

A Model for Evolution of Male Parental Care and Female Multiple Mating

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ABSTRACT: In most animals, males gain a fitness benefit by mating with many females, whereas the number of progeny per female is unlikely to increase as a function of additional mates. Furthermore, males of internally fertilizing species run the risk of investing in offspring of other males if they provide parental care. Nevertheless, males of many avian species and a minority of mammalian species provide parental care, and females of various species mate with multiple males. I investigate a two-locus genetic model for evolution of male parental care and female multiple mating in which females gain a direct benefit by multiple mating from the paternal care they thereby elicit for their offspring. The model suggests that, first, male parental care can evolve when it strongly enhances offspring survival and the direct costs of female multiple mating (e.g., loss of energy, risk of injury, exposure to infectious diseases) are greater than its indirect benefit (e.g., acquisition of good genes, increased genetic diversity among offspring); second, female multiple mating can evolve when paternal care is important for offspring survival or the indirect benefit of multiple mating is larger than its direct cost; and, finally, male parental care and female multiple mating can co-occur.

Keywords: breeding system, extrapair paternity, mating system, paternal care, polyandry.

The relative amounts of parental care provided by males and females influence the evolution of mating systems and the intensity of sexual selection (Trivers 1972). In the majority of animal species, males gain a fitness benefit by mating with many females, whereas the reproductive success of females is limited primarily by the number of their ova (Bateman 1948). Besides this, males of internally fertilizing species run the risk of investing in offspring that are not their own if they provide parental care (Trivers

1972). As a consequence, in most mammals, females provide a substantial amount of parental care, including lactation, while males mate polygynously and provide no parental care. Nevertheless, males as well as females of many avian species and a minority of mammalian species do care for their offspring (Clutton-Brock 1991). In addition, male parental care is also documented in ectotherms such as insects (e.g., Smith 1979), fish (Blumer 1979), and frogs (Wells 1981). Moreover, it is known that females of various species actively mate with multiple males (Smith 1988; Birkhead 1998; Gomendio et al. 1998).

Male parental care may be selected for when it improves the survivorship of offspring. Since time and energy are limited, however, a trade-off between parental effort and mating effort exists (Smith 1995; Magrath and Elgar 1997). Hence, the evolutionary outcome is believed to depend on the relative magnitudes of the importance of male parental care for offspring survival and the loss of mating opportunities due to provision of care (Maynard Smith 1977). The importance of male parental care for the survival of young has been investigated in various species of monogamous birds (Bart and Tornes 1989; Mock and Fujioka 1990; Møller 2000). In mammals, male parental care is often seen in carnivores, rodents, and primates (Woodroffe and Vincent 1994). The importance of paternal care is demonstrated in the California mouse (*Peromyscus californicus*; Gubernick et al. 1993; Cantoni and Brown 1997; Gubernick and Teferi 2000) and the Djungarian hamster (*Phodopus campbelli*; Wynne-Edwards 1987).

There may be both indirect (or genetic) and direct benefits of female multiple mating (Halliday and Arnold 1987; Reynolds 1996). Note that female multiple mating is defined here as a female mating with more than one male and does not refer to mating repeatedly with a single male. The indirect benefits of female multiple mating, including acquisition of good genes and increased genetic diversity among offspring, have been investigated intensively in birds (Yasui 1998). The good-genes hypothesis states that females mate with multiple males to acquire sperm from genetically superior males (e.g., Kempenaers et al. 1992; Hasselquist et al. 1996), while the genetic-diversity hy-

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pothesis posits that females can increase their reproductive success by increasing genetic diversity among their offspring in an unpredictable environment (e.g., Ligon and Zwartjes 1995).

Compared with indirect benefits, less attention has been paid to the direct benefits of female multiple mating although the latter may possibly generate strong selection, particularly in those species in which male parental care is important for offspring survival. In such species, females may compete for the finite amount of parental care provided by males. If this is the case, female multiple mating may be favored because females can thereby increase the number of potential caregivers (Stacey 1982; Kempnaers 1993). Sussman and Garber (1987) argued, for example, that female promiscuity in tamarins and marmosets may be a means to obtain caring males for their offspring.

Even if female multiple mating is selected for by such a direct benefit, however, it will not necessarily evolve. Suppose that, in a strictly monogamous species with biparental care, a mutant female occurs that mates with more than one male. If offspring of such a female receive more paternal care than offspring of strictly monogamous females, the frequency of this mutant will increase in the population. Once female multiple mating becomes prevalent, however, it may no longer pay for males to provide parental care since paternity of a caring male is lowered. Consequently, males may withdraw their parental care and, hence, the direct benefit of female multiple mating will be diminished.

