Supplementary Material

Evolution of male strategies with sex-ratio dependent payoffs:

connecting pair bonds with grandmothering

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1 Model

We model male reproductive strategies in a discrete model. A difference-equation model is employed to explore the effects of pair bonding, paternity stealing, and partner availability. Males are categorised based on their inherited reproductive strategies. We assume here that offspring fully inherit the strategy of their father. Three male strategies are modelled: dependant carers, P; multiple maters, M; mate guarders, which includes those searching for mates, S, and those actively guarding their mates, G. Division of males adopting a guarding strategy into those currently guarding mates and those searching for females to guard allows us to distinguish the number of unguarded and eligible females available for conception at each time step, as well as the number of actively searching males.

The population of eligible and available females (who are not currently guarded) is defined as F. As each guarding male is restricted to guarding one female (a restriction which can be later loosened), G also represents the number of guarded females. Thus the total population of females, guarded and unguarded, is given by $F + G$, and the total population of males is given by $P + M + S + G$. However, we define eligible males as those who are not currently guarding, which is the population of males actively looking for females to mate. This is represented by $\hat{M} = P + M + S$.

We model these strategies as pure strategies, with offspring inheriting the strategy of their fathers. In this way we model a system wherein we can track the fitness of each pure strategy, determining the overall benefit of each. Developing a model that incorporates switching between strategies would be a novel inclusion, but is beyond the scope of this investigation. This assumption of pure strategies further follows from the model developed in Schacht and Bell [2016].

A series of events happens at each time step. Let X_n be the population size of X, any given population, at a certain time $t = n\Delta t$. This indexes the population as it changes every generation, a time period of about 10 years. To calculate the dynamics that occur within each time step, let $X_{n,i}$ be the population size of X at each sub-step $i = 1, 2, 3, 4$ where the sub-steps represent the sequential events below:

1. Breaking pair bonds,

2. Mating events,

3. Death,

4. Offspring become adults.

In order to progress from $t = n\Delta t$ to $t = (n+1)\Delta t$, we must first go through each sub-step i in order. At $i = 4$, population sizes are assigned to the time step, $t = (n+1)\Delta t$.

We allow existing pair bonds to first be under pressure of break up. This changes the number of eligible males and females who can then re-enter the mating population. With these eligible populations, mating and reproduction occurs, then death. At the end of the time step, surviving offspring reach independence and transition to the eligible population.

Further, we seek to investigate the effect of the ASR on the long-term equilibrium strategy when grandmothering effectively removes females from the eligible pool. To achieve this removal, we impose sex-specific adult removal rates that are dependent on target ASRs.

A female-biased ASR is imposed with increased male removal rates, and vice versa. If male removal is higher than corresponding female removal, a female-biased population will result, and vice versa. This manipulation is distinct from empirical differences in mortality rates of the sexes, with mortality generally higher in males across the mammals including our closest primate cousins.

Pair bond breakup

For sub-step $i = 1$, guarded pairs can break up due to random effects. A specifically defined proportion of bonds are allowed to break up. This can be interpreted in terms of a male deciding to stop guarding a female and begin searching for another, or a female choosing to leave. However, from [Hawkes et al., 1995], we emphasize the interpretation of male-male competition. For mathematical simplicity, we parametrize pair-bond break up with a constant, β.

When pair-bond break up occurs, guarding males return to the searching compartment, and females return to eligibility. Thus at each step,

$$
\begin{aligned}
P_{n,1} &= P_n, \\
M_{n,1} &= M_n, \\
S_{n,1} &= S_n + \beta G_n, \\
G_{n,1} &= G_n - \beta G_n, \\
F_{n,1} &= F_n + \beta G_n.
\end{aligned}
$$

Multiple-mating and caring males do not undergo change at this intermediate time-step.

