Individual variation in parental care drives divergence of sex roles

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Abstract

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

Introduction

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

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[12] 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[13]. 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[14,15]. This viewpoint is, in turn, hotly
44 debated[16-19]. Another debate in the literature is on whether and how the relative abundance of males
45 and females drives parental sex roles[20]. 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[21]. 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[22,23]. Last, but not least, there is debate in the literature
51 on the role of sexual selection in determining parental sex roles[12,14,24]. All these debates are intricate
52 in themselves; moreover, they are interwoven, because initial investments, sex ratios, and sexual
53 selection are mutually dependent[12].

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[25] 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[26] pointed out mistakes
63 and erroneous conclusions in the study of Kokko and Jennions[25]. 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[27,28,29], including
70 parental behaviour[30,31,32]. Various studies have shown that such variation is often shaped by
71 diversifying selection[33,34], and that it can have important evolutionary implications[35,36].

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

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[37].

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.

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[25] predicted the evolution of
98   egalitarian biparental care for this scenario. Correcting a mistake in the fitness calculations, Fromhage
99   and Jennions[26] 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
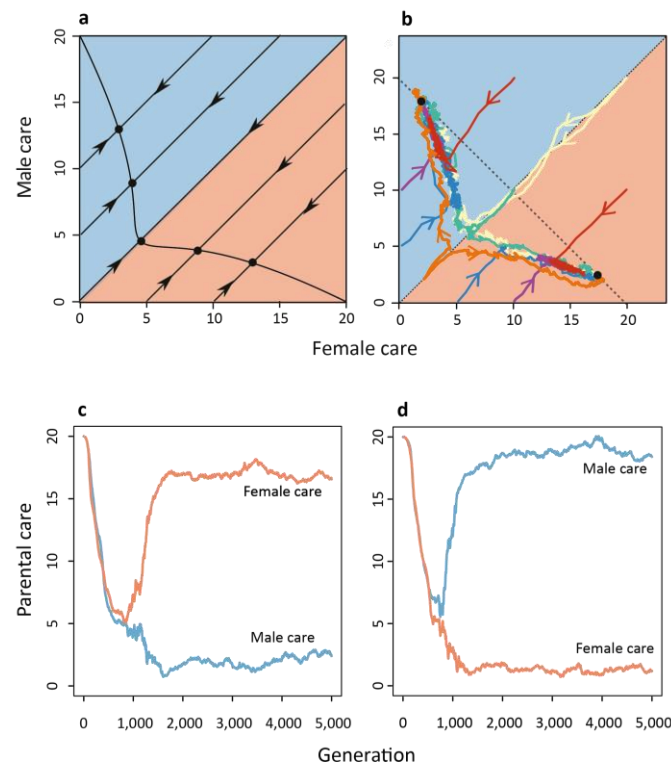
Fig. 1 | Evolution of sex-biased parental roles in the absence of sexual selection. The graphs depict evolutionary trajectories when mating is at random and males and females do not differ in mortality rates or other life-history parameters. **(a)** For this scenario, the selection gradient method predicts 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
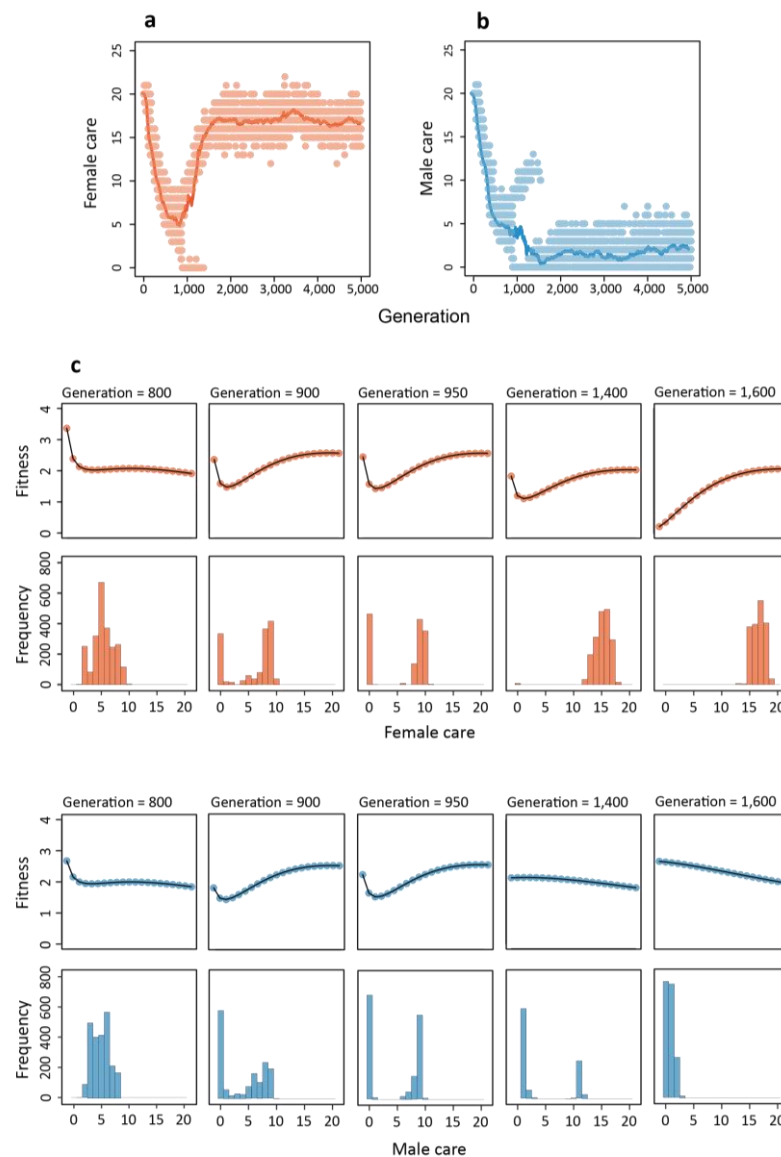
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Fig. 2 | Sex role divergence driven by individual variation in parental roles. Evolution of **(a)** female and **(b)** male care for the simulation in Fig. 1c. Lines show the average care level of females (red) and males (blue) in the population, while 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[12,38,39]

