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Sex roles and the evolution of parental care specialization

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

1. Introduction

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

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

investment in offspring is usually predicted to remain the dominant provider, and consequently to experience less competition for mates. These theoretical predictions are consistent with patterns of parental investment and mating competition across a wide range of animal taxa [19–22].

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

Across species, costly mating traits in one sex almost invariably co-occur with substantial parental investment (or, in some cases, nuptial gifts) by the other sex, an observation that has long drawn the attention of theorists [17,43,44]. Surprisingly, however, most formal models of sexual selection treat parenting patterns as fixed (e.g. via fixed sex-specific 'time-outs' for reproduction) [7,44–48]. On the other hand, theory on parental investment often neglects sexual selection entirely, or models its strength via fixed parameters [4,14,16,18,23,24]. In other words, most models ignore the potential feedback between parental care and sexual selection as care patterns, sexually selected traits and preferences evolve [49]. However, a small but growing body of literature has begun to correct this omission by explicitly modelling the coevolution of care and competition in males and females [5,6,15,50].

Here, we expand the recent model of Fromhage & Jennions [6] to study how care specialization coevolves with sex roles (i.e. sex-specific behavioural patterns) in mating competition and parental investment. In many species, parental investment consists of two or more distinct activities (e.g. egg provisioning, brooding or oxygenation of eggs, defence against predators or offspring provisioning [43]). Due to time and resource constraints, a single individual may not provide multiple types of care as effectively as an individual specialized in a subset of care types [40–42]. We show that such inefficiencies can lead to sex specialization in parental investment, with males and females adopting distinct roles. Care specialization broadens the conditions under which biparental investment can evolve in lineages that historically had uniparental care [24]. Ecological changes in the costs or benefits of different care types, or in the sex ratio at maturation, can then select for partial or full reversals of sex roles in mating and parenting. Our model provides a plausible evolutionary route from the ancestral condition of female-only care to systems with male-biased care and strong female mating competition. In line

with the empirical evidence, however, it also predicts that such transitions should be rare.

2. Model

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

Our model assumes that all processes (e.g. mating, mortality) occur continuously in time and that generations are overlapping. Individuals alternate between two possible states: searching or competing for mates (time-in) and providing or recovering from parental investment (time-out). During time-in, individuals mate at instantaneous rates of a (for females) or \tilde{a} (for males), which depend on the values of their mating traits. After mating, individuals enter time-out for a duration of T or \tilde{T} . If still alive, they then return to time-in. During both time-in and time-out, individuals experience mortality at an instantaneous rate of μ or $\tilde{\mu}$. To vary the mean relatedness between carers and offspring, we suppose that each breeding event involves n females and \tilde{n} males (e.g. all offspring sired by a single pair if $n = \tilde{n} = 1$, mixed paternity if $\tilde{n} > 1$ or mixed maternity if $n > 1$). Parental care benefits equally all offspring produced in a given breeding event. We focus mainly on the case where both males and females have full parentage of all offspring they invest in ($n = \tilde{n} = 1$), as this is the most common mating system in which substantial male care and female mating competition evolve (but see electronic supplementary material for results with mixed parentage).

(a) Mating rates and mortality

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

$$\mu(x) = \mu_{\min}(1 + x^{1.5}). \quad (2.1)$$

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

Mating traits are also under sexual selection due to their effects on individual mating rates. Mating rates are given by $a = Mx\tilde{n}r_{\text{O}}^{1/2}$ for females and $\tilde{a} = Mx\tilde{n}r_{\text{O}}^{-1/2}$ for males [6,18], where r_{O} is the operational sex ratio (i.e. the ratio of males to females in time-in). The operational sex ratio depends on both the sex ratio at maturity (MSR) and sex-specific mortalities (see electronic supplementary material). The parameter M accounts for species-specific factors like population density and movement capacity.