Mating

At each mating step, we first adjust searching and guarding populations by allowing new bonds to form. The probability that an eligible female gets guarded by a searching male is a frequency-dependent term $S_{n,1}/\hat{M}$. Thus, at this step, we have

$$
\begin{aligned}
P_{n,2} &= P_{n,1}, \\
M_{n,2} &= M_{n,1}, \\
S_{n,2} &= S_{n,1} - B_S(\mathbf{X}_{n,1}), \\
G_{n,2} &= G_{n,1} + B_S(\mathbf{X}_{n,1}), \\
F_{n,2} &= F_{n,1} - B_S(\mathbf{X}_{n,1}).
\end{aligned}
$$

To determine the number of paternities for males using each strategy at each time step, we define the number of paternities available to each strategy based on the number of females available, and the number of males actively searching for mates. Mating events depend on the number, F, of eligible females able to conceive at this time. We assume mating functions $B_i(\mathbf{X})$ for each actively searching population $i = P, M, S$, that are dependent on the vector of all populations, $\mathbf{X}$. These define the number of paternities for each strategy, prior to stealing by multiple maters.

Table 1 outlines the approximation of the mating functions used. This approximation is developed under the assumption that caring and guarding males are assigned females before multiple-mating males. In female-biased populations, we assume that the excess number of females present due to the female-biased sex ratio are assigned to multiple-mating males, since we are considering only social monogamy. In a male-biased situation, paternities are assigned as an average of the population. Each strategy gets a fraction of the available females, proportional to the number of males adopting each strategy.

The mating function defines the number of paternities assigned to each strategy, and can be interpreted as the probability of finding a female to mate. In female-biased populations, this birth function allows caring

Mating function, $B_i(X)$	Value when female-biased	Value when male-biased
$B_P(\mathbf{X})$	P	$F\frac{P}{\hat{M}}$
$B_S(\mathbf{X})$	S	$F\frac{S}{\hat{M}}$
$B_M(\mathbf{X})$	$F-P-S$	$F\frac{M}{\hat{M}}$

Table 1: Mating function used, constructed with different frequency-dependent paternity payoffs, where $\hat{M} = P + S + M$, the total population of actively searching males.

males and guarders to obtain paternities prior to multiple maters. Caring and guarding males are 'first-in-line' for paternities. The construction given in Table 1 outlines the birth function used in this model. The remaining paternities are assigned to multiple maters, as they are able to mate multiply. In the case of a male-biased sex ratio, paternities are assigned proportionally to each of the searching categories of male strategies, P, M, S.

Parameters of paternity stealing are also introduced, with multiple-mating males given the opportunity to steal the paternities of caring and guarding males. Assuming that paternities of the offspring of carers' and guarders' mates can be stolen by multiple maters, we denote the proportion of paternities stolen by multiple maters as k_i where $i = P, G$ denotes the total paternities of those mates. We define ϵ_i, where $i = P, G$, as the availability of paternities to stealing by multiple-mating males. This value is restricted to between $[0, 1]$, as its interpretation corresponds to the availability of corresponding females that are taken by multiple-mating males. The paternities of a given female are fully susceptible to multiple-mating males when $\epsilon_i = 1$, and completely unavailable when $\epsilon_i = 0$. An alternative interpretation of this parameter is that it indicates guarding efficiency. If ϵ_G is high, this corresponds to low guarding efficiency, and so $(1 - \epsilon_G)$ can be interpreted as the guarding effectiveness.

Thus, the probability that the offspring of a given strategy has been sired by a multiple-mating male is,

$$k_i = \frac{\epsilon_i M}{1 + \epsilon_i M}.$$

This corresponds to the proportion of paternities assigned to the guarding or caring strategies, that are stolen by multiple-mating males. By its mathematical definition, $k_i \in [0, 1]$.

This is a simplification of the cuckoldry term used in Schacht and Bell [2016]. Rather than using a transition matrix to calculate the probability that a caring male is caring for a mate's offspring without his paternity, we simplify this to a straightforward variable parameter dependent on female availability, as described above.

Given that k_P and k_G are representations of the proportion of paternities sired by multiple-mating males, we adjust the offspring born to each strategy by these values. Thus, the number of paternities for males using each strategy is given by, $C_{n,2}^X$, where $X = P, M, G$. We further break up offspring born to multiple-mating males into those who receive care benefits from being brought up by caring males, $C^{M,P}$, and those who receive no such benefit, including those whose mothers are mated by guarding males, $C^{M,G/M}$. Therefore,

$$C_{n,2}^G = bG_{n,2}(1 - k_G),$$
$$C_{n,2}^P = bB_P(\mathbf{X}_{n,1})(1 - k_P),$$
$$C_{n,2}^{M,P} = bB_P(\mathbf{X}_{n,1})k_P,$$
$$C_{n,2}^{M,G/M} = bB_M(\mathbf{X}_{n,1}) + bG_{n,2}k_G,$$

where b is the probability that a female gives birth in the time step, and k_i is the proportion of paternities stolen by multiple maters from each strategy $i = P, G$.

