Can Females Gain Extra Paternal Investment by Mating with Multiple Males? A Game Theoretic Approach

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ABSTRACT: Although females may require only one mating to become inseminated, many female animals engage in costly mating with multiple males. One potential benefit of polyandrous mating is gaining parental investment from multiple males. We developed two game theoretic models to explore this possibility. Our first model showed that male care of multiple females' offspring evolves when male help substantially increases offspring fitness, future mating opportunity is limited, and group size is small. In our second model, we assumed that males invest in the offspring of former mates and evaluated the fitness consequences of female monogamous and polyandrous mating strategies. Females benefit only from limited polyandry, that is, mating with several males. Polyandry is discouraged because females must share male investment with other polyandrous females, and paternal care is likely to experience diminishing returns. Females may enhance their access to male investment by competing with rival females and monopolizing investment, however. The results support the argument that females can gain paternal investment by mating with several males in small social groups (e.g., dunnocks *Prunella modularis*). The results do not support the argument that females can gain paternal investment from pronounced multiple mating in large social groups, however, as observed in many primate species.

Keywords: female multiple mating, polyandry, nonprocreative mating, paternal investment, mating benefits, mating strategy.

In Bateman's (1948) landmark experiments with *Drosophila*, he showed that male production of offspring increases as a function of the number of mated females but that female production of offspring does not increase after mating with multiple males. In many animals, however, females mate with multiple partners (Birkhead and Moller 1992; Andersson 1994) and, among primates in particular, do so during nonfertile periods (e.g., Wilson et al. 1982; Cords et al. 1986; Wallen 1990; Dixson 1992; Brockman and Whitten 1996; Strier and Ziegler 1997; Soltis et al. 1999). Moreover, mating is a potentially costly activity (Bercovitch 1983; Reynolds and Gross 1990; Manson 1994).

Potential benefits from multiple mating by females include ensuring insemination (Gromko et al. 1984), avoiding genetic incompatibility (Zeh and Zeh 1996, 1997), promoting sperm competition (Yasui 1997), producing genetically diverse offspring (Stearns 1987), avoiding infanticide (Hrdy 1979), acquiring courtship food (Thornhill 1976), and acquiring additional parental investment from males (Stacey 1982).

The paternal investment hypothesis has been advanced to explain the co-occurrence of polyandrous mating and parental investment by multiple males in birds (e.g., dunnocks *Prunella modularis* [Davies 1992], alpine accentors *P. collaris* [Davies et al. 1996; Nakamura 1998], Galápagos hawks *Buteo galapagoensis* [Faaborg et al. 1995]), and mammals (e.g., tamarins *Saguinus* spp. [Garber 1997]). The explanation has also been invoked to explain very pronounced multiple mating by females in primates forming large, multimale, multifemale social groups (Taub 1980, 1984). Indeed, females in such groups are well known for mating with many males (e.g., Small 1990; Sprague 1991; Brockman and Whitten 1996; Dixson 1998; Soltis et al. 1999). The paternal investment explanation has been criticized, however, in part because male-infant interactions may benefit males rather than infants (e.g., Paul et al. 1996).

Beginning with Trivers (1972), theoretical models have examined the conditions that favor investment in offspring rather than desertion. Maynard Smith (1977), for example, showed that the decision to invest in offspring or desert rests fundamentally on the trade-off between the value of

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parental investment and the probability of future matings. Stacey (1982) presented a similar model and extended it to allow for investment by multiple males. Other models have considered the relationship between the evolution of male parental care and paternity confidence (Maynard Smith 1978; Whittingham et al. 1992; Westneat and Sherman 1993; Houston 1995). No models have explicitly examined the investment benefits to females who mate with multiple males.