(b) Parental investment and offspring survival

Offspring require two types of parental investment to survive (e.g. egg production and post-hatching care, or provisioning and defence). We assume that offspring survive to reach maturity (i.e. their first time-in) with probability

$$S = \exp\left(-\frac{\alpha_1}{\tau_{1\text{ all}}}\right) \exp\left(-\frac{\alpha_2}{\tau_{2\text{ all}}}\right). \quad (2.2)$$

Here, $\tau_{1\text{ all}}$ represents the total expected parental investment into care of type 1 that a brood receives, summed across all contributing parents; similarly, $\tau_{2\text{ all}}$ represents the total expected investment into type-2 care (see below). Each factor $\exp(-\alpha_i/\tau_{i\text{ all}})$ is a sigmoidal function of expected parental investment, showing diminishing returns as investment increases. The parameters α_1 and α_2 determine the amount of parental investment needed to achieve a given offspring survival probability (larger α_i means greater investment is needed).

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

$$\tau_{\text{total}} = p_0 T + \int_0^T \mu e^{-\mu t} t dt = \frac{1 - e^{-\mu T}}{\mu}. \quad (2.3)$$

Females allocate a proportion q of their parental investment to type-1 care and the remainder $1 - q$ to type-2 care. We assume that it is inefficient for the same individual to provide both types of care, so that all parental investment is discounted by a factor of $d = 1 - \gamma q(1 - q)$. The parameter γ represents the efficiency benefit of specializing in a single type of care. If $\gamma = 0$ then offspring survival is identical when cared for by two unspecialized parents or by two specialized parents, provided the overall duration of parental investment in each care type is the same. Larger values of γ correspond to more-efficient care by parents that specialize in a single care type. For a female playing T and q , her *effective* contributions to each care type are then $\tau_1 = qd\tau_{\text{total}}$ and $\tau_2 = (1 - q)d\tau_{\text{total}}$ (and analogously for males). We assume that $0 \leq \gamma < 3$, which ensures that τ_1 and τ_2 are strictly increasing functions of q and $1 - q$, respectively (proof in electronic supplementary material). The effective parental investment that a brood receives from all contributing parents combined is $\tau_{1\text{ all}} = n\tau_1 + \tilde{n}\tilde{\tau}_1$ for type-1 care and $\tau_{2\text{ all}} = n\tau_2 + \tilde{n}\tilde{\tau}_2$ for type-2 care.

(c) Fitness and selection trajectories

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

In some cases, we found local equilibria that were not stable to large-effect mutations in care specialization. For instance, populations with unspecialized female-only care (i.e. with $\tilde{T} = 0$ and $q = 1/2$) could sometimes be invaded by caring males, but

only if the males were highly specialized in one care type (e.g. $\tilde{q} = 0$). In such cases, we first allowed the population to evolve gradually towards the local equilibrium, then introduced the mutation of large effect, and allowed gradual evolution towards a final, globally stable equilibrium (e.g. figure 1e,f). This approach is consistent with the assumption that mutations of large effect are rare. Our qualitative results are, however, unaffected by the numerical details of this approach.

3. Results

Our model predicts three possible types of stable equilibria: female-only care, male-only care and biparental care. When there is no inefficiency in providing both types of care (figure 1a,b), only uniparental care is stable. The sex that initially provided more care ends up caring alone, while the non-caring sex competes more strongly for mates. When the need for specialization is moderate (figure 1c,d), either uniparental or biparental care can evolve, depending on the initial conditions. When the need for specialization is high (figure 1e,f), only biparental care is stable. The evolution of sex roles is predicted to be highly conservative, in that each of three equilibria is generally highly stable once it has evolved.

(a) Sole carers are generalists, joint carers are specialists

Under biparental care, each sex fully specializes in one care type as long as there is *any* inefficiency in providing both types of care. In other words, at biparental equilibria, we always have either $(q, \tilde{q}) = (0, 1)$ or $(q, \tilde{q}) = (1, 0)$ whenever the need for specialization $\gamma > 0$ (see red circles in figure 1c-f, which indicate full specialization). If there is no inefficiency in providing both care types (i.e. $\gamma = 0$), then biparental care is unstable (figure 1a,b). The relative amount of care provided by each sex depends on the sex ratio at maturity (figure 2) and the relative need for each type of care (α_1 and α_2 : figure 3) (see below).