Death/removal

Death occurs at sub-step $i = 3$ and is defined by adult mortality/removal rate, r_A, and immature mortality rate, r_C. Further, immature mortality is modified if a dependant is cared for by a caring male. Given these mortality/removal rates the probability of death, μ_A and μ_C can be determined, assuming an exponential distribution. Survival is determined by $(1 - \mu_i)$ where i is either adult, A, or immature, C. We further distinguish

male and female death/removal rates in order to impose changes to the adult sex ratio. By setting a target sex ratio, and adjusting female removal rate by this target sex ratio, we manipulate the female removal rate in order to obtain different adult sex ratios at equilibrium. This is given by

$$\mu_{A,m} = 1 - \exp\left(-r_A \cdot \Delta t\right),$$
$$\mu_{A,f} = 1 - \exp\left(-r_A \cdot \text{SR} \cdot \Delta t\right).$$

Figure S1: Male and female probability of removal, $\mu_{A,m}$ or $\mu_{A,f}$, according to target sex ratios.

Guarding males whose female mates die (or leave the population), return to searching, and females paired with guarding males who die (or leave the population) return to eligibility. Thus, populations are defined at this sub-step by

$$P_{n,3} = (1 - \mu_{A,m})P_{n,2},$$
$$M_{n,3} = (1 - \mu_{A,m})M_{n,2},$$
$$S_{n,3} = (1 - \mu_{A,m})S_{n,2} + \mu_{A,f}(1 - \mu_{A,m})G_{n,2},$$
$$G_{n,3} = (1 - \mu_{A,m})(1 - \mu_{A,f})G_{n,2},$$
$$F_{n,3} = (1 - \mu_{A,f})F_{n,2} + (1 - \mu_{A,f})\mu_{A,m}G_{n,2}.$$

Further, juveniles are also subject to mortality rates, and their survival is also dependent on the survival of their mother:

$$C_{n,3}^G = (1 - \mu_C)(1 - \mu_{A,f})C_{n,2}^G,$$
$$C_{n,3}^P = (1 - \mu_{PC})(1 - \mu_{A,f})C_{n,2}^P,$$
$$C_{n,3}^M = (1 - \mu_C)(1 - \mu_{A,f})C_{n,2}^{M,G/M} + (1 - \mu_{PC})(1 - \mu_{A,f})C_{n,2}^{M,P}.$$

The mortality rate of paternally cared dependants is modified by a parameter of benefit of care, c. The value of the benefit of care is defined between 0 and 1, with $c = 0$ corresponding to equal survival of the offspring of caring males with the offspring of guarding and multiple mating males, and $c = 1$ corresponding to the juvenile immortality of the offspring of caring males. We define the benefit of dependant care as restricted to the juvenile years.

We assume that care benefit, c, alters the rate of mortality, r_c, by a factor of $(1 - c)$. Then the probability of dependant survival can be expressed as

$$1 - \mu_{PC} = 1 - (1 - \exp\left[-r_{PC}\Delta t\right])$$
$$= \exp\left[-r_c(1 - c)\Delta t\right]$$
$$= (\exp\left[-r_c\Delta t\right])^{1-c}$$
$$= (1 - \mu_C)^{1-c}.$$

Offspring become eligible

This sub-step corresponds to recruitment to the mating population, children becoming adults. Thus, half of each child compartment still alive at sub-step $i = 3$ moves to adult male compartments. We assume the other

Parameter	Assumption	
	Our model	S & B model
Care, c	Care benefits the survival of juveniles. Females can only have one offspring per time step, whose survival depends on her mate's strategy.	Care increases the birth rate of females, resulting in a larger number of surviving offspring. Females can have one to two surviving offspring per time step.
Theft of paternities from caring males, ϵ_P or k	ϵ_P defines the availability of the paternities of carers' mates' offspring to theft by multiple maters.	Cuckoldry, k, of the paternities of paternally caring males by multiple-mating males.
Theft of paternities from guarding males, ϵ_G	Guarding inefficiencies modelled in a similar way to the theft of paternities from caring males.	No theft. Guarding provides certainty of paternity.
Pair bond breakup, β	Guarding pairs break up at a constant rate.	Pairs remain together until death.