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'[40] (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[41]: 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[1-4]. 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[18,26]. 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[13], 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[14,15]. 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[42,43]. Second, the sex with the shorter pre-mating period has a higher variance in mating success,
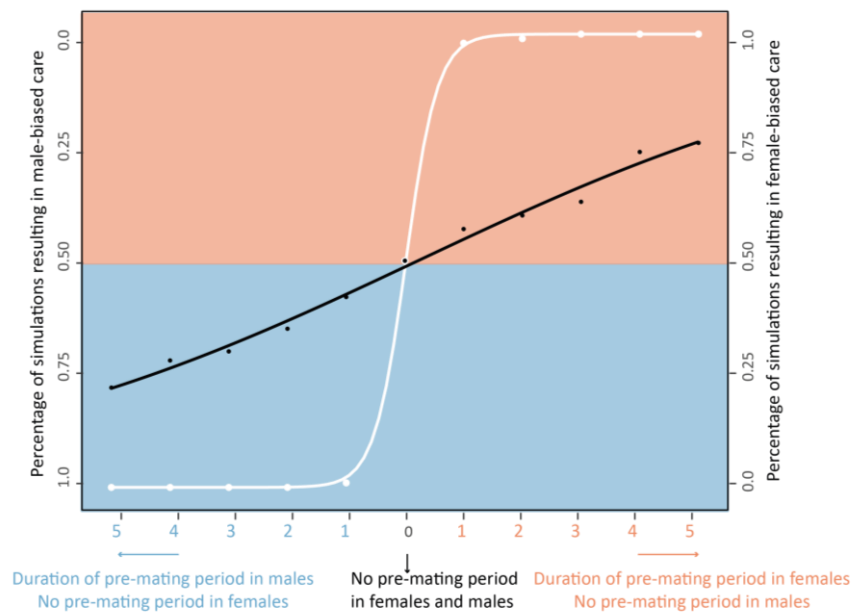
Fig. 3 | A pre-mating investment bias selects for parental sex roles. Percentage of simulations resulting in male-biased care (left axis) or female-based care (right axis) depending on the duration of the pre-mating period in either males (blue) or females (red). Mortality in the pre-mating period was 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[44]. 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[44], 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[9,10,11].
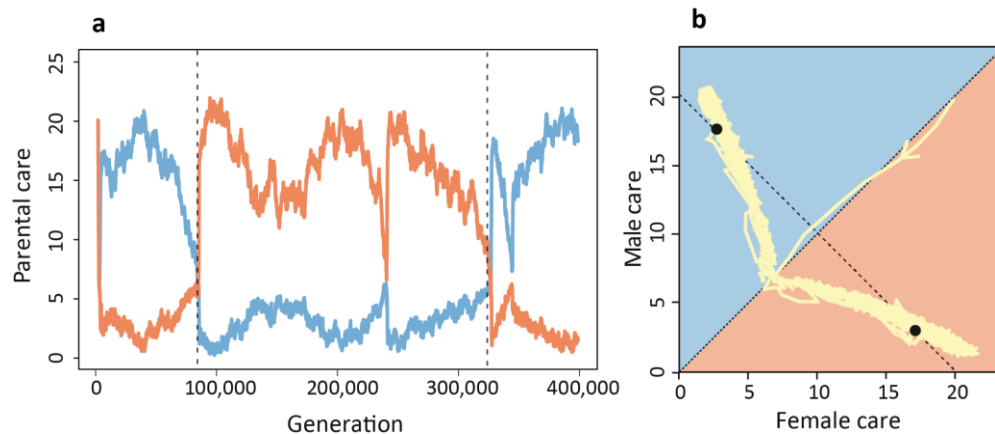
Figure 4 | Evolutionary lability of parental sex roles. Whenever simulations were run for extended periods of time, transitions occurred between the two stable equilibria. In other words, long