To understand either the evolution of male parental care or female multiple mating, it is necessary to consider both phenomena simultaneously. Harada and Iwasa (1996) and Iwasa and Harada (1998) developed game-theoretic models in which females modify the paternity to maximize the amount of parental care provided by males. These models assume, however, that the opportunity cost of a male is independent of the strategies adopted by other individuals in the population (see "Discussion"). Kokko (1999) analyzed an evolutionarily stable strategy (ESS) model for the evolution of cuckoldry and paternal care in which such frequency dependence is incorporated. However, her model does not consider the possibility that females can increase the number of potential caregivers by multiple mating.

In this article, I formulate a two-locus genetic model to investigate the simultaneous evolution of male parental care and female multiple mating in which the cost of male parental care (i.e., loss of mating opportunity) and the direct benefit of female multiple mating (i.e., increasing number of potential caregivers) depend on the frequencies of the strategies in both sexes. Female multiple mating may also entail such direct costs as loss of energy, risk of injury, and/or exposure to infectious diseases. My model

suggests, first, that male parental care is likely to evolve when it strongly enhances offspring survival and the direct cost of female multiple mating is greater than its indirect benefit; second, that female multiple mating can evolve when paternal care is essential for offspring survival or the indirect benefit of multiple mating outweighs its direct cost; and, finally, that male parental care and female multiple mating can be maintained in a polymorphic state.

The Model

The model assumes a population of haploid organisms for the sake of simplicity. Although there may be cases where diploidy would alter the outcome, those are not common (Maynard Smith 1982, pp. 40–53; Grafen 1991). Changes in gene frequencies at two autosomal diallelic loci are of interest. The first locus, X , which is expressed only in females, governs female mating behavior. An X_1 female mates with only one male, while an X_2 female mates with k males ($k > 1$). I assume that mating decisions are made exclusively by females. Since female multiple mating entails direct costs, the probability that an X_2 female gives birth to offspring and raises them successfully is reduced to $1 - s$ relative to that for an X_1 female ($s \geq 0$). Specifically, $1 - s$ is the relative viability of the offspring of a polyandrous female in the absence of paternal care. I will also consider the case of $s < 0$, which corresponds to the case when indirect benefits of female multiple mating are so large as to outweigh the direct costs. The allele frequencies of X_1 and X_2 are denoted by $1 - x$ and x .

The second locus, Y , which is expressed only in males, determines male parenting behavior. A Y_1 male mates polygynously and does not care for offspring. A Y_2 male also mates polygynously but stays with one of his mates chosen at random, if he has any, and cares for her offspring. Male parental care is provided at the expense of mating effort so that a Y_2 male mates with $1 - c$ times fewer females than a Y_1 male does, where c represents the cost of lost mating opportunities due to paternal care ($0 < c < 1$). Male care enhances offspring survival so that offspring cared for by males is $1 + bm$ times more likely to survive relative to offspring without paternal care, where b represents the importance of male parental care for offspring survival ($b > 0$) and m is the expected number of caring males for each offspring (see below in this section). It is assumed that the amount of parental care provided by males is independent of their paternity in the offspring. The allele frequencies of Y_1 and Y_2 are denoted by $1 - y$ and y . I assume that females limit the number of matings and males mate with as many females as possible. Sex ratio is assumed to be unity. Generations are discrete, and there is no age structure.

The life history is as follows. First, matings occur. The

number of matings for each mating type is shown in table 1. It is assumed that there are N males and N females in the population, where N is very large but not necessarily constant across generations. Since each X_1 female mates once and each X_2 female mates k times, the total number of matings is $N\alpha$, where $\alpha = 1 - x + kx$. As a result of the difference in mating effort between Y_1 and Y_2 males, the former participates in a fraction, $(1 - y)/\beta$, of these matings, while for the latter the fraction is $(1 - c)y/\beta$, where $\beta = 1 - y + (1 - c)y$. The number of matings a Y_2 male gives up as the cost of parental care is $c\alpha/\beta$ on average (see table 1), which is an increasing function of x and y . Frequencies of haplotypes X_1Y_1 , X_1Y_2 , X_2Y_1 , and X_2Y_2 are denoted by u_1 , u_2 , u_3 , and u_4 , respectively ($u_1 + u_2 + u_3 + u_4 = 1$). Thus, we have

$$x = u_3 + u_4, \tag{1a}$$

$$y = u_2 + u_4, \tag{1b}$$

$$D = u_1u_4 - u_2u_3, \tag{1c}$$

where D is the linkage disequilibrium.