Table 2: Table summarising and comparing assumptions and parameters used within the difference-equation model developed here and the model developed by Schacht and Bell [2016].

half become adult females. Full strategy inheritance is also assumed. Therefore the difference equations are given by

$$P_{n+1} = P_{n,3} + \frac{1}{2}C_{n,3}^P,$$

$$M_{n+1} = M_{n,3} + \frac{1}{2}C_{n,3}^M,$$

$$S_{n+1} = S_{n,3} + \frac{1}{2}C_{n,3}^G,$$

$$G_{n+1} = G_{n,3},$$

$$F_{n+1} = F_{n,3} + \frac{1}{2}\left(C_{n,3}^P + C_{n,3}^M + C_{n,3}^G\right).$$

These are the population values of the next time step.

If we combine all sub-steps the full dynamics of the system are given by the difference equations

$$P(t + \Delta t) = (1 - \mu_{A,m})P(t) + \frac{b}{2}(1 - \mu_{C,m})^{1-c}(1 - \mu_{A,f})B_P(\mathbf{X})(1 - k_P),$$

$$M(t + \Delta t) = (1 - \mu_{A,m})M(t) + \frac{b}{2}(1 - \mu_{C,m})(1 - \mu_{A,f})\left[B_M(\mathbf{X}) + k_G B_S(\mathbf{X})\right]$$

$$+ \frac{b}{2}(1 - \mu_{C,m})^{1-c}(1 - \mu_{A,f})\left[B_P(\mathbf{X})k_P\right],$$

$$S(t + \Delta t) = (1 - \mu_{A,m})\left[S(t) + \beta G(t) - B_S(\mathbf{X})\right] + \mu_{A,f}(1 - \mu_{A,m})\left[G(t) - \beta G(t) + B_S(\mathbf{X})\right]$$

$$+ \frac{b}{2}(1 - \mu_{C,m})(1 - \mu_{A,f})\left[B_S(\mathbf{X}) + G(t) - \beta G(t)\right],$$

$$G(t + \Delta t) = (1 - \mu_{A,m})(1 - \mu_{A,f})\left[G(t) - \beta G(t) + B_S(\mathbf{X})\right],$$

$$F(t + \Delta t) = (1 - \mu_{A,f})\left[F(t) + \beta G(t) - B_S(\mathbf{X})\right] + \mu_{A,m}(1 - \mu_{A,f})\left[G(t) - \beta G(t) + B_S(\mathbf{X})\right]$$

$$+ \frac{b}{2}\left[(1 - \mu_{C,f})(1 - \mu_{A,f})\left\{G(t) - \beta G(t) + B_S(\mathbf{X}) + B_M(\mathbf{X})\right\}\right.$$

$$\left. + (1 - \mu_{C,f})^{1-c}(1 - \mu_{A,f})B_P(\mathbf{X})\right],$$

where $B_i(X)$, with $i = P, S, M$, represent the birth function of each strategy and X is the vector of strategies in the population, $\mathbf{X} = (P, M, S, G, F)$.