In this article, we use a game theoretic approach (Maynard Smith 1982) to examine the power of the paternal investment hypothesis as an explanation for multiple mating by females. We chose game theory to model this problem because the success of the male strategy of investing in multiple females' offspring and the female strategy of mating with multiple males both depend on what strategy other individuals follow. In the first model, we examine the conditions under which males will invest in offspring of their mate(s) rather than seek additional mating opportunity (parental vs. mating effort). In the second model, male investment in offspring is assumed, and we examine the conditions under which it pays females to mate with multiple males rather than with just one male (benefit of male investment vs. cost of mating). We use our results to evaluate the application of the paternal-investment hypothesis to several species in which females are known to mate with multiple males.

Model 1: The Evolution of Male Investment

To explore the evolution of male care, we analyze a simple model of male investment in multiple females' offspring when females do not exercise mate choice. This analysis allows us to examine the conditions under which males benefit from investing in offspring of mate(s), considering that the size of social groups might vary and influence payoffs to parental care.

Each generation, unrelated individuals are randomly sampled into groups of $2N$, with N adult males and N adult females in each group. Next, all males mate at random within the group as many times as their strategy dictates, and some males begin caring for future offspring (e.g., by nest building, provisioning the female, or other investment), also as their strategy dictates. Each female produces offspring sired by one of her mates from within the local group, selection occurs based on offspring quality, and, finally, new groups are formed each generation by randomly sampling from among all offspring in all groups (the metapopulation). For species in which either sex disperses, migration rates are large enough per generation to make this infinite-migration assumption an excellent approximation of the actual dynamics.

Males have two reproductive strategies. "Dads" mate with females and invest in the offspring of their mate(s) instead of seeking additional mating opportunity. "Cads" never invest in offspring and instead use their time and energy to pursue additional mates. Let d be the number of matings each dad obtains, and let $(d + c)$ be the number of matings each cad obtains. The d variable represents the baseline number of matings common to both strategies, and c represents the additional number of matings a cad can achieve by not caring for the offspring of his mates. Another model might specify these additional matings as increased gamete production, giving cads an edge in sperm competition. In either case, cads use their time and energy to mate more (and therefore increase paternity), while dads use it to improve offspring quality. Males do not guard females or direct their matings toward specific females, however. We do not include such paternity-assurance strategies in this article but caution that such strategies are likely to favorably affect the evolution of male investment.

Under the above assumptions, the probability per mating that a particular dad is the father of a given female's child is $1/[(Nd + xc)/N]$, where x is the number of cads in the group of N males. When d is 1 and c is 0, each dad mates with one female and each female is mated once, on average. This expression assumes matings are distributed randomly within the group such that the same male may mate a single female more than once in a row. On average, however, all females are mated an equal number of times. In species with strict mate guarding or mate markets, however, this is unlikely to be a harmless assumption, and the intuitions of the model should be used with caution.

We assume that dads do not know paternity but invest equally in the offspring of former mates. Let R be the total amount of resources a male or female parent has to invest in offspring. Let f be the relative value of male investment to female investment, such that if $f = 2$, then each unit of male investment has twice the effect on offspring quality as one unit of female investment. The fitness of a dad in a group with N total males and x cads is then

$$W(D|x) = d\frac{1}{(Nd + xc)/N} \times \left[R + \frac{fR}{d} + \frac{(N-1-x)d}{N}\left(\frac{fR}{d}\right)\right]. \quad (1)$$

In the brackets of equation (1), a female contributes R units of investment to her offspring. The dad whose fitness we are calculating contributes fR units of investment divided equally among all the females with whom he has mated. Finally, $(N - 1 - x)d/N$ other dads in the group also, on average, mate with the same female and add their

investment, fR/d, to the offspring of the dad whose fitness we are calculating. The sum in brackets thus gives the expected amount of investment (from all males) in a single offspring of a female with whom the dad has mated.

It follows from equation (1) that the fitness of a cad in a group of N total males and x cads other than himself is

$$W(C|x) = (d + c)\frac{1}{[Nd + (x + 1)c]/N} \times \left[R + \frac{(N - 1 - x)d}{N}\left(\frac{fR}{d}\right)\right]. \quad (2)$$

The cad gives up fR/d units of investment in each potential offspring and gains an additional c mating over a dad.