Second, females breed and raise offspring with or without the assistance of males. Let m_{ij} be the expected number of caring males for offspring from an X_i - Y_j mating (a mating of an X_i female and a Y_j male). There are two cases to be distinguished. (1) When $(1 - c)\alpha/\beta < 1$, each Y_2 male mates at most once. Some Y_2 males never mate and, hence, do not provide any care. In this case, offspring of an X_1 - Y_2 mating are always cared for by the Y_2 male because the female is his only mate ($m_{12} = 1$). Offspring of an X_2 - Y_1 mating may be cared for by Y_2 males with whom the female has mated. Thus, $m_{21} = k \times$ (proportion of matings in which Y_2 males participate). Offspring of an X_2 - Y_2 mating may be cared for by the Y_2 male and/or other Y_2 males with whom the female has mated. The expected number of caring males is the same as for offspring of an X_2 - Y_1 mating ($m_{21} = m_{22}$). (2) When $(1 - c)\alpha/\beta \geq 1$, however, every Y_2 male mates at least once and, hence, all of them provide care. In this case, offspring of an X_1 - Y_2 mating is cared for by the Y_2 male with probability $1/(\text{number of mates per } Y_2 \text{ male})$, since the Y_2 male cares for offspring

of one of his mates chosen randomly. Offspring of an X_2 - Y_1 mating and of an X_2 - Y_2 mating can be cared for by Y_2 males with whom the female has mated: $m_{21} = m_{22} = k \times$ (proportion of matings in which Y_2 males participate)/(number of mates per Y_2 male). In either case, offspring from an X_1 - Y_1 mating do not receive any paternal care because the female has mated monogamously with a male who provides no parental care ($m_{11} = 0$). Each m_{ij} is calculated from table 1 separately for the above two cases (table 2).

Multiple mating by a female increases the number of potential caregivers. The excess number of caring males for an X_2 female compared with an X_1 female is $(1 - c)(k - 1)y/\beta$ if $(1 - c)\alpha/\beta < 1$, and $(k - 1)y/\alpha$ otherwise (see table 2). Note that the former is an increasing function of y and the latter increases with y and decreases with x . Assuming that the number of fertilized eggs per female is independent of the number of her mates and that paternity is equal among males that share a mate, the frequency of surviving offspring from each mating is obtained as shown in table 3, where $\phi_1 = 1 + bm_{12}$ and $\phi_2 = (1 - s)(1 + bm_{21}) = (1 - s)(1 + bm_{22})$.

From table 3, the haplotype frequencies in the next generation, u'_1 , u'_2 , u'_3 , and u'_4 , are

$$u'_1 = \frac{u_1}{2\bar{w}} [1 - x + \phi_2x + 1 - y + (1 - c)\phi_1y] - R, \tag{2a}$$

$$u'_2 = \frac{u_2}{2\bar{w}} [(1 - c)\phi_1(1 - x) + (1 - c)\phi_2x + 1 - y + (1 - c)\phi_1y] + R, \tag{2b}$$

$$u'_3 = \frac{u_3}{2\bar{w}} [1 - x + \phi_2x + \phi_2(1 - y) + (1 - c)\phi_2y] + R, \tag{2c}$$

$$u'_4 = \frac{u_4}{2\bar{w}} [(1 - c)\phi_1(1 - x) + (1 - c)\phi_2x + \phi_2(1 - y) + (1 - c)\phi_2y] - R, \tag{2d}$$

Table 1: Number of matings for each mating type

Female	Male				Total
	X_1Y_1	X_1Y_2	X_2Y_1	X_2Y_2	
X_1Y_1	Nu_1^2/β	$Nu_1u_2(1 - c)/\beta$	Nu_1u_3/β	$Nu_1u_4(1 - c)/\beta$	Nu_1
X_1Y_2	Nu_2u_1/β	$Nu_2^2(1 - c)/\beta$	Nu_2u_3/β	$Nu_2u_4(1 - c)/\beta$	Nu_2
X_2Y_1	kNu_3u_1/β	$kNu_3u_2(1 - c)/\beta$	kNu_3^2/β	$kNu_3u_4(1 - c)/\beta$	kNu_3
X_2Y_2	kNu_4u_1/β	$kNu_4u_2(1 - c)/\beta$	kNu_4u_3/β	$kNu_4^2(1 - c)/\beta$	kNu_4
Total	$Nu_1\alpha/\beta$	$Nu_2(1 - c)\alpha/\beta$	$Nu_3\alpha/\beta$	$Nu_4(1 - c)\alpha/\beta$	$N\alpha$

Note: $\alpha = 1 - x + kx$; $\beta = 1 - y + (1 - c)y$.

where

$$\bar{w} = (1 - x)[1 - y + (1 - c)\phi_1 y] + \phi_2 x \beta, \quad (2e)$$

$$R = \frac{r}{2\bar{w}} \{u_1 u_4 [(1 - c)\phi_1 + \phi_2] - u_2 u_3 [1 + (1 - c)\phi_2]\}, \quad (2f)$$

and r is the recombination fraction between the two loci ($0 \leq r \leq 1/2$). Equations (1) and (2) allow us to trace the per-generation change of the allele frequencies, x and y , and the linkage disequilibrium, D .