2 Further sensitivity analyses

Benefit of care and potential of theft from caring males

As highlighted in the main text, care only persists in populations at near equal sex ratios and where carers have certain paternity, i.e., stealing of paternities does not occur ($\epsilon_P = 0$). This can be seen in the top right panel of Figure S2, where $\epsilon_P = 0$ and care persists around a near equal sex ratio. Once theft is introduced with $\epsilon_P = 0.2$ in the panel below, this region disappears.
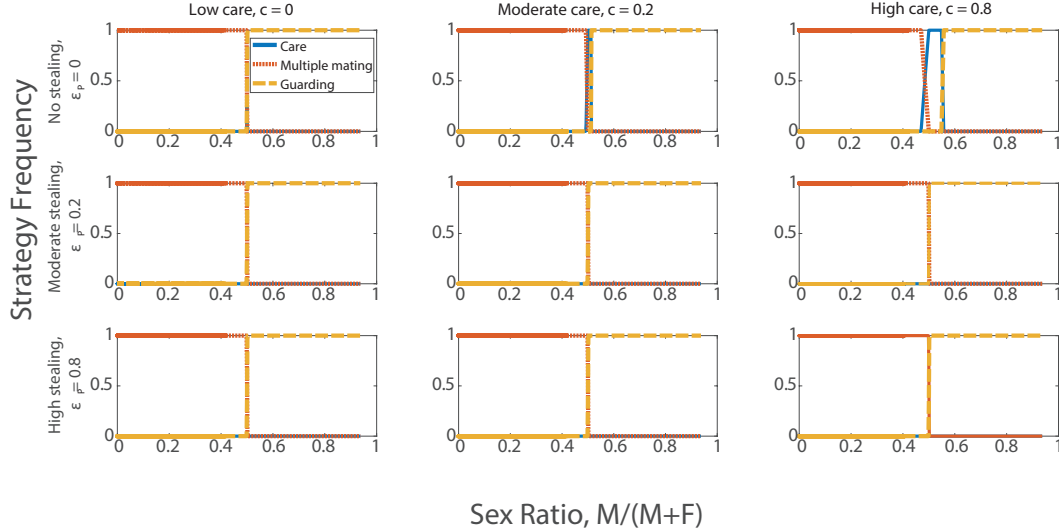

Figure S2: The effect of different parameters of the benefit of care on the equilibrium strategies given different sex ratios, fully efficient guarding ($\epsilon_G = 0$), and low pair bond breakup ($\beta = 0.1$). In the top right panel, care persists in a small region of ASRs around an equal sex ratio. In all other parameter sets, multiple mating persists at female-biased sex ratios (ASR< 0.5), and guarding wins at all male-biased sex ratios (ASR ≥ 0.5).

If inefficient guarding is introduced, comparing Figure S2 to Figure S3, we note that care can win at lower survival benefits, c, than in the case of fully efficient guarding, and also in very male-biased populations. This can be seen in comparing the top row of Figure S2 with the top row of Figure S3. Care wins for larger regions in Figure S3 than in the top row of Figure S2. However, as was described in the main text, we note that the first row represents an unrealistic case, where $\epsilon_G > \epsilon_P$, meaning that the mates of guarding males are more available than that of caring males. In these cases, care wins as it mimics the effects of guarding. We present the results here in Figure S3 to show the equilibrium strategies for a range of different parameter values.

Further, in the right column of Figure S3, care wins over strategies of multiple mating and guarding at male-biased sex ratios. However, upon further inspection of these populations, it is found that given these parameter values, these populations have progressed to extinction. Thus, the persistence of care does not accurately represent the takeover of this strategy.

