Electronic supplementary material

This material relates to the following paper:

Henshaw JM, Fromhage L, Jones AG (2019) Sex roles and the evolution of parental care specialization. *Proc. R. Soc. B* 20191312.

Proof that τ_1 and τ_2 are strictly increasing functions of q and $1 - q$ when $\gamma < 3$

Here we show that an individual's effective contribution to parental investment for a given care type (τ_1 or τ_2) is a strictly increasing function of the proportion of resources devoted to that care type (q or $1 - q$ respectively), as long as the benefit of specialisation $\gamma < 3$. Consider an individual with fixed duration of parental investment T. The individual's effective contribution to type-1 care is given by (see main text):

$$\tau_1 = q\big(1 - \gamma q(1 - q)\big) \cdot \frac{1 - e^{-\mu T}}{\mu} \qquad [\text{S1}]$$

Taking the first derivative with respect to the proportion q of resources devoted to type-1 care yields:

$$\frac{\partial \tau_1}{\partial q} = \big(1 + \gamma q(3q - 2)\big) \cdot \frac{1 - e^{-\mu T}}{\mu} \qquad [\text{S2}]$$

The second derivate in q is similarly:

$$\frac{\partial^2 \tau_1}{\partial q^2} = 2\gamma(3q - 1) \cdot \frac{1 - e^{-\mu T}}{\mu} \qquad [\text{S3}]$$

The minimum value of $\frac{\partial \tau_1}{\partial q}$ occurs when $\frac{\partial^2 \tau_1}{\partial q^2} = 0$, which occurs when $q = \frac{1}{3}$. Substituting this back into equation S2 yields

$$\left.\frac{\partial \tau_1}{\partial q}\right|_{q=\frac{1}{3}} = \left(1 - \frac{\gamma}{3}\right) \cdot \frac{1 - e^{-\mu T}}{\mu} \qquad [\text{S4}]$$

If $\gamma < 3$, then $\frac{\partial \tau_1}{\partial q}$ is positive at its minimum value, and hence positive everywhere.

Consequently, τ_1 is a strictly increasing function of q whenever $\gamma < 3$. By symmetry, τ_2 is also a strictly increasing function of $1 - q$.

Operational sex ratio

Here we calculate the operational sex ratio (i.e. the ratio of males to females in time-in), assuming fixed values for all parameters (including the sex ratio at maturation, MSR). All individuals begin their reproductive lives in time-in. The probability that a female survives any given time-in is $p_I = \frac{a}{a+\mu}$ and the probability that she survives time-out is $p_O = e^{-\mu T}$. The expected number of times that a female enters time-in is consequently given by the geometric series $1 + p_I p_O + (p_I p_O)^2 + \cdots = \frac{1}{1 - p_I p_O}$. The average duration of each time-in is $\frac{1}{a+\mu}$. Consequently, the expected total time that a female spends in time-in over her lifetime is:

$$L_I = \frac{1}{1 - p_I p_O} \cdot \frac{1}{a + \mu} = \frac{1}{a(1 - p_O) + \mu} \tag{S5}$$

We write $\tilde{L}_I$ for the analogous male variable. Given our assumptions of continuous breeding with overlapping generations, the operational sex ratio must obey:

$$r_O = r \cdot \frac{\tilde{L}_I}{L_I} \tag{S6}$$

where r is the ratio of males to females at maturity (MSR). Solving this equation yields:

$$r_O = r \frac{\mu}{\tilde{\mu}} + \frac{A}{2\tilde{\mu}^2} \left(A + \sqrt{A^2 + 4r\mu\tilde{\mu}} \right) \tag{S7}$$

where

$$A = Mx\tilde{x}[rn(1 - p_O) - \tilde{n}(1 - \tilde{p}_O)] \tag{S8}$$

2

Note that in some previous models [6,18], sexual selection was incorporated by allowing only a proportion of individuals (k for females, $\tilde{k}$ for males) to mate while in time-in. The expression for the operational sex ratio r_O in these models should consequently contain a factor $k/\tilde{k}$ [6]. In our model, by contrast, all individuals are 'qualified to mate'. We incorporate sexual selection by assuming that an individual's mating rate is a function of its mating trait x or $\tilde{x}$. As a result, the factor of $k/\tilde{k}$ does not arise in our model.