Case 1: $s = 0$

First, consider the simplest case that assumes no indirect benefit or direct cost of female multiple mating (i.e., $s = 0$). A line of equilibria and two equilibrium points exist, which are given below in the form of $(\hat{x}, \hat{y}, \hat{D})$. The results of local stability analysis are also given.

1. The set of points $(\hat{x}, 0, 0)$ ($0 \leq \hat{x} \leq 1$) forms a line of equilibria. When $c < b/(1 + b)$, the segment of the line ($x^* \leq \hat{x} \leq 1$) is neutrally stable (the maximum eigenvalue equals unity), where

$$x^* = \begin{cases} \frac{b - c}{b + c(k - 1)} & \text{if } c < \frac{b(k - 1)}{(1 + b)k - 1} \\ \frac{b - (1 + b)c}{b(1 - c)} & \text{if } c \geq \frac{b(k - 1)}{(1 + b)k - 1}. \end{cases} \quad (3)$$

The other part of the line is unstable. When $c \geq b/(1 + b)$, the entire line is neutrally stable.

- 2. $E_2(0, 1, 0)$ is always unstable.
- 3. $E_3(1, 1, 0)$ is always unstable.

Figure 1 shows the equilibria and the directions of change in the allele frequencies. The three-dimensional space is projected on to the xy -plane. The arrows indicate the directions of change in allele frequencies on the left, right, and upper boundaries of the unit square ($0 \leq x \leq 1, 0 \leq y \leq 1$). Numerical analysis suggests that there are no other equilibria and that the neutrally stable segment

Table 2: Expected number of caring males for offspring of each mating

Female	Male			
	If $(1 - c)\alpha/\beta < 1$		If $(1 - c)\alpha/\beta \geq 1$	
	Y_1	Y_2	Y_1	Y_2
X_1	0	1	0	$\beta/[(1 - c)\alpha]$
X_2	$(1 - c)ky/\beta$	$(1 - c)ky/\beta$	ky/α	ky/α

of the line of equilibria is globally stable. An example of the numerical analysis is shown in figure 2.

From the above analysis, two inferences can be drawn. First, male parental care never evolves. Although the Y_2 allele can increase temporarily, it is always eliminated at equilibrium. Second, polymorphism can be maintained at the X locus. Hence, monandrous and polyandrous females can coexist at equilibrium. It is obvious, however, that these results depend heavily on the assumption $s = 0$ because, in this case, female multiple mating is evolutionarily neutral when no males provide parental care (i.e., $y = 0$). This assumption may be rather unrealistic. As shown below, a minimal amount of cost on female multiple mating can change the results drastically.

Case 2: $0 < s < 1$

Now I introduce a cost to female multiple mating into the model. Any indirect benefit of female multiple mating is assumed so small as not to confer a net advantage. Five equilibrium points are found analytically in this case:

- 1. $E_0(0, 0, 0)$ is stable if and only if

$$c > \frac{b}{1 + b}; \quad (4)$$

- 2. $E_1(1, 0, 0)$ is always unstable;
- 3. $E_2(0, 1, 0)$ is stable if and only if

$$c < \frac{b}{1 + b} \quad \text{and} \quad s > \frac{b(k - 1)}{1 + bk}; \quad (5)$$

- 4. $E_3(1, 1, 0)$ is always unstable; and
- 5. $E_4(b\{[k(1 - s) - 1] - s\}/[(k - 1)s], 1, 0)$ exists if and only if

$$\frac{b(k - 1)}{(1 + b)k} < s < \frac{b(k - 1)}{1 + bk}. \quad (6)$$

Given that it exists, it is stable if and only if

$$s > \frac{(k - 1)[b + c(k - 1)]}{(1 + b)k + c(k - 1)^2}. \quad (7)$$

The outcome of the model can be classified into seven distinct patterns, as shown in figure 3 according to the parameter values (see appendix for details). No two of the five corner or edge equilibria described above are stable at the same time. Numerical work suggests that whenever an equilibrium point is locally stable it is also globally stable and that whenever none of the five equilibria is stable there is a stable internal equilibrium. An example of the numerical work is shown in figure 4.

When the cost of male parental care is small relative to its benefit, specifically

$$c < \frac{b}{1+b} \quad (8)$$

holds, y reaches a polymorphic equilibrium (fig. 3A, 3C) or converges to 1 (fig. 3E, 3F). Hence, male parental care evolves in this case. Provided (8), it can be shown that when s is sufficiently small, x reaches a polymorphic equilibrium (fig. 3A, 3C, 3E); otherwise x converges to 0 (fig. 3F). Hence, female multiple mating can be maintained if its direct cost is small. When (8) does not hold, however, the cost of male parental care is large relative to its benefit. In this case, both x and y converge to 0 (fig. 3B, 3D, 3G), and, hence, neither male parental care nor female multiple mating evolve.