Theft by multiple mating males

Further investigation of different parameter choices demonstrates the effect of varying availabilities of paternities to theft by multiple mating males. Qualitative behaviour is similar for both low and high levels of care benefit, seen in Figure S4 and S5 respectively. The first column of Figure S4 shows that care persists only where $\epsilon_G > \epsilon_P$; the paternities of guarded females are more available to theft than that of caring males. Again, this smuggles guarding effects into care, as described in the main text and in the definition of parameters given in the model description. The left column of Figure S5 also demonstrates this. If counter to our definitions, $\epsilon_G \geq \epsilon_P$, i.e., caring supplies higher paternity assurance than guarding, then care can persist in a close to equal sex ratio.
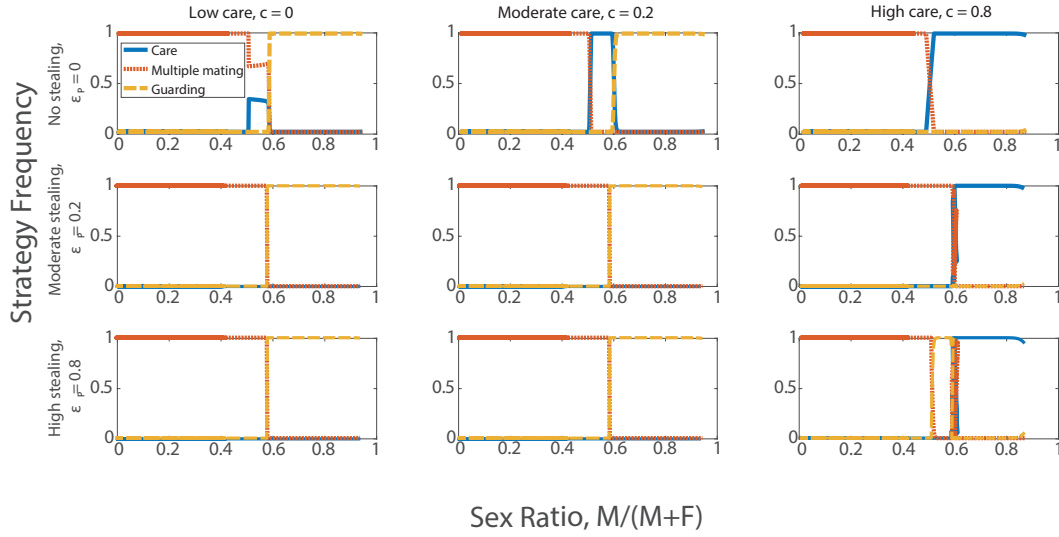
Figure S3: The effect of different parameters of the benefit of care on the equilibrium strategies given different sex ratios, inefficient guarding ($\epsilon_G = 0.1$), and low pair bond breakup ($\beta = 0.1$). Here, where theft from guarders occurs, the benefit to guarding is smaller than in Figure S2 and thus, care persists in all cases where theft from carers does not occur ($\epsilon_P = 0$, in the top row). In the right column, care also persists in male-biased ASRs, but further investigation shows that these populations are extinct and are therefore not considered.
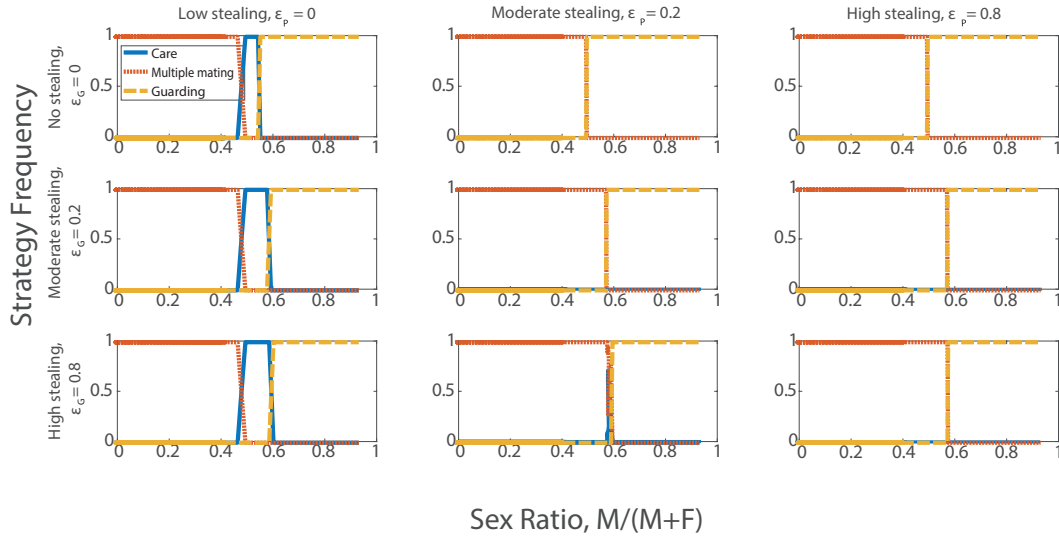

Figure S4: The effect of the availability of the paternities of females to theft by multiple-mating males. High, moderate, and low availabilities, ϵ_P and ϵ_G, are presented. Other parameters are that of $c = 0.8$ (or high survival benefit to care), and low pair bond breakup ($\beta = 0.1$). The left panels show persistence of care, where theft from carers does not occur ($\epsilon_P = 0$). In the other panels, multiple mating wins in female-biased populations, and guarding wins at male-biased. The ASR at which the switch between these winning strategies occurs is dependent on how available the paternities of offspring of mates of guarding males are to theft by multiple maters, ϵ_G.