By contrast, uniparental carers always provide both types of care, as otherwise their offspring would not survive. For these parents, the optimal allocation of parental effort depends on both the relative importance of each care type and the need for specialization. If the two care types are equally important ($\alpha_1 = \alpha_2$) and the need for specialization is not too great ($\gamma \leq 2$), then sole carers provide both care types equally ($q = 1/2$: see blue circles in figure 1a-d, which indicate no specialization). If one type of care is more necessary than the other, sole carers unsurprisingly invest more in that type of care (e.g. $q > 1/2$ when $\alpha_1 > \alpha_2$: data not shown). In the interesting case where $\gamma > 2$, the inefficiency of providing both care types is so severe that sole carers always evolve partial specialization, even when both types of care are equally important (small purple circles in figure 1e,f). However, uniparental care is unstable in this case: the non-caring sex is under selection to start providing the more neglected type of care (figure 1e,f).

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

Under biparental care, biases in the sex ratio at maturation select for both greater parental investment and greater competition (i.e. larger mating trait values) by the more common sex

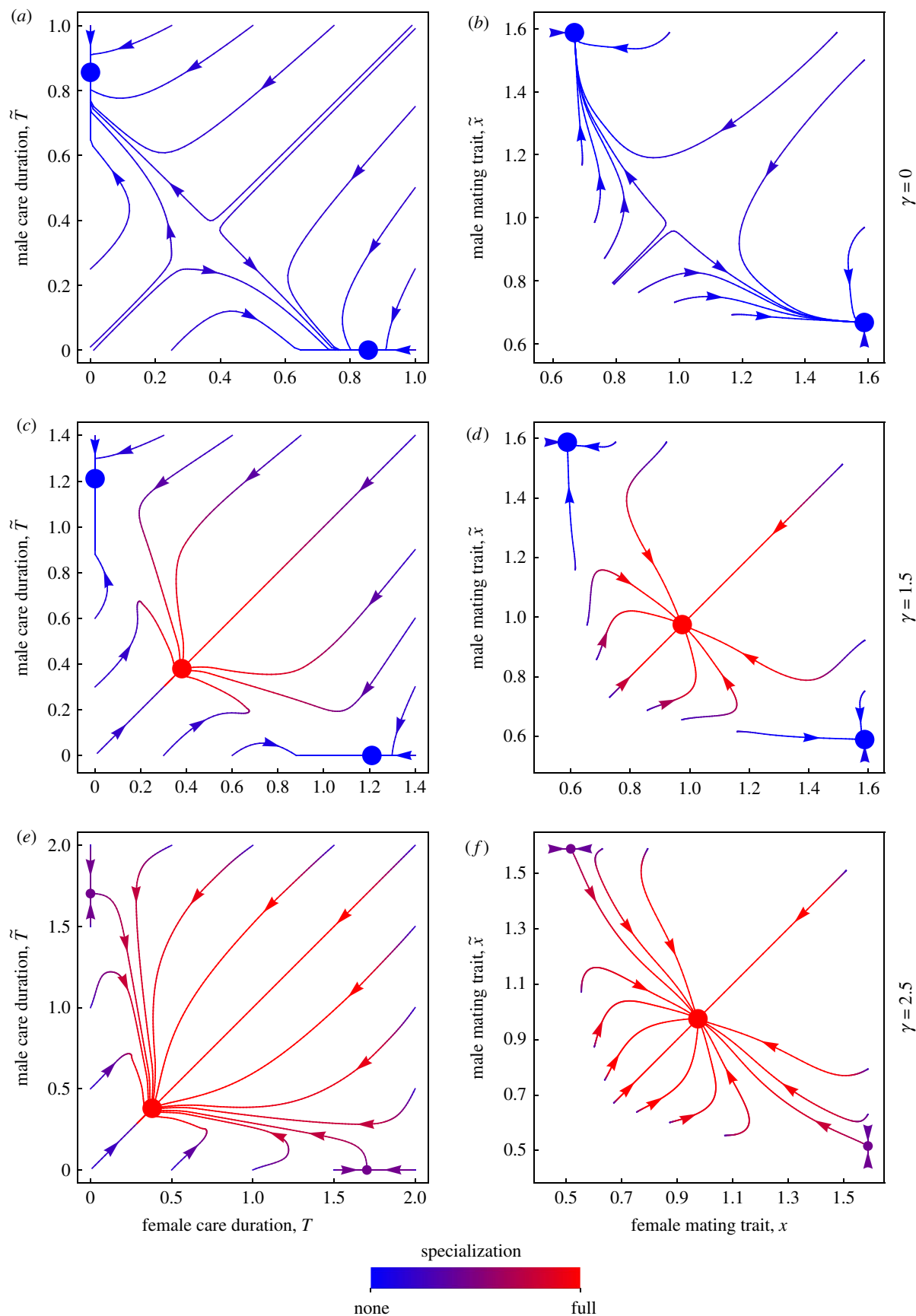


Figure 1. The evolution of care duration (T and \tilde{T} : *a,c,e*), the mating trait (x and \tilde{x} : *b,d,f*) and the average level of care specialization (line colouring) when the only sex asymmetry is in the initial strategies. Arrows indicate the direction of evolution. Large circles indicate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