Consider first whether dads can invade a population of cads. When cads are common ($x \cong N - 1$), almost all groups consist of N cads. The fitness of a cad is then (from eq. [2])

$$W(C|N - 1) = (d + c)\frac{1}{(Nd + Nc)/N} \times \left\{R + \frac{[N - 1 - (N - 1)]d}{N}\left(\frac{fR}{d}\right)\right\} = R.$$

The rare dad, however, is almost always present in a group of $N - 1$ cads. Then the fitness of a dad is (from eq. [1])

$$W(D|N - 1) = d\frac{1}{[Nd + (N - 1)c]/N} \times \left\{R + \frac{fR}{d} + \frac{[N - 1 - (N - 1)]d}{N}\left(\frac{fR}{d}\right)\right\} = d\frac{N}{[N(d + c) - c]}R\left(1 + \frac{f}{d}\right).$$

Thus, dads will invade when

$$\left(\frac{N}{N - 1}\right)f > c. \quad (3)$$

When groups are large, this is approximately

$$f > c. \quad (4)$$

Dads will invade a population of cads when the relative value of male investment (f) exceeds the average number of extra matings to a cad (c). One way to think of c is the opportunity cost a dad pays for investment, while f is the opportunity cost a cad pays for pursuing additional matings.

To understand the effect of group size on the invasion criterion, consider that when groups are small, $N/(N - 1)$ approaches 2 (which is the minimum group size), increasing the left side and the likelihood that dads will invade (eq. [3]). This results from the fact that small groups have fewer cads who freeload off the investment of dads, and thus, the dad receives a larger share of the benefits of his own investment. In either condition, however, male investment can most easily evolve when male care (f) is quite valuable relative to the number of additional mating opportunities (c) and when social groups (N) are small.

Now consider when cads may invade a population of dads. When dads are common ($x \cong 0$), dads will almost always be in groups with $N - 1$ other dads. Cads, however, will, on average, exist in groups with $N - 1$ dads and zero other cads. Under these circumstances, the condition for cads to invade dads can be derived from expressions (1) and (2). The expression specifying when cads will invade a population of dads is complicated and difficult to interpret. When groups are large, $(N - 1)/N$ is approximately 1, however, and the expression specifying when cads invade dads becomes

$$\left(\frac{d + 1}{d}\right) < N\left(\frac{c - 1}{c}\right) + \frac{N - 1}{f}. \quad (5)$$

Expression (5) is more difficult to interpret than the previous result (expression [3]), but examining the effect of each parameter is revealing. Just as we saw for the invasion of dads, larger group sizes (higher N) encourage invasion of cads. Likewise, when cads obtain more extra matings (c is large), cads are more likely to invade dads. Low value of male investment (f) also encourages cads to invade. Finally, a higher baseline number of matings for both strategies (d) also encourages the evolution of cads. This results from the fact that dads create an additional public good with each female in whom they invest and simultaneously receive a smaller share of that public good. Cads always receive a share of the good disproportionate to their investment because they contribute nothing to the production of this public good.

Figure 1 plots the zones of the mixed and pure equilibria for varying c and f for four representative values of N. When groups are small, the range of values giving rise to dads is larger. As N increases, both the range giving rise to cads and the range of mixed equilibria containing both