Guarding inefficiencies

For parameter sets exploring the effect of guarding inefficiencies, β and ϵ_G, multiple mating is the persistent strategy at female-biased sex ratios, and guarding is the persistent strategy at very male-biased sex ratios. This can be seen in Figures S6 and S7. The panels on the right of Figure S6 show care persisting at very male-biased populations, but further exploration of these long-term equilibria show that these populations are extinct. When the size of the total population is close to 0, care is a winning strategy as it produces surviving juveniles, when levels of care benefit are high, as is the case of Figure S6, but not Figure S7 (comparing the right column of Figure S6, where care is high, $c = 0.8$, with that of Figure S7, where care is low, $c = 0.2$).
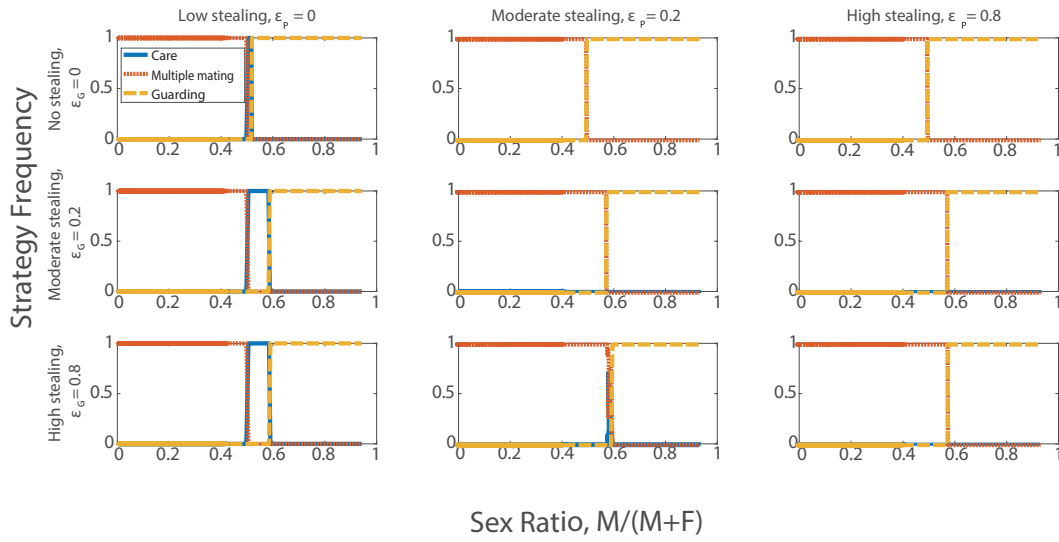
Figure S5: The effect of availability of paternities to theft by multiple maters. Different combinations of high, moderate, and low availabilities, ϵ_P and ϵ_G, are presented. Other parameters are low care benefit ($c = 0.1$), and low pair bond breakup ($\beta = 0.1$). Where care here is low, the region within which care persists in the left column, is smaller than that of Figure S4. Again, in the other panels, multiple mating wins in female-biased populations, and guarding wins at male-biased. The ASR at which the switch between these winning strategies occurs is dependent on how available the paternities of offspring of mates of guarding males are to theft by multiple maters, ϵ_G.