Fitness of typical males and females

We now use an adaptive dynamic approach to calculate evolutionary trajectories for the coevolution of parental care duration, the mating trait, and care specialisation in each sex. We begin by deriving the fitness of typical males and females in a population where all individuals play the same sex-specific strategies. Each breeding event results in an average of nb offspring, where n is the number of females and b is the average brood size. The survival probability of each offspring is S, which depends on the parental investment of all contributing males and females (see main text). For a female, the probability of surviving any given time-in is $p_I = \frac{a}{a+\mu}$ and the probability that she survives time-out is $p_O = e^{-\mu T}$. Her total number of breeding events is then given by the geometric series

$p_I + p_I^2 p_O + p_I^3 p_O^2 + \cdots = \frac{p_I}{1-p_I p_O}$. A typical female's expected lifetime fitness is consequently:

$$W = \frac{p_I}{1 - p_I p_O} \cdot S \cdot b \qquad [S9]$$

Male fitness is similarly given by:

$$\widetilde{W} = \frac{\tilde{p}_I}{1 - \tilde{p}_I \tilde{p}_O} \cdot \frac{n}{\tilde{n}} \cdot S \cdot b \qquad [S10]$$

Since every offspring has exactly one mother and one father, consistency requires that the total fitness of males and females in the population should be equal. This is sometimes known as the 'Fisher condition' [59]. To verify that the Fisher condition is met in this model, we must show that $\frac{W}{\widetilde{W}} = r$, where r is the adult sex ratio. By taking the ratio of [S9] to [S10] and substituting in the definitions $p_I = \frac{a}{a+\mu}$ and $\tilde{p}_I = \frac{\tilde{a}}{\tilde{a}+\tilde{\mu}}$, we have:

$$\frac{W}{\widetilde{W}} = \frac{a\tilde{n}}{\tilde{a}n}\left(\frac{\tilde{a}(1-\tilde{p}_O)+\tilde{\mu}}{a(1-p_O)+\mu}\right) = \frac{a\tilde{n}L_I}{\tilde{a}n\tilde{L}_I} \qquad [S11]$$

From the main text, the mating rates are given by $a = Mx\tilde{x}nr_O^{1/2}$ and $\tilde{a} = Mx\tilde{x}\tilde{n}r_O^{-1/2}$. Substituting in these values and using equation [S6] then gives us $\frac{W}{\widetilde{W}} = r$, as required.

Fitness of male and female mutants

Next we derive the fitness of male and female mutants, which we then use to calculate the selection gradients. Expressions relating to mutants are marked with a star and are analogous to the expressions relating to typical individuals (see main text and above). Consider a mutant female playing $\sigma^* = (T^*, q^*, x^*)$ in a population where all other females play σ and all males play $\tilde{\sigma}$. Her probabilities of surviving time-in and time-out are

$p_I^* = \frac{a^*}{a^*+\mu^*}$ and $p_O^* = e^{-\mu^* T^*}$ respectively. Her mating rate is $a^* = Mx^*\tilde{x}nr_O^{1/2}$ and her

mortality rate is $\mu^* = \mu_{\min}(1 + x^{*1.5})$. Her effective contributions to parental investment of

each type are $\tau_1^* = q^* d^* \tau_{\text{total}}^*$ and $\tau_2^* = (1-q^*)d^*\tau_{\text{total}}^*$, where $\tau_{\text{total}}^* = \frac{1-e^{-\mu^* T^*}}{\mu^*}$ and

$d^* = 1 - \gamma q^*(1-q^*)$. The expected survival probability of her offspring is

$S^* = \exp\left(-\frac{\alpha_1}{\tau_{1\,\text{all}}^*}\right)\exp\left(-\frac{\alpha_2}{\tau_{2\,\text{all}}^*}\right)$, where $\tau_{1\,\text{all}}^* = \tau_1^* + (n-1)\tau_1 + \tilde{n}\tilde{\tau}_1$ and