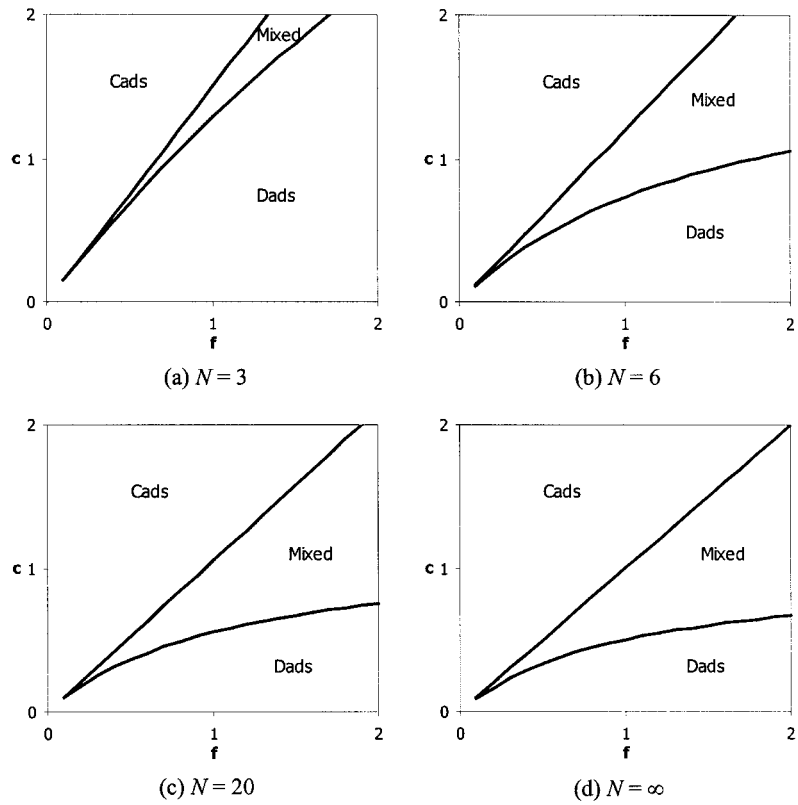

Figure 1: Plots of zones of equilibria for the dads and cads model for $d = 1$ and variables f, c, and four values of N. The top line is the invasion condition for dads to invade cads. The bottom curve is the invasion condition for cads to invade dads. In between these two conditions is a zone of mixed equilibria. *a*, Small social groups in which dads have high fitness. *b*, Slightly larger social groups in which cads have made substantial inroads. *c*, *d*, Large social groups in which cads have high fitness. While extreme values of f and c can compensate for the effects of group size, increasing group size quickly reduces the regions in which dads do well.

dads and cads increase. Note that the effect of group size is strong at small values; even moderate group sizes quickly erode the range of conditions that give rise to dads.

When both conditions are satisfied (expressions [3] and [5]), a stable mixture of dads and cads exists in the population, and some males invest in the offspring of mates while others do not. The internal equilibrium proportion of cads and dads is reached when the fitness of dads averaged across all groups is equal to the expected fitness of cads averaged across all groups (app. A). The mixed equilibria are affected in the same ways and by the same parameters as the ESS conditions, and therefore, additional analysis of those conditions is not very revealing in this case.

Model 2: Polyandry and Male Parental Investment

In this model, we examine the conditions under which it is adaptive for females to mate with multiple males, given that males already invest in offspring. Again, assume a metapopulation from which individuals are randomly sampled into groups each generation, with N females and N males in each group. Females control the number of males with whom they mate but do not control other females' mating. Each male divides his resources for parental investment (B) between the females with whom he mates. Males do not differ in quantity or quality of investment. Females pay a cost (C) for each male with whom they mate.

Females have two strategies. Monogamous females (M) mate with one male in the group, each with a different male, with a fitness $W(M)$; polyandrous females (P) mate with all males in the group, with a fitness $W(P)$. Monogamous females each mate with a different male because males do not differ in quality of investment (i.e., we removed polygyny threshold effects; Orians 1969). Let x equal the number of other $(N - 1)$ females in the group mating polyandrously. Then,

$$W(M|x) = \frac{B}{x+1} - C. \tag{6}$$

A monogamous female receives investment only from her one mated male (B), but the investment is divided among the number of polyandrous females in the group (x) and herself. She pays the cost of mating with one male. For polyandrous females,

$$W(P|x) = \frac{B(x+1)}{(x+1)} + \frac{B[N-(x+1)]}{(x+1)+1} - CN. \tag{7}$$

The investment received by a polyandrous female is divided into two components: that received from males who have not mated with a monogamous female and that received from males who have mated with a monogamous female. All N males in the group mate with the $x+1$ polyandrous females. The $N-(x+1)$ males mate with an additional monogamous female, however, while the remaining $x+1$ males do not. The investment that the polyandrous female receives from each of the $x+1$ males who mated only with polyandrous females is divided among x other polyandrous females and herself. The investment from each of the $N-(x+1)$ males who mated with an additional monogamous female, however, is divided among x polyandrous females, herself, and the monogamous female. She pays costs of mating with every male.