The mating systems predicted by the model can be classified into four groups. (1) Figure 3F: All males provide parental care and all females mate with only one male each. Since sex ratio is unity and all males have equal chance to mate, monogamy with biparental care is predicted. (2) Figure 3E: Some females mate with more than one male while others mate monogamously. Since every male stays with a female to provide care, the predicted mating system is social monogamy with extrapair paternity associated with biparental care. (3) Figure 3A and 3C: Both male parental care and female multiple mating are maintained in a polymorphic state. The predicted mating system is a mixture of monogamy with biparental care (with or without extrapair paternity) and polygamy without paternal care. (4) Figure 3B, 3D, and 3G: No male provides care and no female mates polyandrously. Hence, monogamy without paternal care is predicted.

In stark contrast to case 1 (i.e., $s = 0$), male parental care can be maintained and sometimes goes to fixation. Since X_2 females suffer a cost, x decreases when the caring males are rare (i.e., y is small) and this results in a greater paternity for Y_2 males so that male parental care can be favored. In spite of the cost, female multiple mating can be maintained in a polymorphic state. In contrast to case

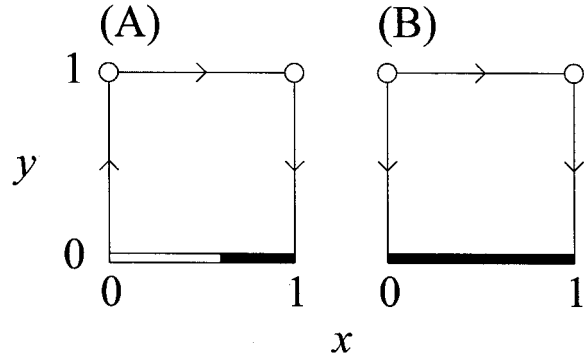


Figure 1: The equilibria and the directions of change in the allele frequencies when $s = 0$. Three-dimensional space is projected onto the xy -plane. Arrows indicate directions of change on the boundaries. The thick line ($y = 0$) represents the line of equilibria, the filled region of which is neutrally stable. Empty circles are unstable equilibrium points. A, $0 < c < b/(1+b)$. B, $b/(1+b) < c < 1$. Examples shown are for the parameter values $b = 0.8$, $k = 2$; for A, $c = 0.2$; for B, $c = 0.6$.

1, the equilibrium is not a neutrally stable line but a globally stable point, at which the cost of female multiple mating is counterbalanced by the improved survival of their offspring due to paternal care.

Case 3: $s < 0$

Finally, I consider the case when the indirect benefit of female multiple mating outweighs its direct cost. Four equilibria are observed: $E_0(0, 0, 0)$ is always unstable; $E_1(1, 0, 0)$ is always stable; $E_2(0, 1, 0)$ is always unstable; and $E_3(1, 1, 0)$ is always unstable.

Numerical work suggests that $E_1(1, 0, 0)$ is always globally stable. Since females always gain a benefit from multiple mating, x increases even when y is small and converges to 1. This leads to a lower paternity for Y_2 males so that male parental care is not favored. Thus, paternal care never evolves, and all females mate with more than one male. The predicted mating system is promiscuity.

Table 3: Frequency of surviving offspring for each mating type

Female	Male				Total
	X_1Y_1	X_1Y_2	X_2Y_1	X_2Y_2	
X_1Y_1	u_1^2	$u_1u_2(1-c)\phi_1$	u_1u_3	$u_1u_4(1-c)\phi_1$	$u_1[1-y+(1-c)\phi_1y]$
X_1Y_2	u_2u_1	$u_2^2(1-c)\phi_1$	u_2u_3	$u_2u_4(1-c)\phi_1$	$u_2[1-y+(1-c)\phi_1y]$
X_2Y_1	$u_3u_1\phi_2$	$u_3u_2(1-c)\phi_2$	$u_3^2\phi_2$	$u_3u_4(1-c)\phi_2$	$u_3\phi_2\beta$
X_2Y_2	$u_4u_1\phi_2$	$u_4u_2(1-c)\phi_2$	$u_4u_3\phi_2$	$u_4^2(1-c)\phi_2$	$u_4\phi_2\beta$
Total	$u_1(1-x+\phi_2x)$	$u_2[\phi_1(1-x)+\phi_2x](1-c)$	$u_3[1-x+\phi_2x]$	$u_4[\phi_1(1-x)+\phi_2x](1-c)$	$(1-x)[1-y+(1-c)\phi_1y]+\phi_2x\beta$

Note: $\phi_1 = 1 + bm_{12}$; $\phi_2 = (1-s)(1 + bm_{21}) = (1-s)(1 + bm_{22})$.