$\tau_{2\,\text{all}}^* = \tau_2^* + (n-1)\tau_2 + \tilde{n}\tilde{\tau}_2$. Her expected fitness is then:

$$W(\sigma^*, \sigma, \tilde{\sigma}) = \frac{p_I^*}{1 - p_I^* p_O^*} \cdot S^* \cdot b \qquad \text{[S12]}$$

For a mutant male playing $\tilde{\sigma}^* = (\tilde{T}^*, \tilde{q}^*, \tilde{x}^*)$, all expressions are analogous to those above,

except that his mating rate is $\tilde{a}^* = M x \tilde{x}^* \tilde{n} r_O^{-1/2}$ and his expected fitness is:

$$\widetilde{W}(\tilde{\sigma}^*, \sigma, \tilde{\sigma}) = \frac{\tilde{p}_I^*}{1 - \tilde{p}_I^* \tilde{p}_O^*} \cdot \frac{n}{\tilde{n}} \cdot \tilde{S}^* \cdot b \qquad \text{[S13]}$$

Selection gradients

As above, we write $W(\sigma^*, \sigma, \tilde{\sigma})$ for the fitness of a mutant female playing the strategy

$\sigma^* = (T^*, q^*, x^*)$ in a population where all other females play $\sigma = (T, q, x)$ and all males

play $\tilde{\sigma} = (\tilde{T}, \tilde{q}, \tilde{x})$. Similarly, $\widetilde{W}(\tilde{\sigma}^*, \sigma, \tilde{\sigma})$ is the fitness of a mutant male playing

$\tilde{\sigma}^* = (\tilde{T}^*, \tilde{q}^*, \tilde{x}^*)$. Selection gradients on female and male mutant strategies are then given

respectively by:

$$\beta = \frac{1}{W} \cdot \frac{\partial W(\sigma^*, \sigma, \tilde{\sigma})}{\partial \sigma^*} \bigg|_{\sigma^* = \sigma}$$

$$\text{and} \qquad \text{[S14]}$$

$$\tilde{\beta} = \frac{1}{\widetilde{W}} \cdot \frac{\partial \widetilde{W}(\tilde{\sigma}^*, \sigma, \tilde{\sigma})}{\partial \tilde{\sigma}^*} \bigg|_{\tilde{\sigma}^* = \tilde{\sigma}}$$
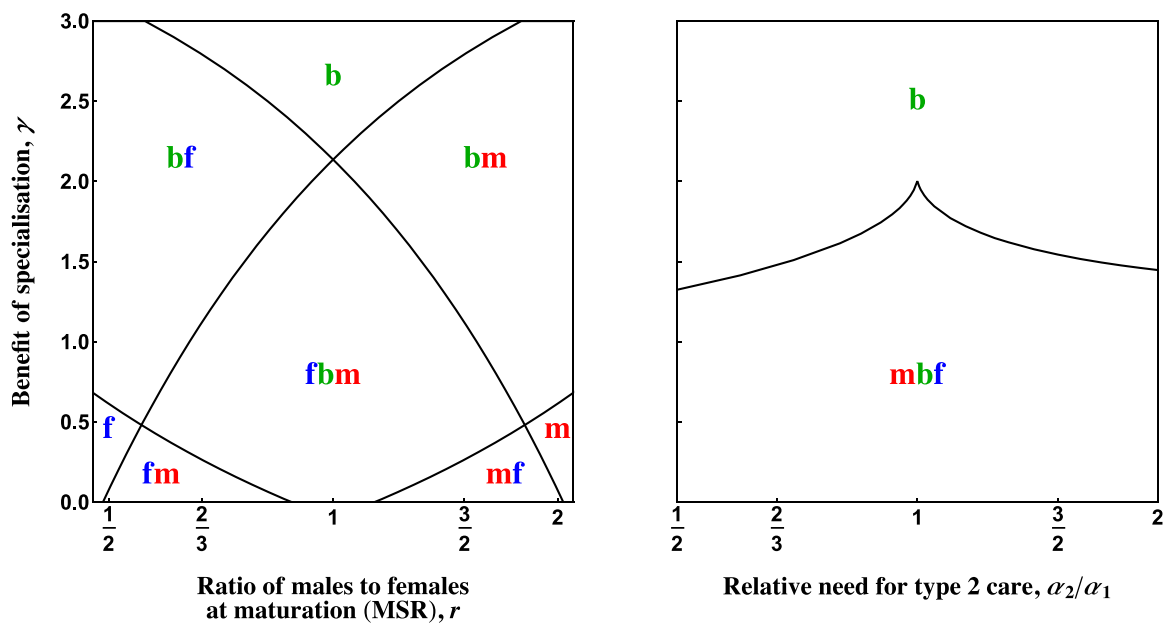
We calculated evolutionary trajectories based on the standard assumption that trait values

