
287 selection-gradient based plots like Fig. 1a should not be over-interpreted, because it is not self-evident  
288 that evolution by natural selection proceeds in the direction of the selection gradient (the direction of  
289 steepest ascent of the fitness landscape). This only happens under restrictive assumptions, such as  
290 weak selection<sup>56</sup>, simple interactions across loci<sup>57</sup>, uncorrelated mutations of similar effect sizes<sup>58</sup>, and  
291 a simple structure of the genetic variance-covariance matrix<sup>59</sup>. A comparison of Fig. 1a and 1b shows  
292 that the gradient method predicts the simulation trajectories reasonably well when the fitness  
293 gradient is steep, but that it fails to detect directional selection away from egalitarian care when the  
294 curve of equilibria is approached (where the fitness gradient is close to zero). One could argue that  
295 the discrepancy between Fig. 1a and 1b is not too surprising, because a curve of equilibria, as predicted  
296 by the analytical model, is structurally unstable<sup>60</sup> meaning that it will disappear if the model is slightly  
297 changes. However, we observed similar discrepancies in the parental synergy scenario where the  
298 gradient method predicts a structurally stable pattern of egalitarian care while the simulation model  
299 predicts the coexistence of two stable equilibria corresponding to either strongly male-biased or  
300 strongly female-biased care.

301 A second limitation of selection gradient methods is their focus on population averages. Averages  
302 have only a clear biological meaning if variation around them is small and symmetrically distributed<sup>61</sup>.  
303 In recent years, it is becoming increasingly clear that in the behavioural domain this assumption is not  
304 satisfied: in virtually all animals studied, individuals differ strongly and systematically in all kinds of  
305 behavioural tendencies<sup>27,28,29</sup> (including parental<sup>30,31,32</sup> and mating behaviour<sup>62,63</sup>), exhibiting so-called  
306 'animal personalities'<sup>64</sup>. Fig. 2 and 5a show that such individual variation in parental strategies, within  
307 and between the sexes, is also to be expected in the evolution of sex roles; in fact, it is shaped by  
308 natural selection (Supplementary Fig. 2). It has been argued before<sup>35,36</sup> that such 'patterned' variation  
309 can strongly affect the course and outcome of evolution. This is clearly exemplified by our model,  
310 where the emergence of a bimodal distribution of care strategies is, in virtually all our simulations, the  
311 first step toward the evolution of sex role specialisation. The take-home message is that 'selection  
312 gradient dynamics' have to be interpreted with care if the emergence of individual variation is to be  
313 expected.

314 A third limitation of selection gradient approaches is their difficulty to include stochasticity. This is  
315 exemplified by our simulations including a pre-mating period (Fig. 3), where a rather subtle effect –  
316 the higher variance in mating success in the sex with the shorter pre-mating period, even in case of  
317 random mating – has a strong effect on the evolutionary outcome, providing a new underpinning for  
318 the Trivers effect.

319 At present, individual-based simulations are not yet very popular in evolutionary studies, presumably  
320 because of the belief that they do not add much to the evolutionary theory toolbox. Our study  
321 demonstrates that such simulations can be a useful check of analytical results, in particular in cases  
322 where the complexity of the evolutionary dynamics necessitates the usage of ‘short-cut’ methods  
323 (such as the selection-gradient method). On top of this, individual-based simulations have other  
324 advantages. They are easy to implement, without the necessity of performing complicated fitness  
325 calculations. For example, the fact that in the simulations each offspring has one mother and one  
326 father automatically guarantees that the ‘Fisher condition’ (that total reproductive success of all  
327 females is equal to the total reproductive success of all males) is satisfied, while the incorporation of  
328 this constraint in analytical models is not obvious<sup>14,25,65,66</sup>. Stochasticity, spatial structure, and  
329 environmental variation can easily be included in simulation models, in a variety of ways. The life cycle  
330 of the individuals can be much more intricate (and realistic) than in analytical models. Perhaps most  
331 importantly, individual interactions can be implemented in a natural way<sup>37</sup>. We have demonstrated  
332 how the evolution of mate choice can be included in the model, instead of representing sexual  
333 selection by constant parameters. This is relevant, because mating strategies and parental strategies  
334 must be allowed to evolve side by side in order to study evolutionary feedbacks between them. We  
335 are aware that our model of sexual selection is quite simple, but it is straightforward to include ‘good  
336 genes’ and ‘direct benefits’ variants<sup>67,68</sup>, as well as condition-dependent preferences<sup>69</sup> and  
337 ornaments<sup>70</sup>.