When monogamy is common ($x \cong 0$), monogamous females are in groups with other monogamous females. The fitness of a monogamous female is therefore determined mostly by how she competes against other monogamous females. Likewise, a rare polyandrous female will, on average, be in a group where all other females are monogamous. Under these conditions, from expressions (6) and (7), polyandry can invade monogamy when

$$B > 2C. \tag{8}$$

When polyandry is rare, a polyandrous female acquires half of the investment from all monogamous females in her group. If benefits of male investment are more than twice the costs of mating, then polyandrous females will invade.

When polyandry is common ($x \cong N-1$), a rare monogamous female will be in a group where all other females are polyandrous, and polyandrous females will also be in groups where all other females are polyandrous. Under these conditions, from expressions (6) and (7), monogamy can invade polyandry when

$$CN > B. \tag{9}$$

When polyandry is common, investment is shared with all other females, but costs of mating with all males must be paid. If the cost of mating with all group males is greater than the benefit received from one male, then monogamous females will invade.

Figure 2 plots these invasion conditions and shows the zones of possible equilibria for varying B/C and N. For sizable groups, polyandry resists invasion by monogamy only for very high B/C ratios. A large zone of mixed equilibria may exist for large groups, however, whenever both conditions are satisfied (eqq. [8] and [9]).

The internal equilibrium proportion of polyandrous females ($\hat{p}$) is reached when the expected fitness of polyandrous females is equal to the expected fitness of monogamous females, across all randomly sampled groups. In general, it is not possible to solve for these equilibria analytically, but for variable number of males (N) and B/C ratios, we derived the equilibrium proportions of polyandry ($\hat{p}$) numerically (app. B). Solid lines in figure 3 show the results. When the benefits of male investment are low ($B/C = 5$), polyandry cannot evolve even in small groups. Even with high benefits to male investment ($B/C = 20$), only modest forms of polyandry, that is, mating with a few males, can evolve.

If groups are large ($N \approx 100$), it is possible to derive an analytic solution for the mixed equilibria (app. C). Under that assumption, the equilibrium proportion of polyandry is

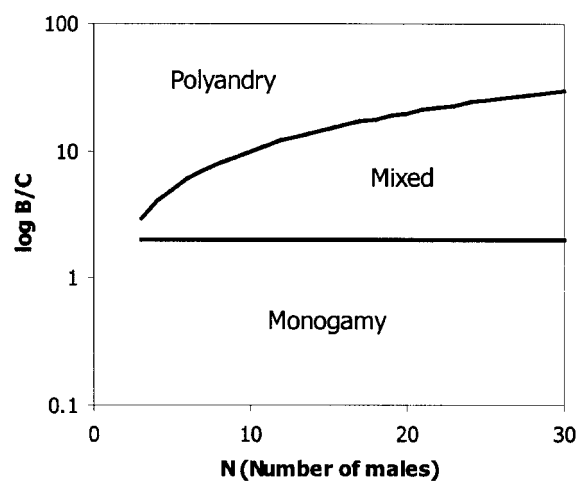

Figure 2: Zones of equilibria for the female polyandry model. The curve on top is the condition for polyandry to invade monogamy. The line on bottom is the condition for monogamy to invade polyandry. The Y-axis shows the log of the ratio of benefits of male care to costs of mating. The X-axis is the number of males in the group (number of mates for a polyandrous female).