change at rates proportional to these gradients (in particular, this assumes weak selection, as

well as similar rates of mutational input and no genetic correlations among traits: [51]).

Evolution of sex roles when parentage is shared

All results in the main text assume serial monogamy ($n = \tilde{n} = 1$), where both males and

females have full parentage of the offspring they care for. Here we consider how these results

change when the parentage of a single brood is shared. We present results for the case of

mixed paternity ($n = 1$, $\tilde{n} > 1$), but results for mixed maternity ($\tilde{n} = 1$, $n > 1$) are completely symmetric, with only the identities of the sexes reversed. We assume that paternity is shared equally among all males contributing to a brood (i.e. sperm competition is a fair raffle). When paternity is shared, males necessarily gain parentage in a larger number of broods on average than females. This is captured in our model by an increase in male mating rate $\tilde{a} = Mx\tilde{x}\tilde{n}r_O^{-1/2}$ as the number of sires per brood $\tilde{n}$ increases. In line with previous studies [6,14,18], we find that mixed paternity selects for reduced male parental investment (Figure S2). This result manifests itself in two ways. First, the basin of attraction (i.e. the set of initial values leading to an equilibrium) is reduced for male-only care and enlarged for female-only care. Second, males provide less care at both male-only and biparental equilibria than they do under monogamy. As expected, the reduction in male care coincides with increased investment by males in mating competition.