338 We do not plead for replacing analytical methods by simulations. Simulations have the big  
339 disadvantage that their outcome can easily be ‘as complicated as reality’, thereby not furthering our  
340 understanding and sharpening our intuition. Instead, we recommend a pluralistic approach<sup>71</sup> where  
341 analytical insights are checked and expanded by individual-based simulations, while the simulation  
342 outcomes are scrutinized with the help of analytical tools (such as the pairwise invasibility plots in  
343 Supplementary Fig. 2 and 7). The hope is to achieve a deeper understanding by a combination of  
344 diverse methods, in the spirit of Richard Levins’ insight<sup>72</sup> (in our own wording): every model is a lie –  
345 all we can hope for is to approach truth by the intersection of independent lies.

## 346 **Methods**

347 **Model structure.** In line with the models of Kokko and Jennions<sup>25</sup> and Fromhage and Jennions<sup>26</sup>, we  
348 consider a population with overlapping generations and discrete time structure. To be concrete, we  
349 assume that a time unit corresponds to one day. The population consist of females and males that, on  
350 each day, can be in one of the following states: juvenile, pre-mating, mating, or caring. In each of the  
351 four states, there is a fixed mortality rate, which can be sex-specific. Unless stated otherwise, all  
352 mortalities were set to 0.001 day<sup>-1</sup>. Therefore, the expected lifespan of an individual is 1000 days, a



353 value that we consider a proxy for generation time. Offspring mortality is density dependent, thus  
354 ensuring a limited population size. In our baseline scenario, population size fluctuates around 2000  
355 females and 2000 males.

356 The life cycle of our model organisms is illustrated in Supplementary Fig. 1. Offspring that survive the  
357 period of parental care spend a fixed number of days (the maturation time) in the juvenile state. In all  
358 simulations reported, the maturation time of both sexes was equal to 20 days. After maturation, the  
359 surviving individuals enter the pre-mating state, corresponding to a condition where they prepare for  
360 mating (e.g. territory establishment; nest building; replenishment of gametes). After a fixed sex-  
361 specific number of days, the pre-mating state changes into the mating state. Unless stated otherwise,  
362 the pre-mating period was set to zero, meaning that individuals move to the mating state without  
363 delay. Once in the mating state, individuals seek for mating opportunities. In our baseline scenario,  
364 females and males mate at random, but we also consider a mate-choice scenario where females have  
365 a preference for certain male ornaments. On a given day, mating is modelled as follows: one by one,  
366 a female in the mating state is selected at random. As long as there are still males in the mating state,  
367 the female encounters one of these males at random. In the random mating scenario, such an  
368 encounter always results in mating; in the mate-choice scenario, the male can be rejected if its  
369 ornamentation does not fit to the preference of the female (see below). When mating does occur,  
370 both the male and the female immediately leave the mating state and both enter the caring state.  
371 When a female-male encounter does not result in mating, both individuals stay in the mating state,  
372 but they are no longer available for mating on that day. Hence each individual in the mating state can  
373 only have one encounter per day, and a female and a male both lose one day if their encounter does  
374 not result in mating. Mating will stop for the day when no more males in mating state are available  
375 and/or when all females in mating state have made their mating decisions. All remaining individuals  
376 stay in the mating state, but they will only have a new mating opportunity on the following day.