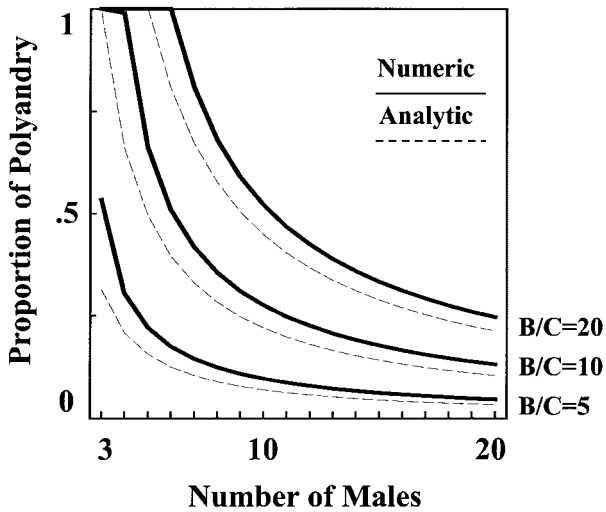

Figure 3: The effect of B/C ratios and the number of males (N) on the equilibrium proportion of polyandry. Solid lines show the numerical solution (app. B), and dashed lines show the analytical solution (app. C). Lowest two lines: $B/C = 5$; middle two lines: $B/C = 10$; top two lines: $B/C = 20$. Default parameter for diminishing returns to male investment (a) is 0.60 in both solutions (app. B, C). Equilibrium proportions of polyandry can be interpreted to be the proportion of polyandrous females or the extent of polyandry in each female (i.e., the proportion of $N - 1$ additional group males with whom all females mate).

$$\hat{p} = \left(\frac{1}{N-1}\right)\left(\frac{B}{C} - 2\right). \tag{10}$$

The level of polyandry in expression (10) is proportional to the ratio B/C and group size (N). This expression yields qualitatively similar results as the numerical solution but underestimates slightly the frequency of polyandry at equilibrium, as shown by the dashed lines in figure 3. With low benefits to male investment ($B/C = 5$), polyandry cannot evolve at any group size. Even with very high benefits ($B/C = 20$), only modest levels of polyandry evolve. Although the zone of mixed equilibria in figure 2 may be quite large for very large N, monogamy or mild forms of polyandry seem to dominate most such equilibria.

One of the reasons that polyandry is difficult to evolve in the above model is that male investment must be shared among all other polyandrous females. A polyandrous female could increase parental investment by excluding other females from mating and reproducing. An individual female who monopolizes male parental investment has fitness $W(P_{\text{monopolizer}}) = NB^a - N(C_m + C_e)$. Such females should simply increase the number of mated males (N) until the costs of mating (C_m) and excluding other females (C_e) exceed the diminishing returns to investment (B^a), where a represents diminishing returns ($1 > a > 0$).

Discussion

Review of Results

Our first model showed that males are favored to seek additional matings rather than invest in offspring under a wide variety of conditions (fig. 1). Echoing earlier work (Trivers 1972; Maynard Smith 1977; Stacey 1982), investing males are favored when the value of male care is substantial and future mating opportunity is limited. Furthermore, favorable conditions for male investment in multiple females' offspring are optimized when groups are minimally small (fig. 1). When group sizes are larger, noninvesting males free ride off of those males who do invest in offspring.

Our second model indicated that mating with multiple males for parental investment can explain modest levels of polyandry, provided the benefit of a male's investment is at least 10 times the cost of mating (fig. 3). The paternal investment hypothesis cannot explain pronounced polyandry, however, even when benefits of investment are substantial compared to the costs of mating. First, when many females mate with multiple males, they have to share benefits of investment with other polyandrous females while also paying costs of mating with many males. Second, diminishing returns to male investment make the costs of mating increasingly prohibitive. When females pay additional costs of monopolizing male mating and paternal investment by excluding other females, however, higher levels of polyandry may evolve, but diminishing returns to investment should still limit polyandry.

Empirical Evidence

Dunnocks (*Prunella modularis*) are polygynandrous birds in which females possess exclusive territories and males compete to defend them (Davies 1992). Females use aggression to inhibit rival female mating while vocalizing to attract male mates (Langmore and Davies 1997) and actively seek matings with beta males despite mate guarding by alpha males (Davies 1985; Davies et al. 1996). Males feed the offspring of former mate(s) in relation to their proportional access to the mother(s) during fertile periods (Davies et al. 1992), and offspring survival is higher with more than one male helper (Houston and Davies 1985; Davies and Hatchwell 1992).