periods of male- or female-biased care were followed by rapid switches to a situation where most of the care 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[45]. They occur, for example, in ecological systems[46,47], in the
187   climate system[48], and in physical systems[49] (think of the spontaneous reversal of polarity in magnets[50]).
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[1-4]. 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[51]. 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[52,53]. Here we introduce
199   parental synergy in our model in line with earlier modelling studies[26,52]: 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 σ is a positive parameter (In the additive model considered until now, $\sigma = 0$). In the
202   analytical model of Fromhage and Jennions[26], 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
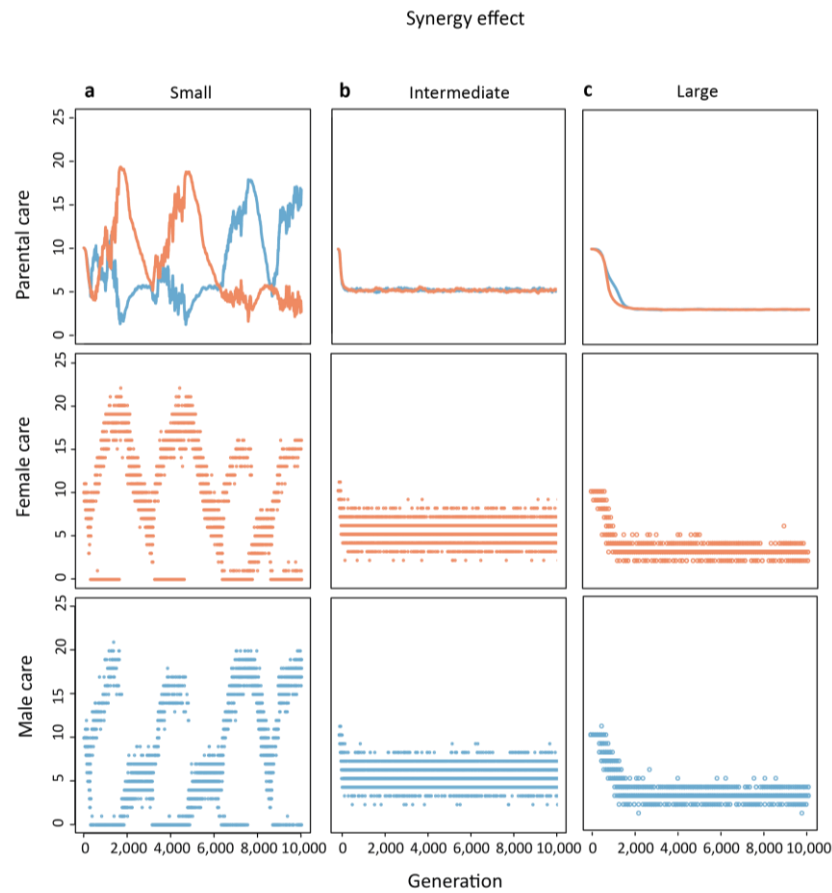
Figure 5 | Evolution of parental roles when biparental care has a synergistic effect. Representative simulations for the case that the effects of the parents on offspring survival are not additive but synergistic. **(a)** In case of weak synergy ($\sigma = 0.05$), evolution leads to a rapid succession 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