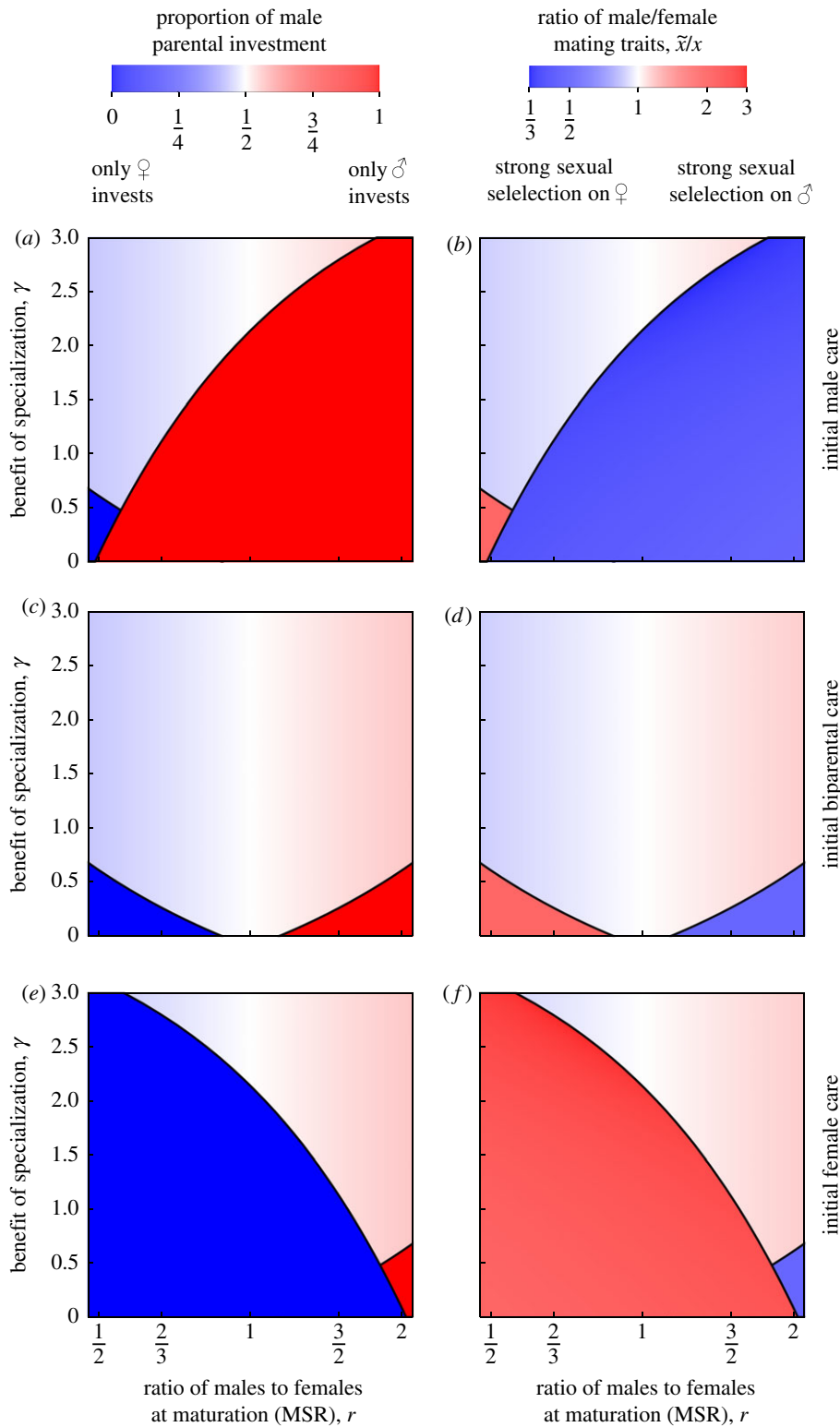


Figure 2. Equilibrium proportion of male care $\tilde{T}/(T + \tilde{T})$ (a,c,e) and the ratio of male to female mating traits \tilde{x}/x (b,d,f) for populations that initially show male-only care (a,b), biparental care (c,d) and female-only care (e,f). All panels are shown with variation in the benefits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

(lighter coloured regions in figure 2c,d). Similarly, under uniparental care, individuals of the caring sex provide greater parental investment, in absolute terms, when they outnumber the non-caring sex at maturation (data not shown). This

increase in parental investment is accompanied by an increase in mating competition in the caring sex, although the non-caring sex remains the more competitive of the two (figure 2b,f).