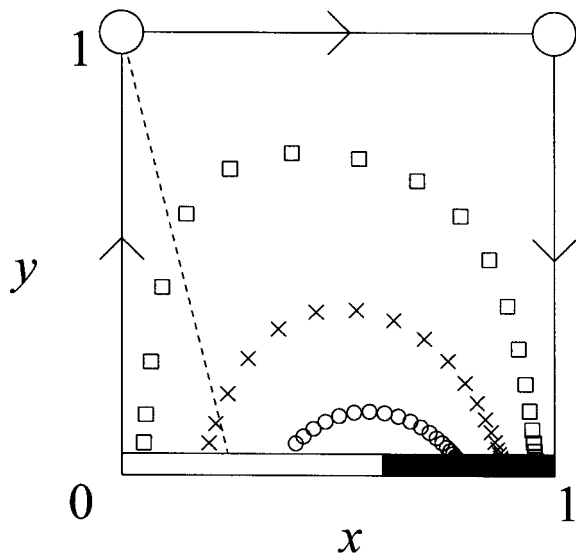


Figure 2: A numerical analysis of the case $s = 0$. Sample trajectories are plotted at intervals of five generations. The broken line represents the boundary between the two cases distinguished in table 2, below which $(1 - c)\alpha/\beta < 1$. Each trajectory starts from $y = 0.05$, $D = 0$, and (squares) $x = 0.05$; (crosses) $x = 0.2$; (circles) $x = 0.4$. The parameter values are $b = 0.8$, $c = 0.2$, $k = 2$, and $r = 0.5$.

Discussion

The model investigated in this article suggests that male parental care is likely to evolve when it improves the survivorship of offspring and the direct costs of female multiple mating (e.g., loss of energy, risk of injury, exposure to infectious diseases) are large enough to overwhelm its indirect benefits (e.g., acquisition of good genes, increased genetic diversity among offspring). It is also suggested that female multiple mating can be favored when male parental care is important for offspring survival or the indirect benefits of female multiple mating are greater than its direct costs. Furthermore, the model indicates that both male parental care and female multiple mating can be maintained simultaneously.

When there are no indirect benefits or direct costs of female multiple mating, male parental care never evolves (case 1). Female multiple mating is maintained in a polymorphic state as an evolutionarily neutral trait (fig. 1). When the cost of female multiple mating is incorporated, however, the outcome is altered drastically (case 2). In this case, the evolutionary consequences are primarily dependent on the relative magnitudes of the importance of male parental care for offspring survival, b , and the cost of lost mating opportunities due to paternal care, c (fig. 3). When b is large relative to c (i.e., eq. [8]), both male parental care and female multiple mating may evolve, whereas nei-

ther is favored with a small b . When the indirect benefit of female multiple mating is large enough to outweigh its direct cost, the outcome is again entirely different (case 3). In this case, male parental care is always eliminated while female multiple mating always prevails.