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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[52]. Many models on the evolution of parental roles therefore represent

226 mating patterns by a parameter that cannot change in time[25,26]. 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[54], 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
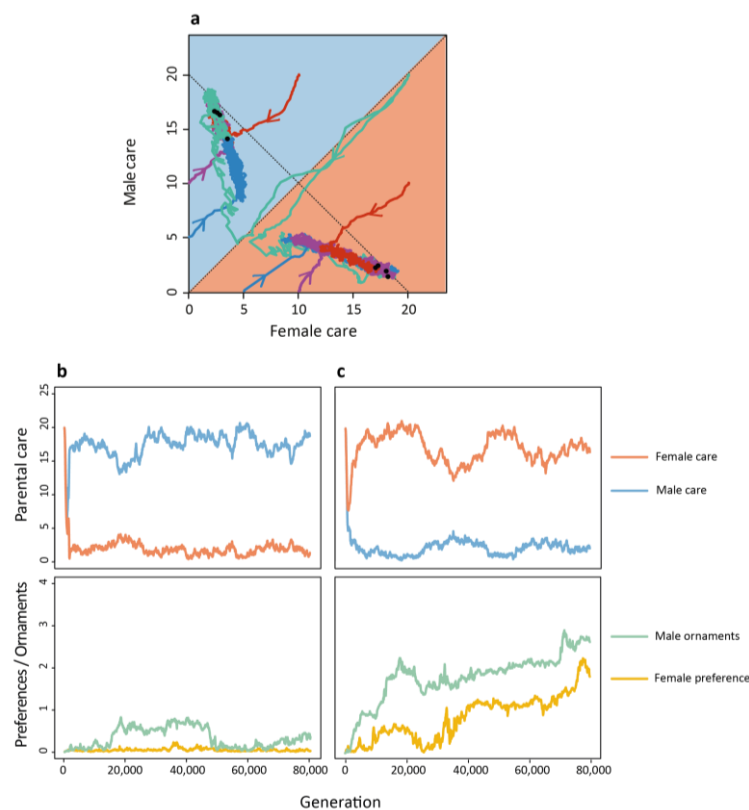

Figure 6 | Joint evolution of mating and parental strategies. (a) If parental care strategies evolve alongside with the evolution of female preferences for a costly male ornament, all simulations result in one of two alternative equilibria. **(b)** One equilibrium is characterized by male-biased care, 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.

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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.

Discussion

254 Here we investigated an individual-based simulation implementation of a modelling framework[25] 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[25] or to a line (or curve) of equilibria[26] 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'[12] 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[25,26]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[12]. 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 competiveness. 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[25] and Fromhage & Jennions[26] 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[56], simple interactions across loci[57], uncorrelated mutations of similar effect sizes[58], and
291   a simple structure of the genetic variance-covariance matrix[59]. 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[60] 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[61].
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[27,28,29] (including parental[30,31,32] and mating behaviour[62,63]), exhibiting so-called
306   'animal personalities'[64]. 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[35,36] 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[14,25,65,66]. 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[37]. 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[67,68], as well as condition-dependent preferences[69] and
337   ornaments[70].

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[71] 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[72] (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.

Methods

347   **Model structure.** In line with the models of Kokko and Jennions[25] and Fromhage and Jennions[26], 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^{-1}. 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   σ 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

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393 dependent: it is given by $S(T_{tot})/(1+\gamma N)$, where N is the current population size and the parameter

394 γ 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[73]. 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[52], 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 κ and α 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 βs^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 ε 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 $\varepsilon_{max} = 0.05$.

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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 β; density
438 dependence γ; mutation rate μ), 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[25] and Fromhage and Jennions[26]. 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[25] and Fromhage and Jennions[26], 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.

Data availability

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

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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Author contributions

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

Competing interests

The authors declare no competing interests.