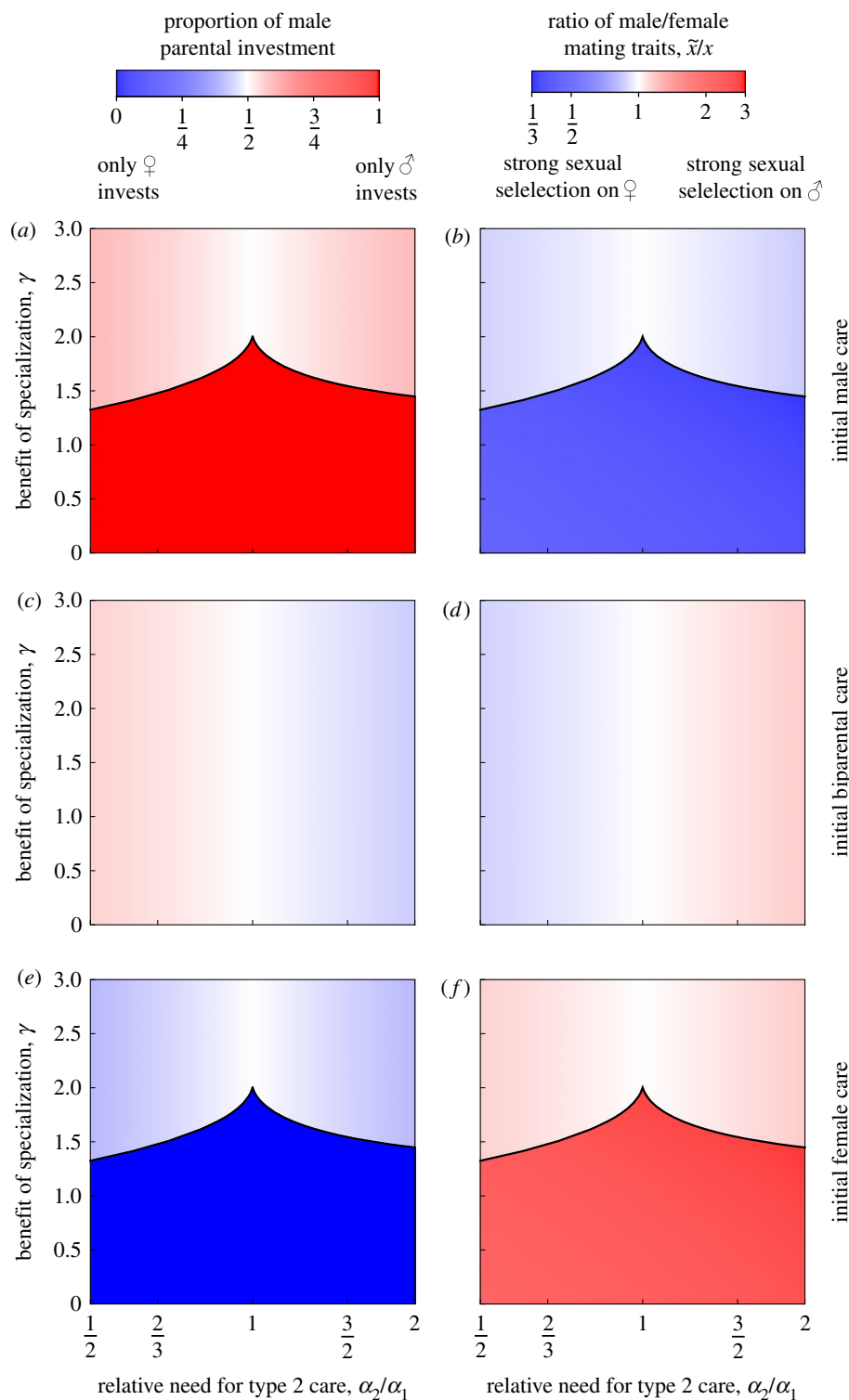


Figure 3. Equilibrium proportion of male care $\tilde{T}/(T + \tilde{T})$ (*a,c,e*) and the ratio of male to female mating traits \tilde{x}/x (*b,d,f*) for populations that initially show male-only care (*a,b*), biparental care (*c,d*) and female-only care (*e,f*). All panels are shown with variation in the benefits of specialization γ and the importance of type-2 care relative to type-1 care, α_2/α_1 . For the case of biparental care (*c,d*), we assume without loss of generality that males and females initially specialize in type-1 and type-2 care, respectively. Abrupt colour changes indicate where uniparental care is unstable and transitions to biparental care (upper region of *a,b,e,f*). In this case, the initially caring sex ends up specializing in the more important type of care (e.g. in type-2 care when $\alpha_2/\alpha_1 > 1$). Biparental care is always stable under the parameter values illustrated here (*c,d*). Under uniparental care, the non-caring sex competes more strongly for mates (dark blue regions in left panels correspond to dark red regions in right panels and vice versa). Similarly, under biparental care, the sex that cares more competes less (colour transitions in lighter coloured regions are reversed between left and right panels). All panels are shown with $\alpha_1 = 0.1$, $\mu_{\min} = 0.01$ and $r = n = \tilde{n} = 1$.

This simple pattern, which applies within care systems, is complicated by transitions among systems. Biparental care can transition to uniparental care when the MSR is highly biased and the need for specialization is low (lower corners of figure 2*c,d*). This results in an abrupt change in sex roles.

In the biparental system, the more common sex both cares and competes slightly more than the less common sex (i.e. both T and x are larger in the more common sex). By contrast, under uniparental care, the more common sex provides all the care, while competition is much stronger in the less common