377 Once a mating has occurred, the mated couple produces a clutch of offspring. Offspring survival  
378 strongly depends on the amount of parental care received. The female care duration  $T_f$  and the male  
379 care duration  $T_m$  are heritable traits that may differ between individuals. The evolution of  $T_f$  and  $T_m$   
380 is the core subject of our study. We interpret  $T_f$  and  $T_m$  as the 'intended' cared duration: if one of the  
381 parents dies during the care period, this intended care duration is replaced by the actual care duration  
382 (the time from mating to death). To consider the possibility of synergy between the two parents, we  
383 assume that their total parental effort is given by  $T_{tot} = T_f + T_m + \sigma T_f T_m$  where the 'synergy' parameter  
384  $\sigma$  is non-negative. Unless stated otherwise, we assume that  $\sigma = 0$ , meaning that each parent has an  
385 independent additive effect on total care. Offspring survival is proportional to  $S(T_{tot}) = T_{tot}^2 / (T_{tot}^2 + D^2)$ ,  
386 an increasing sigmoidal function of total parental care. The parameter  $D$  may be viewed as a measure  
387 of the care demand of offspring: the function  $S$  has a turning point at  $T_{tot} = D$ , implying that the  
388 marginal benefits of care are maximal when the total parental effort matches  $D$ . Throughout, we  
389 consider the case  $D = 20$ , i.e. the offspring demand the equivalent of 20 days of care. When the care  
390 period  $T_f$  (resp.  $T_m$ ) has passed, the corresponding parent changes into the pre-mating state. When  
391 the longest-caring parent stops caring, the surviving offspring enter the infant state. As mentioned  
392 above, population size is regulated in our model by assuming that offspring survival is density



393 dependent: it is given by  $S(T_{tot})/(1+\gamma N)$ , where  $N$  is the current population size and the parameter  
394  $\gamma$  quantifies the degree of density dependence. This form of density regulation ensures that expected  
395 lifetime reproductive success (the fitness measure used by analytical approaches; see below) does  
396 indeed predict the course and outcome of evolution<sup>73</sup>. Our choice  $\gamma = 0.003$  ensured relatively large  
397 populations (about 2000 females and 2000 males) with limited genetic drift and demographic  
398 stochasticity.

399 At the start of a new day, the survival of each individual was checked according to the individual's sex-  
400 and state-specific mortality. Non-survivors were removed from the population.

401 **Sexual selection.** In part of our study, we consider a mate-choice scenario where females can evolve  
402 a preference  $p$  for a male trait of size  $s$ , where  $p$  and  $s$  are both heritable traits. In line with Kokko and  
403 Johnstone<sup>52</sup>, we assume that the probability that a female with preference  $p$  that encounters a male  
404 with trait size  $s$  will actually mate with this male is given by the logistic expression  
405  $(1+\kappa \exp(\alpha(p-s)))^{-1}$ . For all non-negative values of  $p$ , this expression increases with  $s$  (hence all  
406 females have a preference for males with larger ornament sizes), and the rate of increase is positively  
407 related to  $p$  (hence females with a large value of  $p$  discriminate more strongly against males with a  
408 small trait size). The parameters  $\kappa$  and  $\alpha$  are scaling factors that affect the intensity of sexual  
409 selection. The mate-choice simulations shown are all based on the parameter values  $\kappa = 0.02$  and  
410  $\alpha = 2$ . For these parameters, an 'unattractive' male with  $s = 0$  is accepted for mating with probability  
411 0.98 by a female with a preference value  $p = 0$  (hence,  $p = 0$  is almost undistinguishable from  
412 random mating) and with probability 0.48 by a female with preference value  $p = 2$ . We assume that  
413 male ornamentation is costly: each time step, the survival probability of a male with trait size  $s$  is  
414 reduced by a percentage  $\beta s^2$ , where we chose  $\beta = 10^{-6}$ .