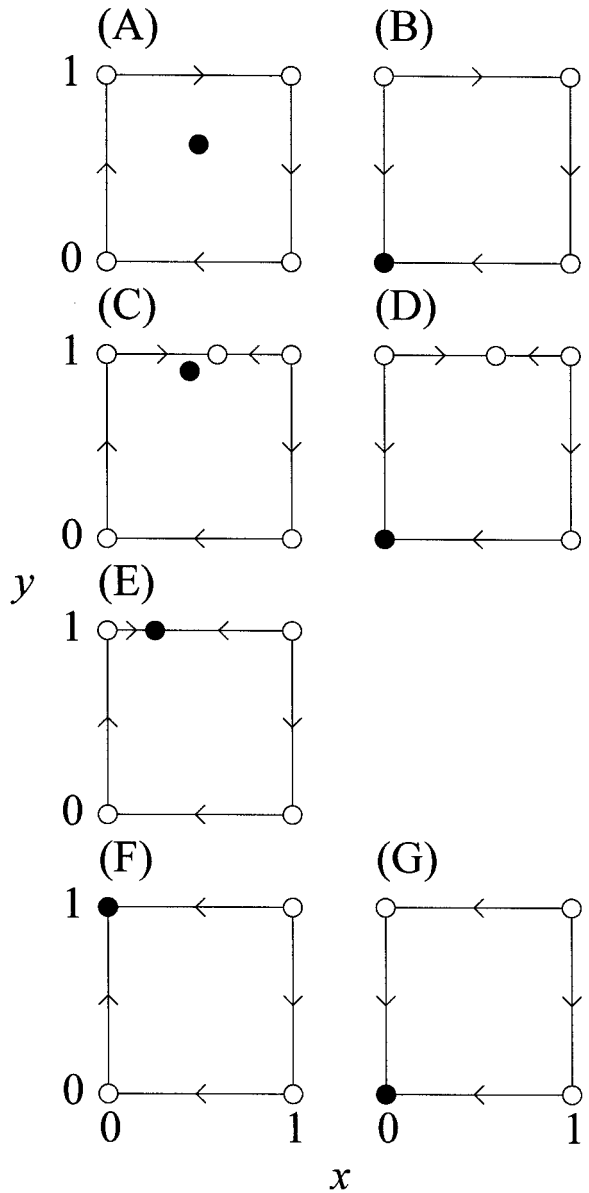


Figure 3: The equilibria and the directions of change in the allele frequencies when $0 < s < 1$. Empty and filled circles represent unstable and stable equilibrium points, respectively. The outcome of the model can be classified into seven patterns according to the parameter values (see appendix for details). The examples shown are for the parameter values $b = 0.8$, $k = 2$, $r = 0.5$; for A, $c = 0.2$, $s = 0.2$; for B, $c = 0.6$, $s = 0.2$; for C, $c = 0.2$, $s = 0.25$; for D, $c = 0.6$, $s = 0.25$; for E, $c = 0.2$, $s = 0.28$; for F, $c = 0.2$, $s = 0.4$; and for G, $c = 0.6$, $s = 0.4$.

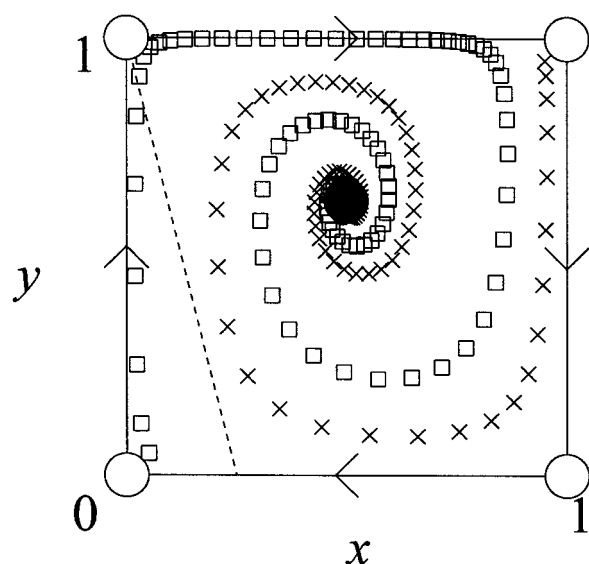


Figure 4: A numerical analysis of the case $0 < s < 1$. Sample trajectories are plotted at intervals of five generations. The broken line represents the boundary between the two cases distinguished in table 2, below which $(1 - c)\alpha/\beta < 1$. Each trajectory starts from $D = 0$. Squares, $x = y = 0.05$; crosses, $x = y = 0.95$. The parameter values are the same as in figure 3A: $b = 0.8$, $c = 0.2$, $k = 2$, $r = 0.5$, $s = 0.2$.

Female Multiple Mating

This model indicates that the evolutionary outcome concerning female multiple mating is primarily dependent on the magnitude of its indirect benefit. That is, female multiple mating is most likely to evolve when its indirect benefit is large relative to its direct cost (i.e., $s < 0$). This is consistent with a comparative study (Petrie et al. 1998) that found a positive correlation between the level of extrapair paternity and the amount of genetic variability across bird species. As they claimed, the amount of genetic variability can be a measure of indirect benefits for females from extrapair mating, since if there is little variation in genetic quality among males such indirect benefits will be diminished (Petrie and Lipsitch 1994).

However, the model also indicates that female multiple mating can sometimes evolve even when the indirect benefit of female multiple mating is negligible (fig. 3A, 3C, 3E). This is because the direct benefit of female multiple mating (i.e., increasing number of potential caregivers) can outweigh its direct cost provided that the importance of male care for offspring survival is sufficiently large.

Male Parental Care

The model indicates that the evolution of male parental care is restricted to the case when the direct cost of female

multiple mating is large relative to its indirect benefit (i.e., $s > 0$). When $s \leq 0$, the frequency of females that mate with multiple males exceeds a certain threshold above which expected paternity for a male is too low to permit male care to evolve. This, together with the indication that female multiple mating is most likely to evolve when $s < 0$, is in line with comparative studies among avian species (Møller and Birkhead 1993; Møller and Cuervo 2000) in which negative correlations between male contribution to feeding offspring and the frequency of extrapair paternity were found.