sex. The reverse transition from uniparental to biparental care can occur if the MSR is biased in the direction of the non-caring sex and the need for specialization is high (upper left corners of figure 2*a,b*; upper right corners of figure 2*e,f*). Even more extreme transitions—from female-only care directly to male-only care or vice versa—can occur if the need for specialization is low and the MSR is extremely biased towards the non-caring sex (bottom left corners of figure 2*a,b*; bottom right corners of figure 2*e,f*).

(c) Relative importance of the two care types

Biparental care is stable to changes in the relative importance of the two care types (i.e. the magnitudes of α_1 and α_2 : figure 3*c,d*). The sex specializing in the more important care type provides more care, all else being equal, while the other sex competes more strongly (note that we assume without loss of generality that males are initially specialized in type-1 care). This can result in strong sex biases in care even under biparental care. Uniparental care can be invaded by biparental care if the benefits of specialization are high enough (upper regions of figure 3*a,b,e,f*). In this case, the initially caring sex specializes in the more important care type, while continuing to provide more care and compete less. Existing sex roles are consequently preserved, although in a less pronounced form, after the transition to biparental care. For any given benefits of specialization γ , biparental care invades more easily when the two care types differ in importance (figure 3*a,b,e,f*). This is because partial specialization by the caring sex creates an opportunity for the non-caring sex to specialize in the complementary care type.