Alpine accentors (*Prunella collaris*) form polygynandrous groups, with several adult males and females in a single territory (Nakamura 1998). Dominant females interrupt mating attempts by lower-ranking females. Males feed the chicks of former mates, and offspring fitness increases in a linear fashion with the number of males provisioning the nest until about five male helpers are present,

at which point increases begin to level off (Nakamura 1998).

The communal marmosets and tamarins (*Callitrichidae*) live in small, mixed-sex social groups with variable mating systems (Goldizen 1987; Garber 1994, 1997; Goldizen et al. 1996). Dominant females suppress the reproduction of rival females (Abbott 1984; Epple and Katz 1984; Kleiman et al. 1988; Abbott et al. 1993). Multiple males contribute to offspring welfare (Goldizen 1987; Ferrari 1992; Garber 1994, 1997), and care from multiple males improves offspring fitness (Goldizen 1987; Wright 1990; Koenig 1995); however, benefits to infants level off with more than four male helpers (Garber 1997). While some have argued that male care may be mating effort, not parenting effort (e.g., Smuts and Gubernick 1992; van Schaik and Paul 1997), most evidence shows that male care of infants is not associated with increased mating opportunity (Price 1990; Tardif and Bales 1997).

We believe that the paternal investment model for female multiple matings applies well to the above three taxa, in which females monopolize male mating, males invest in offspring of former mates, and male help increases offspring fitness. Consistent with the model, the benefits of male care are limited. In both alpine accentors and the Callitrichid monkeys, for example, benefits increase up to about four or five males, after which additional male care no longer increases offspring fitness.

The paternal-investment hypothesis has also been invoked to explain the very pronounced promiscuity of Barbary macaques (*Macaca sylvanus*; Taub 1980, 1984), which reside in large, multimale, multifemale groups of 12–59 individuals (Mehlmen 1989). Primate species residing in such groups usually consist of related adult females and unrelated males (Pusey and Packer 1987), and multiple, nonprocreative mating by females is common (sources in the introduction to this article). Male-infant affiliative interactions range from never to extensive (e.g., Taub 1980, 1984; Stein and Stacey 1981; Stein 1984; Smuts 1985; Whitten 1987; Palombit et al. 1997; Borries et al. 1999). It has not been shown that such behavior toward infants actually increases offspring fitness, however, and there is no evidence that females compete against one another for access to male mating and/or paternal investment (e.g., Kuester and Paul 1996). Finally, our theoretical results suggest that the paternal-investment hypothesis is insufficient to account for very pronounced female polyandry, in which females mate with many group males and nongroup males.

Caveats to the Model

Relaxing some of the simplifications in our models could change the results. Relatedness among investing males, for example, could increase investment by males in multiple females' offspring (Stacey 1982). Likewise, mate guarding by investing males could increase the success of that strategy. If males differed in quality of investment, however, polygyny threshold effects could apply (Orians 1969) and less polyandry would evolve. Also, to the extent that males can determine fertile periods, such determinations may reduce the potential for females to receive paternal care from polyandrous mating.

The paternal investment model assumed that males use the unsophisticated rule of dividing resources equally among all former mates. A male who mates with one monogamous and one polyandrous female, however, should invest most or all of his resources in the monogamous female (e.g., Davies et al. 1992). If the equilibrium proportion of polyandry is interpreted as characterizing each female's degree of polyandry, rather than specifying the proportion of polyandrous females in the population, however, then the problem is solved.

Finally, we did not include conflict between the sexes in these models. In the first model, males controlled mating, and in the second model, females did. Both males and females may attempt to restrict the mating behavior of the opposite sex, but neither sex is likely to completely control the other. Conflicts of interest are likely to be evident when females seek polyandry because males may simultaneously seek polygyny to increase mates. Such conflict between the sexes not only occurs in the dunnocks and Callitrichid monkeys but also contributes to the variability in their observed mating systems.

