Supporting Information

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Supporting Text

A Game-Theoretical Analysis of Reproductive Conflict Under Female-Biased Dispersal. Suppose that two females of an older and a younger generation are in competition over shared resources that can support their reproductive efforts. We model this competition using the "tug-of-war" game of Reeve *et al.* (1), which is commonly used to analyze reproductive conflict in cases where each party may exert partial control over the outcome (2, 3). Each female can invest in competitive acts to increase her personal share of the communal resource but only at the cost of depleting the total amount of resource to be shared. This cost reflects the time and/or energy expended on selfish competition that could otherwise be used in cooperative endeavor. Specifically, writing o and y for the competitive effort of the older and younger female, respectively, we assume that total reproductive success of the pair declines with total effort expended on selfish behavior ($o + y$), whereas the shares of reproduction obtained are $o/(o + by)$ for the older female, and $by/(o + by)$ for the younger female, where b is a positive, non-zero constant that reflects the relative competitive ability of the younger female; it is likely that $b \leq 1$, implying that the older female obtains a larger fraction of the resource for a given expenditure of effort, i.e., that she is behaviorally dominant (although we allow for the possibility of a dominant younger female).

In *The Basic Model*, we construct a basic model and present analytical results for the simple case where all females disperse from their natal group to breed and there is no extrapair paternity. In *Relaxing the Assumptions*, we present the results of an extended model in which these assumptions are relaxed.

The basic model. The inclusive fitness payoffs to the two females, I_o and I_y, assuming that both are unrelated themselves but that the older female is related to the younger female's children via her son, are given by

$$I_o(o, y) = \frac{o}{o + by}(1 - o - y) + \frac{1}{2}\left(\frac{by}{o + by}\right)(1 - o - y)$$

$$= (1 - o - y)\left(\frac{1}{2}\left(1 + \frac{o}{o + by}\right)\right) \quad \textbf{[1]}$$

$$I_y(o, y) = (1 - o - y)\left(\frac{by}{o + by}\right). \quad \textbf{[2]}$$

Here, we show that, given the above payoffs, the older female may be expected (regardless of her degree of behavioral dominance, i.e., of the value of b) to refrain from reproduction. In other words, she should commit to zero competitive effort, allowing the younger female to claim all direct reproduction at negligible cost. This is an example of an "endogenous" or "natural" Stackelberg solution in which both players prefer to act in sequence, and both agree on who should move first (3-5). The key difference between a sequential and simultaneous game is one of information: in a sequential game, the second mover can observe the effort level of the first mover before deciding on its response. In a simultaneous game, by contrast, both plays submit blind "sealed bids," i.e., they have no advance information of the action of the other player. Endogenous Stackelberg equilibria are interesting from a biological perspective because they can explain the evolution of commitment strategies that are profitable precisely because they cannot credibly be changed (3, 6). Thus, in the stable Stackelberg solution to the current model, the older female's first move of zero investment is advantageous only if it is perceived to be irreversible by the younger female. We note that permanent sterility as a consequence of rapid reproductive senescence is an effective way for an older female to commit credibly to a first move of zero investment in reproduction.

If the older female commits to some competitive investment o as a first move, the younger female's optimal investment in competition [found by maximization of $I_y(o,y)$] is given by

$$\hat{y}(o) = \frac{1}{b}\left(\sqrt{o(o + (1 - o)b)} - o\right). \quad \textbf{[3]}$$

From this we obtain the payoff to the older female, $I_o[o,\hat{y}(o)] = (1 - o)/2$, which reveals that she does best to commit to zero competitive effort (regardless of the relative competitive ability b of the younger female), allowing the younger female to claim all available reproduction at negligible cost. This leads to a payoff of 1 for the younger female, and ½ for the older female.

If both players make simultaneous sealed bids [as in the analysis of Reeve *et al.* (1)], the stable levels of investment in competition, o^* and y^*, each of which maximizes the relevant player's payoff given the other's investment, are given by

$$o^* = \frac{(2 + b)\sqrt{b(8 + b)} - b(8 + b)}{2(8 - b(7 + b))} \quad \textbf{[4]}$$

$$y^* = \frac{(8 + b) - 3\sqrt{b(8 + b)}}{2(8 - b(7 + b))}. \quad \textbf{[5]}$$

The payoff to the younger female given these values, $I_y(o^*,y^*)$, is always less than 1, and the payoff to the older female, $I_o(o^*,y^*)$, is always less than one half. Thus, both players do worse than if the older female moves first (as described above).