(d) Major transitions in sex roles

Gradual shifts in sex roles, with respect to both parental care and mating competition, can occur in our model when the initial care system is biparental. These shifts in roles can be driven by changes in the MSR or in the relative importance of the two care types (figures 2*c,d* and 3*c,d*). Large differences in the needs for each care type can lead to large sex biases in the amount of care provided. A full transition from female-only to male-only care is also possible, with an accompanying reversal of mating competition. For instance, biparental care might first evolve from female care via increased benefits of specialized care (higher γ : figures 2*e,f* and 3*e,f*). Male-only care could then be favoured by a subsequent reduction in the benefits of specialization, along with a male-biased MSR (figure 2*c,d*). Notably, this scenario requires only two large ecological shifts to precipitate the transitions from uniparental care to biparental care and from biparental care to uniparental care by the other sex. A less likely outcome, which our model predicts should be possible but rare, is a direct transition from female-only care to male-only care, or vice versa. Such a transition requires a low benefit of specialization and a large bias in the MSR (figure 2*e,f*), although it is unclear how such an extreme MSR would arise.

4. Discussion

Here, we model how care specialization shapes the evolution of parental investment and mating competition, and investigate the circumstances under which sex-role transitions in these traits are likely to arise. Our model predicts that a given set

of parameter values can lead to more than one type of care system (male-only, female-only or biparental), depending on the initial strategies for each sex (in fact, all seven possible combinations of stable equilibria occur in some parameter regions: electronic supplementary material, figure S1). The conditions that allow a transition from one parental care system to another are usually much stricter than the conditions for maintaining a given system once it has evolved (figures 2 and 3). For instance, the parameter regions where biparental care is stable once evolved (light-coloured regions in figures 2*c* and 3*c*) are much larger than the parameter regions where biparental care can arise from uniparental care (lighter coloured regions in figures 2*a,e* and 3*a,e*). The model consequently predicts that transitions among the three types of equilibrium will be uncommon. These alternative stable states arise because strong mating competition selects for large mating traits in the less-caring sex, which indirectly trade off against parental care. The positive feedback cycle acting on sex roles is consequently relaxed but not eliminated in our model [52].

Our model predicts that males and females should specialize in complementary care types when it is inefficient for a single parent to provide multiple types of care. Care specialization allows for greater evolutionary lability of sex roles than predicted by most previous theory [2,5,6,14–16]. In particular, (i) increases in the efficiency of care specialization can select for transitions from uniparental to biparental care; (ii) under biparental care, if the relative importance of one care type increases, then the sex providing that care type evolves to care more and compete less; and (iii) biases in the sex ratio at maturity select for greater care by the more common sex, although the effect on mating competition is more complicated. Together, these factors enable the evolution of varied sex roles, including transitions between female-only, male-only and biparental care.

Although parental care specialization occurs in many taxa [43], the efficiency of specialization has to our knowledge never been measured empirically (but see [40,42] for interesting related work). Efficiency benefits may result if, for example, some important care activities are both demanding and exclusive of other activities. In convict cichlids, for instance, females spend most of their time tending offspring, leaving them little time to defend the territory or chase intruders, tasks that consequently fall to the male [39]. Our model is formulated in terms of the benefit to offspring of parental specialization, but equivalent predictions apply if specialization reduces the costs of care to parents. Any efficiency gains could be quantified most easily in systems where specialization is facultative, e.g. when individuals switch from specialized to unspecialized caring strategies upon the death or desertion of a partner [40,42]. For instance, offspring and parental outcomes could be compared between one joint brood cared for by both parents and two half-sized broods each cared for by one parent. We note, however, that differences in parental effort may also affect the results of such manipulations [53].

Our model assumes that changes in the parameter values are ecological in origin, or at least not directly caused by shifts in parental or mating behaviour. Optimal parental investment in care activities—e.g. provisioning, defence, brooding, or oxygenation—may be particularly sensitive to ecological factors. For instance, the need to oxygenate broods depends on temperature and dissolved oxygen levels, while the benefits of offspring defence depend on the density of

potential predators [54–56]. Temporal or spatial variation in these factors should consequently affect the relative need for different care types (e.g. α_1 and α_2 in our model), leading to sex-role variation within or among biparental species where males and females specialize in different care types. Similarly, changes in how strongly offspring depend on their parents (e.g. the evolution of precocial versus altricial young in birds) may affect the benefits of care specialization (γ) [56–58].