415 **Reproduction and inheritance.** For simplicity, we consider a population of haploid individuals that  
416 may differ in their alleles at four gene loci. The  $T_f$ -locus and the  $p$ -locus are only expressed in females,  
417 and the  $T_m$ -locus and the  $s$ -locus are only expressed in males. The alleles at the  $T_f$ -locus and the  
418  $T_m$ -locus determine the duration of maternal and paternal care, respectively. The allele at the  $p$ -locus  
419 determines the degree of female preference, while the allele at the  $s$ -locus determines the size of the  
420 male trait. In our baseline scenario (random mating), the  $p$ -allele and the  $s$ -allele are not expressed.  
421 Offspring inherit their alleles from their parents' subject to mutation. In a first step, the allele at each  
422 locus is drawn at random from one of its parents. Moreover, offspring sex is determined at random,  
423 with equal probability. In a second step, mutations could occur with probability  $\mu = 0.005$  per locus.  
424 If a mutation occurs at the  $T_f$ -locus or the  $T_m$ -locus, the current allele is either increased or decreased  
425 by 1, with equal probability. This ensures that the parental care times  $T_f$  and  $T_m$  are natural numbers.  
426 If a mutation occurs at one of the other two loci, a small mutational step of size  $\varepsilon$  was drawn from a  
427 Cauchy distribution (with location parameter 0 and scale parameter 0.01) and added to the current  
428 value of  $p$  or  $s$ , respectively. We used the Cauchy distribution (rather than a normal distribution)  
429 because it allows for occasional larger step sizes. However, we limited mutational step sizes to a  
430 maximum value of  $\varepsilon_{\max} = 0.05$ .

431 **Initialization and replication.** In all simulations, the  $p$ - and the  $s$ -locus were initialized at  $p = s = 0$ . The  
432  $T_f$ -locus and the  $T_m$ -locus were initialized at different values (leading to the different trajectories in  
433 Fig. 1b and 6a); each time, we started with a monomorphic population. For each parameter  
434 combination, we ran at least 100 replicate simulations. In all cases, the outcome was highly repeatable,  
435 allowing us to focus on one or two replicates. As partly documented in the Supplement, we also ran  
436 numerous simulations for model variants that differed from the baseline model in its parameter values  
437 (state- and sex-specific mortalities; offspring demand  $D$ ; cost of ornamentation  $\beta$ ; density  
438 dependence  $\gamma$ ; mutation rate  $\mu$ ), the survival function  $S(T_{tot})$ , the mate choice function, or the  
439 distribution of mutational step sizes. In all cases, we arrived at the same conclusions as reported in  
440 the manuscript. We therefore conclude that our results and conclusions are quite robust.

441 **Mathematical analysis.** As a standard of comparison for our individual-based simulations, Fig. 1a  
442 shows the trajectories of the corresponding deterministic model, making use of the fitness gradient  
443 method described in Kokko and Jennions<sup>25</sup> and Fromhage and Jennions<sup>26</sup>. In a nutshell, this method  
444 calculates the selection gradient (indicating the strength and direction of selection) in males and  
445 females for each combination of parental care parameters  $(T_f, T_m)$ . This gradient points into the  
446 direction of steepest ascend of the fitness landscape, where fitness is defined by expected lifetime  
447 reproductive success. Under the assumption that evolution will proceed in the direction of the  
448 selection gradient, evolutionary trajectories as in Fig. 1a are obtained. Our model is inspired by the  
449 model of Kokko and Jennions<sup>25</sup> and Fromhage and Jennions<sup>26</sup>, but it differs from the former models in  
450 various respects. In the Supplement, we discuss these differences and demonstrate that our main  
451 results are also recovered for the earlier models, again indicating the robustness of our results and  
452 conclusions.

## 453 **Data availability**

454 This study is theoretical; no new empirical data were generated.

## 455 **Code availability**

456 The C++ simulation code and a Mathematica file with an implementation of the fitness gradient  
457 method are available for download from <https://github.com/xiaoyanlong/evolution-of-sex-roles>.

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## 604 **Author contributions**

605 Both authors conceived the study and developed the model. X.L. performed the computational work  
606 and analysed the data. Both authors interpreted the results and wrote the manuscript.

## 607 **Competing interests**

608 The authors declare no competing interests.