Conclusions

Game theoretic analyses showed that male investment in multiple females' offspring is favored when male care increases offspring fitness, future mating opportunity is limited, and group size is small. Under such circumstances, females may benefit from polyandry and receive paternal investment from more than one male. Such benefits decline, however, after mating with more than several males because females must share paternal investment with other polyandrous females, and male investment is likely to experience diminishing returns.

The game theoretic analyses show that the paternal-investment hypothesis is unlikely to explain very pronounced polyandry, however. We wish to emphasize that the second model assumes the best-case scenario for the evolution of investment from multiple males, in that the investing male strategy is already an ESS. Even when it is assumed that males divide investment equally among their former mates, however, females only gain from mating with a few males. Therefore, the paternal investment hypothesis should be applied with caution when attempting to explain the very pronounced female promiscuity ob-

served in some species, such as that observed in large, multimale, multifemale primate groups.

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APPENDIX A

Solving for the Equilibrium Proportion of Cads Numerically

The internal equilibrium proportion of cads, $\hat{p}$, is reached when the expected fitness of cads averaged over all groups is equal to the expected fitness of dads averaged over all groups. Assuming random formation of groups, the expected fitness of dads is (from eq. [1])

$$E(W(D)) = \sum_{x=0}^{N-1} k(x)\left\{d\frac{1}{(Nd + xc)/N} \times \left[R + \frac{fR}{d} + \frac{(N-1-x)d}{N}\left(\frac{fR}{d}\right)\right]\right\}, \tag{A1}$$

where $k(x)$ is the binomial probability that a dad finds himself in a group with x cads. The expression for $E(W(C))$ is similarly derived from equation (2). For various values of the parameters f, d, c, x, N, and R, the equilibrium value of p was calculated using the interval halving method (VISUAL BASIC program by R.M. available upon request). The equilibrium $\hat{p}$ is that value reached when $E(W(D)) = E(W(C))$.

APPENDIX B

Solving for the Equilibrium Proportion of Polyandry Numerically

Like the previous model, the internal equilibrium proportion of polyandrous females cannot be solved analytically without a simplifying assumption (app. C) but can be solved numerically. The internal equilibrium is reached when the expected fitness of polyandrous females averaged over all groups is equal to the expected fitness of monogamous females averaged over all groups. Let $B = B^a$, where a represents diminishing returns to male investment ($0 < a < 1$). Assuming random formation of groups, the expected fitness of monogamous females is (from eq. [6])

$$E(W(M)) = \sum_{x=0}^{N-1} k(x)\left\{\frac{B}{x+1} - C\right\}, \tag{B1}$$

where $k(x)$ is the binomial probability that a monogamous female finds herself in a group with x polyandrous females. The expression for $E(W(P))$ is similarly derived from equation (7). For various values of the parameters B, C, and N, the equilibrium value of p was calculated using the interval halving method (QBASIC program by J.S. available upon request). The equilibrium $\hat{p}$ is that value reached when $E(W(M)) = E(W(P))$. Solid lines in figure 3 show the results.

APPENDIX C

Solving for the Equilibrium Proportion of Polyandry Analytically

Assuming large groups, x is approximately $p(N-1)$ in every group, where p is the proportion of $N-1$ females who are polyandrous. Let $B = B^a$, where a represents diminishing returns to male investment ($0 < a < 1$). The equilibrium proportion of polyandry, $\hat{p}$, is found by equating the fitnesses shown in equations (6) and (7) and solving for p,

$$\frac{B}{\hat{p}(N-1)+1} - C = \frac{B[\hat{p}(N-1)+1]}{\hat{p}(N-1)+1} + \frac{B(1-\hat{p})(N-1)}{\hat{p}(N-1)+2} - CN, \tag{C1}$$

and for $N \cong (N-1)$,

$$\hat{p} = \left(\frac{1}{N-1}\right)\left(\frac{B}{C} - 2\right). \tag{C2}$$

The dashed lines in figure 3 show that the analytical results are qualitatively similar to the numerical results.

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