Further, the higher the availability of the paternities of guarders' mates' offspring to theft by multiple maters, the higher the ASR at which guarding takes over the population. This is further explored in Figure 3 of the main text.
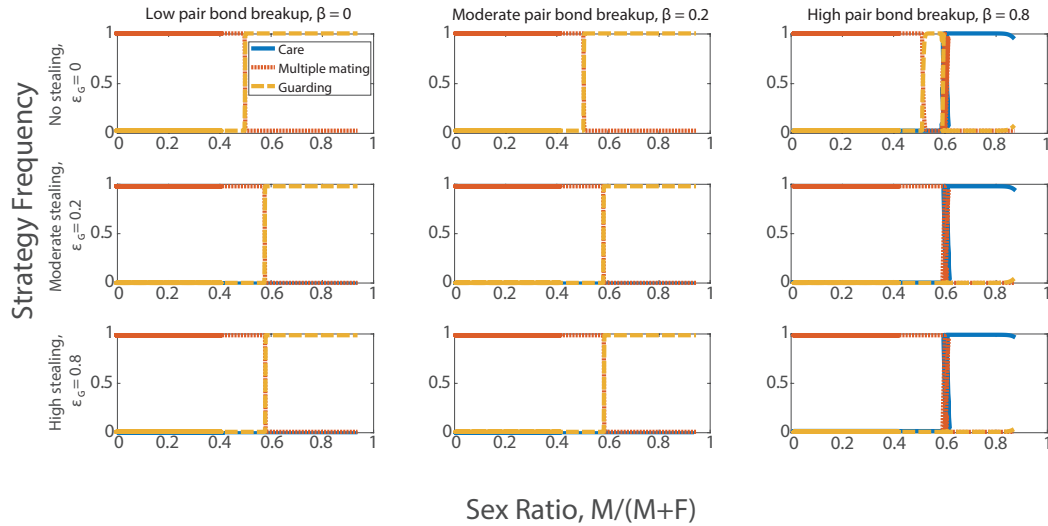

Figure S6: The effect of changes to parameters of guarding inefficiency, at high care benefit ($c = 0.8$). Different combinations of parameters quantifying pairbond break up, β, and theft of paternities from guarders, ϵ_G, are presented. The right column shows care persisting at male-biased ASRs, but further investigation into the populations show extinction. For other combinations of parameter regions, multiple mating wins when female-biased, and guarding persists when male-biased.

References

Ryan Schacht and Adrian V Bell. The evolution of monogamy in response to partner scarcity. *Scientific Reports*, 6, 2016.
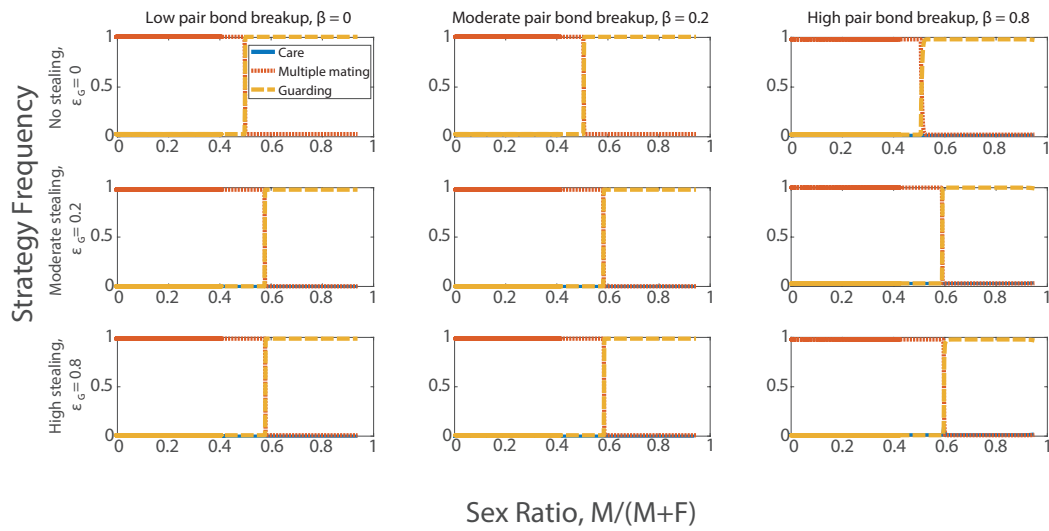
Figure S7: The effect of changes to parameters of guarding inefficiency, at low care benefit ($c = 0.2$). Different combinations of parameters quantifying pairbond break up, β, and theft of paternities from guarders, ϵ_G, are presented. Where care is lower, and theft of the paternities of carer's mates' offspring is high, multiple mating persists in all female-biased populations, and guarding in all male-biased populations.

Kristen Hawkes, Alan R Rogers, and Eric L Charnov. The male's dilemma: increased offspring production is more paternity to steal. *Evolutionary Ecology*, 9(6):662–677, 1995.