With regard to species in which females gain a considerable amount of indirect benefit from multiple mating, my model predicts that males do not provide parental care unless there is also a large direct cost to female multiple mating. A large cost of female multiple mating may be given rise to by a male response against that behavior. Westneat and Sherman (1993) investigated a static optimization model for the effect of parentage on the evolution of parental behavior. They distinguished two mechanisms by which a parent responds to reduced parentage in the offspring. On one hand, if individuals are able to assess their parentage, they may adjust their parental effort accordingly (facultative response). If individuals cannot assess the parentage, on the other hand, the level of parental effort may be modified through evolutionary time (non-facultative response). In this model, since I assume a trade-off between a male's parental effort and mating effort, the latter mechanism works as a necessity, whereas the former is not formulated explicitly. Male facultative response may work as a large direct cost of female multiple mating and, as a result, may play a role in the evolution of male parental care (see Gowaty 1996). Indeed, a theoretical work by Kokko (1999) supports this contention.

There may be some other factors that can encourage the evolution of male parental care. First, males may be able to control the behavior of their mates and/or other males to prevent the paternity from being lowered (i.e., mate guarding). If so, expected paternity for a male can be kept high so that male care may evolve even when $s \leq 0$. Second, if females prefer to mate with those males who are willing to care for their offspring, such males may obtain a larger number of mates than those who do not provide paternal care. Third, in some species, individuals may imitate behavior of their parents (i.e., cultural transmission; see Cavalli-Sforza and Feldman 1981). If a male is more likely to imitate the behavior of his social father, who provides parental care for him but may not be genetically related to him, than that of his biological father, who shares genes with him but does not provide care, male caring behavior will be transmitted more efficiently to the next generation than in this model, in which male

behavior is assumed to be determined genetically. Further theoretical work taking such effects into account is needed.

*Coexistence of Male Parental Care and
Female Multiple Mating*

Iwasa and Harada (1998) developed a game model in which females allocate the paternity in order to obtain the maximum amount of paternal care. It was suggested that each female mates exclusively with one male at the evolutionarily stable state given that males provide any parental care (See also Harada and Iwasa 1996). Their results are in contrast to those of my model, in which both male parental care and female multiple mating can be maintained simultaneously at equilibrium (fig. 3A, 3C, 3E). This may be due to frequency-dependent selection included in my model. Iwasa and Harada (1998) assumed that the cost of paternal care depends only on the amount of care, while in my model, it depends on the frequencies of the strategies in both sexes (i.e., x and y). Analogously, Webb et al. (1999) extended models of mate desertion that assume a constant remating probability for a deserting male (Maynard Smith

1977, model 2; Maynard Smith 1982, pp. 126–130). They found that a mixed-strategy ESS, which is never observed in the original models, can emerge when the remating probability is frequency-dependent (see also Yamamura and Tsuji 1993).

In conclusion, I suggest that the evolution of male parental care and female multiple mating is largely affected by the relative magnitudes of the direct cost and the indirect benefit of female multiple mating among other factors. Allowing the cost of lost mating opportunities due to paternal care to be frequency dependent, it is found that male parental care and female multiple mating can co-occur. Further theoretical work that considers such factors as male mate guarding, female mate choice, and cultural transmission is clearly needed.

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APPENDIX

Details of the Outcome in Case 2

The outcome of the model in case 2 can be classified into seven distinct patterns. Figure 3 shows examples in the form of a 4×2 matrix. Each row and each column of the matrix is specified by a condition that is to be satisfied. In other words, each pattern emerges if and only if the two conditions specified by the row and the column are met simultaneously. Each of the four rows (from top to bottom) corresponds to

$$0 < s < \frac{b(k-1)}{(1+b)k}, \quad (\text{A1a})$$

$$\frac{b(k-1)}{(1+b)k} < s < \frac{b(k-1)}{1+bk} \quad \text{and} \quad s < \frac{(k-1)[b+c(k-1)]}{(1+b)k+c(k-1)^2}, \quad (\text{A1b})$$

$$\frac{b(k-1)}{(1+b)k} < s < \frac{b(k-1)}{1+bk} \quad \text{and} \quad s > \frac{(k-1)[b+c(k-1)]}{(1+b)k+c(k-1)^2}, \quad (\text{A1c})$$

and

$$\frac{b(k-1)}{1+bk} < s < 1, \quad (\text{A1d})$$

respectively. Each of the two columns (from left to right) corresponds to

$$0 < c < \frac{b}{1+b}, \quad (\text{A2a})$$

and

$$\frac{b}{1+b} < c < 1, \quad (\text{A2b})$$

respectively. The pattern represented by figure 3C, for instance, emerges if and only if (A1b) and (A2a), which correspond to the second row and the first column, are satisfied. Note that equations (A1c) and (A2b) are never met simultaneously.

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