Finally, if the younger female commits to some competitive investment y as a first move, the older female's optimal investment in competition [found by maximization of $I_o(o,y)$] is given by

$$\hat{o}(y) = \begin{cases} \sqrt{\frac{1}{2}by(1 - (1 - b)y)} - by, & \text{for } y < \frac{1}{1 + b} \\ 0, & \text{for } y \geq \frac{1}{1 + b} \end{cases}. \quad \textbf{[6]}$$

From this we obtain the payoff to the younger female,

$$I_y(\hat{o}(y), y) = \begin{cases} \sqrt{2by(1 - (1 - b)y)} - by, & \text{for } y < \frac{1}{1 + b} \\ 1 - y, & \text{for } y \geq \frac{1}{1 + b} \end{cases}. \quad \textbf{[7]}$$

Maximization of the above expression reveals that if the younger female moves first she does best to commit to a level of effort

$$y_1 = \begin{cases} \frac{(2 - b) - \sqrt{b(2 - b)}}{2(2 - b(3 - b))}, & \text{for } b < 1 \\ \frac{1}{1 + b}, & \text{for } b \geq 1 \end{cases} \quad \textbf{[8]}$$

This once again leads to a payoff for the younger female, $I_y[\hat{o}(y_1),y_1]$ that is always less than 1, and a payoff for the older female, $I_o[\hat{o}(y_1),y_1]$ that is always less than ½. So once again, both players do worse than if the older female moves first.

Given the above results, it pays both players to allow the older female to move first and commit to zero competitive effort, following which the younger female will claim all direct reproduction at negligible cost. The equilibrium solution preferred by both players, in other words, is for the older female to cede reproductive status to the younger.

Relaxing the assumptions: An extended model. In this section, we explore the consequences of relaxing the assumptions of zero extrapair paternity and strict female dispersal. We solve for the stable levels of competitive effort and examine the relative stability of the sequential versus simultaneous forms of the game.

Let p denote the probability that a female's offspring is fathered by an extrapair male who is unrelated to any of the other group members. With probability s females stay in their natal group to breed: s is therefore the probability that the older female is the mother of the younger female. We assume for simplicity that the schedule of reproductive investment depends on average sex-specific population rates of dispersal and is not adjusted facultatively to the particular social environment in which an individual finds itself. This is a common assumption in patch-structured genetic models (7-9) and is reasonable in the absence of evidence for facultative adjustment at an individual level (although we do not rule out the possibility of such adjustment).

Given these assumptions the inclusive fitness payoff to the older female is

$$\bar{I}_o(o, y) = (1 - s)I_o(o, y) + sI_m(o, y) \quad [9]$$

where $I_o(o,y)$ is the inclusive fitness payoff of an older female in a group in which the younger female is an immigrant, and $I_m(o,y)$ is the inclusive fitness payoff to a mother in reproductive conflict with her daughter. These two functions are given by

$$I_o(o, y) = \frac{o}{o + by}(1 - o - y) + \frac{1 - p}{2}\left(\frac{by}{o + by}\right)(1 - o - y)\,. \quad [10]$$

and

$$I_m(o, y) = \frac{o}{o + by}(1 - o - y) + \frac{1}{2}\left(\frac{by}{o + by}\right)(1 - o - y)\,, \quad [11]$$

Averaging across social contexts in which an allele present in a younger female might find itself, the inclusive fitness payoff to the younger female is

$$\bar{I}_y(o, y) = (1 - s)I_y(o, y) + sI_d(o, y). \quad [12]$$

where $I_y(o,y)$ is defined in Eq. **2**, and $I_d(o,y)$ is the inclusive fitness payoff to a daughter in reproductive conflict with her mother, given by

$$I_d(o,y) = \frac{by}{o + by}(1 - o - y) + \left(1 - \frac{p}{2}\right)\left(\frac{o}{o + by}\right)(1 - o - y) \quad [13]$$

This formulation assumes that the rate of extrapair paternity is the same for older and younger females and that philopatric females mate with unrelated males from outside the group.

The extended model does not yield simple analytical solutions, so we solve using numerical methods and present graphical results for illustrative cases. First, we calculate the equilibrium values of o and y for three cases: (*i*) where the older female commits to a first move; (*ii*) where both females choose their level of competitive effort simultaneously; and (*iii*) where the younger female commits to a first move. We then calculate the inclusive fitness payoff to both females for these three cases. If both females prefer to act sequentially rather than simultaneously and both agree on the order of play, the outcome is a natural Stackelberg equilibrium (as in the basic model above). If one or both players prefer to act simultaneously or both prefer to adopt the same role in a sequential game, the stable outcome is the simultaneous sealed-bid equilibrium (3, 10).

The results of varying the rate of extrapair paternity on the stable levels of effort are shown in SI Fig. S1. Assuming that all females disperse to breed, we find that where $p < 1$, both players still favor an equilibrium in which the older female commits to a first move, but in this case her best effort is greater than zero. Thus, for $0 < p < 0.5$, the model predicts that the older female should commit to low reproductive effort in the face of reproductive competition from the younger female.

The effects of varying the rate of female philopatry (while holding extrapair paternity at zero) are shown in SI Fig. S2. Increasing s has a similar effect on the stable efforts invested in reproduction as does increasing p. In the example shown, however, there is a threshold level of female philopatry above which the older female no longer prefers to commit to a first move and instead gains a higher payoff in the simultaneous game. In this region, the stable outcome is for both females to submit simultaneous sealed bids (but note that even in this region the younger female's stable effort exceeds that of the older female).