The sex ratio at maturation (MSR) likely depends on complex interactions between ecological and evolutionary factors, which we do not model here explicitly. Biases in the MSR may result either from skewed sex ratios at conception (i.e. primary sex ratios) or from sex-biased mortality during early development or juvenile stages [59]. For instance, population-level bias in the primary sex ratio can occur when the relationship between parental investment and offspring fitness differs between male and female offspring. Such differences can favour overproduction of the competitive sex by carers that are in good condition (i.e. the Trivers–Willard hypothesis: [60]). Similarly, selection for costly mating traits in the competing sex (e.g. due to size advantage in contests) may favour riskier juvenile growth trajectories that generate larger mating traits when successful [61]. Such factors could lead to feedback effects of mating competition on the MSR that are not accounted for in our model. Feedback is perhaps more likely when mating success is an accelerating function of investment in sexually selected traits (in contrast with our model, where the relationship is assumed linear).

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

Several limitations of the model should be kept in mind. First, we model mating competition via a hypothetical ‘mating trait’ that is assumed *a priori* to increase an individual’s mating rate. We consequently do not model whether opposite-sex individuals should prefer mates with higher mating trait values (i.e. this is not a preference-trait model: see [45,46,67]). The assumptions of our model are most plausible when the mating trait is interpreted as mate search effort [5,7,68], an armament used in mating competition [69], or an ornament that exploits perceptual biases [70,71], rather than an ornament that coevolves with active mate choice [45,46,67].

Second, our model assumes that the benefits of a given care type are not synergistic between the sexes, in the sense that the value of a female investing x and her partner investing y is identical to one parent investing $x + y$. In biparental systems, this assumption selects for males and females to specialize fully in complementary care types. In reality, there may be synergistic benefits when both parents participate in the same care type (e.g. offspring provisioning or nest defence

may be considerably more effective when both parents participate) [6,23,72]. This situation might favour the evolution of incomplete specialization by males and females, an outcome that does not occur in our model. Further, the evolution of biparental care from uniparental ancestors is driven by care specialization in our model, with the consequence that specialization and biparental care evolve in tandem. An alternative scenario would be for unspecialized biparental care to evolve first (e.g. due to synergy), followed by care specialization whenever the latter is efficient. Under either scenario, sex roles in parental care and mating competition would be sensitive to ecological factors influencing the costs and benefits of sex-limited care types once care specialization has evolved (see above).

Third, our model permits the evolution of exclusively male parental investment, with no investment at all by females. In nature, however, female investment in offspring is apparently never negligible, possibly because in most organisms, only females have evolved to provision the zygote directly. The evolution of parenting roles may consequently be more constrained than predicted by our model. More generally, coevolution between care effort and the ability to care (e.g. lactation in female mammals) may constrain sex-role evolution because the lack of co-adaptations for caring creates an entry barrier for the non-caring sex [16,73].

Lastly, our model assumes that important mating system parameters like the operational sex ratio are constant over time. In many species, however, such parameters change dynamically due to factors like the seasonality of breeding conditions or sex-biased mortality [74–76]. These fluctuations can lead to sex-role variation within a single population over time. In the two-spotted goby (*Gobiusculus flavescens*), for instance, the operational sex ratio shifts dramatically over the course of a breeding season due to male-biased mortality. Male courtship and mating competition is consequently replaced by female courtship and competition as the season progresses [75,76].

One important prediction of our model is that a given regime of parental investment and mating competition, once it evolves, remains relatively stable under a broad range of conditions. Empirical evidence suggests that the evolution of mating and parenting systems is characterized by strong phylogenetic inertia, such that clades of closely related species, despite sometimes varying greatly in ecology, often share similar sex-role patterns [77,78]. Our model sheds light on the origins of such conservatism: transitions in sex roles are predicted to occur only under restrictive conditions, whereas the conditions for maintaining a particular sex-role pattern may be broad. We expect, however, that our model does not describe the only mechanism of sex-role transitions. Rather, the considerable taxonomic and life-history diversity of species with unusual sex roles suggests that multiple mechanisms are at play. Considerable scope remains for theory on how exceptions to the dominant sex-role patterns arise, and why they arise so rarely.

Data accessibility. This article has no additional data.

Authors’ contributions. J.M.H. conceived the ideas and designed the model. J.M.H., L.F. and A.G.J. wrote the manuscript.

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