Figure S1: Stability plot for female-only, male-only and biparental care, shown against variation in the benefits of specialisation γ (both panels), the sex ratio at maturity r (left panel), and the importance of type-2 care relative to type-1 care, α_2/α_1 (right panel). In each region, letters indicate which types of parental care can be stable (b = biparental, f = female, m = male). If ecological change causes a population to move from one parameter region to another, there are two possible outcomes: (1) if the letter representing the current equilibrium is still present in the new region, the current care system remains stable; (2) if the current letter is absent from the new region, the population transitions to the equilibrium represented by the *first-listed* letter in the new region. For example, if a biparental population moves to a region marked 'mf', then male-only care evolves. If a population with female-only care moves to a region marked 'bf', then female care remains stable. In general, biparental care evolves more easily when the benefits of specialisation γ are higher, whereas deviations from unity in the MSR can select for uniparental care by the more common sex. Shown with $\mu_{\min} = 0.01$, $n = \tilde{n} = 1$, $\alpha_1 = 0.1$ (both panels), $\alpha_2 = 0.1$ (left panel only), and $r = 1$ (right panel only).
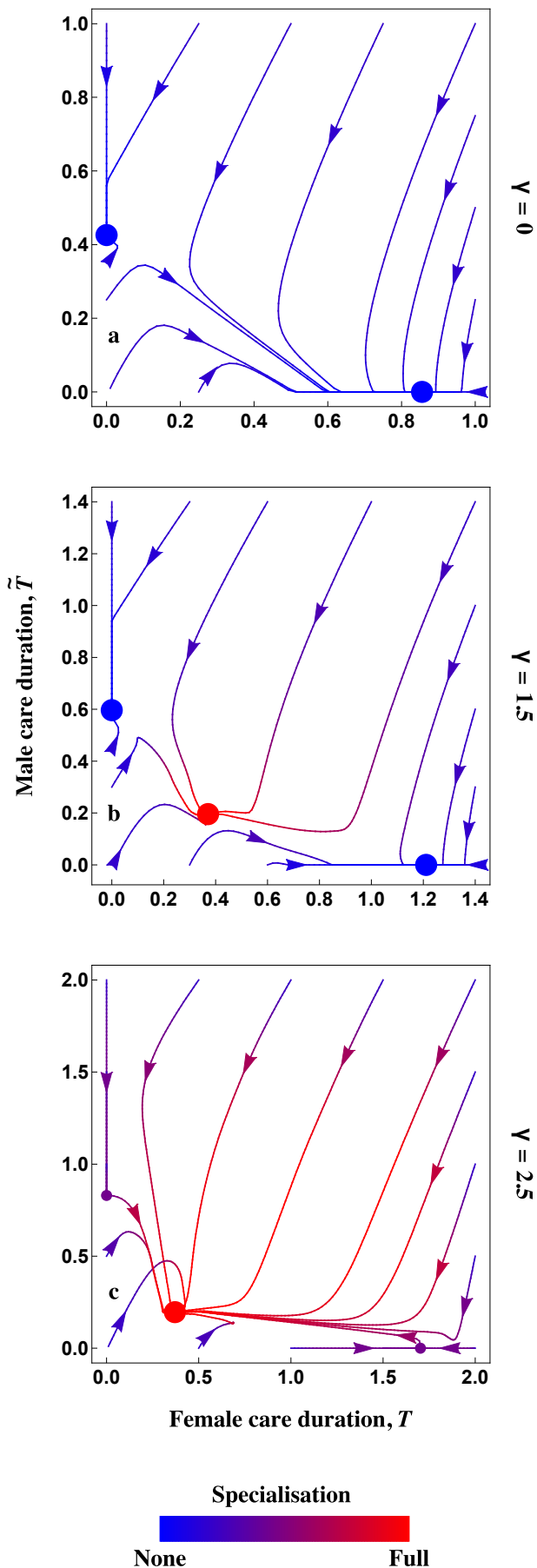
Figure S2: The evolution of care duration (T and $\tilde{T}$) and the average level of care specialisation (line colouring) when paternity is shared ($n = 1$, $\tilde{n} = 1.5$). All other parameter values are as in Figure 1 in the main text. Arrows indicate the direction of evolution. Large circles indicate globally stable equilibria; the smaller circles in panel **c** indicate locally stable equilibria that can be invaded by fully-specialised carers of the initially non-caring sex. Shared paternity selects for reduced male parental investment (cf. Figure 1 in the main text), manifested as reduced basins of attraction for male-only care, increased basins of attraction for female-only care, and reduced male parental investment at both male-only and biparental equilibria. The reduction in male care coincides with increased investment in mating competition (not shown).

Table 1: Summary of parameters and variables. Symbols marked with a tilde (like this: $\tilde{x}$) apply to males, whereas unmarked symbols apply to females.

Parameter	Description
$n, \tilde{n}$	Number of females or males that contribute gametes to each brood
$\mu_{\min}$	Minimum rate of mortality
M	Species-specific factor determining mating rate
r	Ratio of males to females at maturity (MSR)
α_1, α_2	Importance of care of type 1 or 2
γ	Benefits of specialisation
Variable	**Description**
$T, \tilde{T}$	Maximum duration of parental care
$q, \tilde{q}$	Proportion of parental investment devoted to type-1 care
$x, \tilde{x}$	Investment in mating trait
r_O	Operational sex ratio (ratio of males to female in time-in)
$a, \tilde{a}$	Mating rate
$\mu, \tilde{\mu}$	Mortality rate
S	Survival probability of offspring
$\tau_{\text{total}}, \tilde{\tau}_{\text{total}}$	Expected duration that an individual provides parental care, including care of both types
$\tau_i, \tilde{\tau}_i$	Effective contribution of an individual to care of type i (where $i = 1,2$)
$\tau_{1\,\text{all}}, \tau_{2\,\text{all}}$	Total care of type 1 or 2 received by a brood
$p_I, \tilde{p}_I$	Probability of surviving any given time-in
$p_O, \tilde{p}_O$	Probability of surviving any given time-out
$W, \widetilde{W}$	Fitness
$\beta, \tilde{\beta}$	Selection gradients on strategies (T, q, x) or $(\tilde{T}, \tilde{q}, \tilde{x})$