Finally, we explore the interaction between the effects of variation in extrapair paternity and variation in female philopatry. In SI Fig. S3, we plot the location of the critical female philopatry threshold s_{crit} as a function of the level of extrapair paternity p, for different values of the strength parameter b. Below the plotted threshold, the stable outcome is for the older female to commit to low reproductive effort as a first move; above the threshold players revert to simultaneous bids. For $b \geq 1$ (i.e., where the younger female is at least as strong as the older female), the natural Stackelberg solution in which the older female commits to low reproductive effort as a first move holds even when dispersal is only slightly female-biased. For lower values of b, however, the region for which the natural Stackelberg solution holds becomes progressively smaller. A combination of relatively high s and low b can, therefore, render the sequential equilibrium unstable given some degree of extrapair paternity. However, provided that younger females are of comparable competitive ability to older females, older females will commit to low reproductive effort in the face of reproductive competition, even when dispersal is only mildly female-biased.

To summarize, a formal analysis suggests that a pattern of female-biased dispersal gives females of a younger generation a decisive advantage in reproductive conflict with older females. For a large region of parameter space, the stable solution is for older females to commit to zero or low reproductive effort when females of the next generation start to breed. Reproductive conflict under female-biased dispersal, therefore, is predicted to lead to an evolutionary separation of reproductive generations of the kind observed in humans.

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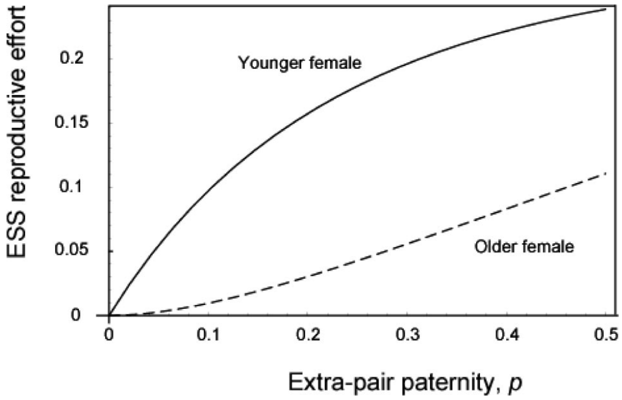

Fig. S1. Evolutionarily stable best efforts of an older and a younger female in a stable sequential game as a function of the level of extrapair paternity p. In the example shown, we assume that all females disperse ($s = 0$), and the older female obtains a larger fraction of the resource for a given expenditure of effort (specifically $b = 0.9$).

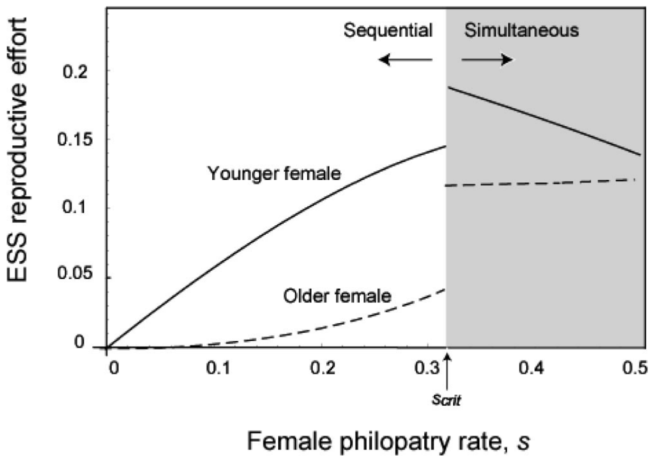

Fig. S2. Stable best efforts of an older and a younger female as a function of the female philopatry rate *s.* Above a threshold level of female philopatry s_{crit}, the sequential solution is unstable because the older female no longer prefers to commit to a first move (other parameters: $b = 0.9$; $P = 0$).

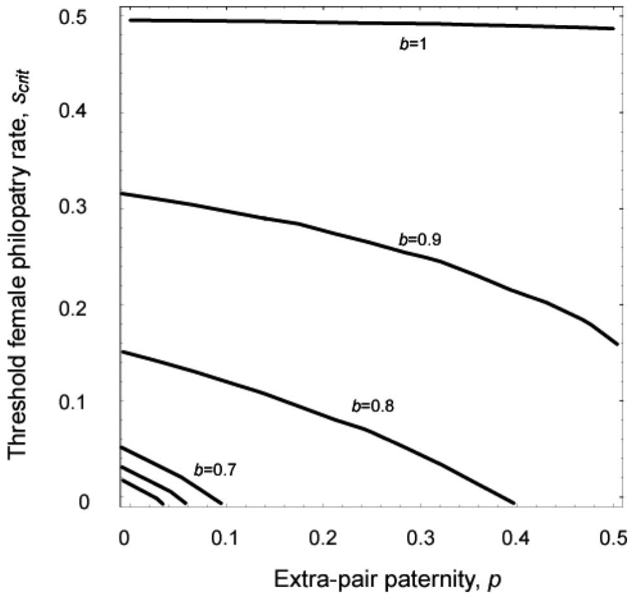

Fig. S3. Threshold level of female philopatry s_{crit} below which the sequential Stackelberg equilibrium is stable, as a function of extrapair paternity rate and the relative competitive strength of the younger female. Above this threshold, the stable solution to the game involves each player making simultaneous sealed bids.