The male's dilemma: increased offspring production is more paternity to steal

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Summary

Large potential effects of male care on the number of offspring females successfully raise are not sufficient to select for caring males because of the pervasive importance of mating competition. Males face a version of 'the social dilemma', in which increased production increases the pay-off for theft. Models of the allocation of male effort partitioned between caring for babies and competing for paternity show that the optimal allocation to care is very low under a wide range of conditions. Like sex allocation where the alternatives are male versus female function or sons versus daughters, the pay-offs to one alternative are always strongly frequency dependent. Because that alternative (male function, sons, male mating effort) pays so well when rare, it cannot remain rare under most conditions. Here we consider the consequences of partitioning mating effort into mate guarding and all other forms of mating conflict. If a male gets all his partner's conceptions while guarding, gaining them at a constant rate, there are two possible regions of stability. The evolutionarily stable strategy (ESS) depends on a parameter scaling the decisiveness of (non-guarding) mating conflict. When marginal returns from conflict decrease with scale, almost all effort goes into guarding. When marginal returns increase, the ESS devotes all effort to mating. Even when the potential effect of care is large, male equilibrium strategies allocate little effort to it. We also report the results of computer simulations showing that care increases if gains from guarding saturate quickly, so that a male is assured of the paternity of most of his partner's offspring with little guarding, and consequently the pool of unguarded conceptions open to competion shrinks sharply. But even when the male's dilemma is very much reduced, it still substantially limits the allocation to care. The results of both computer simulations and mathematical analysis converge with other lines of evidence that mating has much stronger effects than parenting in shaping male strategies.

Keywords: sexual selection; male strategies; mating competition; mating systems; paternal care

Introduction

Males may gain descendants by providing care that increases the number of surviving offspring produced by their mates, but they also gain by competing with other males for additional mating opportunities. The gains (and losses) a male faces in seeking additional matings depend on whether other males are seeking them as well, making pay-offs frequency dependent in a way that the benefits for providing care are not. A consequence of this asymmetry is that whenever males can effectively compete for mating, the ESS is to allocate more to competition and less to care, no matter how much that care could increase the number and survivorship of eggs or infants.

This paper uses a model from conflict theory in economics to pose the problem that mating competition presents for males and then calculates the evolutionarily stable strategies for this problem. A robust result of the models is that mating competition has a different and much

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stronger effect on the optimal allocation of a male's reproductive effort than does the impact he can have on the survival of infants.

Fitness benefits for parental effort have been central to models exploring variation in patterns of care for eggs and infants (reviewed in Westneat and Sherman, 1933). Gains in the number or survival of young due to male care have been used to explain the prevalence of monogamy in birds (e.g. Lack, 1968), its rare occurrence in mammals (e.g. Orians, 1969: Kleiman, 1977) and even to distinguish humans from other primates (e.g. Washburn and Lancaster, 1968; Lovejoy, 1981), accounting not only for variation in human mating systems (e.g. Alexander *et al.*, 1979), but for an array of other aspects of human social life (e.g. Washburn and Lancaster, 1968; Lancaster and Lancaster, 1983). However, recent research often contradicts the expectation that with monogamy males allocate relatively little reproductive effort to mating because their allocation to parenting is crucial. Removal experiments in some bird species demonstrate that male care is not essential to successful fledging. Instead of pay-offs for care, it is strong mating competition among males that enforces monogamy (Davies, 1991). Social pairing commonly occurs with high rates of extra-pair paternity (Westneat *et al.*, 1990; Birkhead and Moller, 1992). The models presented here show that even if male care has strong effects on the number of babies produced, the ESS allocation to mating competition is very large. Surprisingly, the introduction of mate guarding does not increase the allocation to care in the ways expected.

The 'social dilemma' for males

Suppose that males can partition their effort into two kinds of activities, those that increase the number of offspring females successfully raise and those that increase the fraction of these offspring carrying their genes. They can either care for babies or seek paternity. Posed this way the problem for males is a version of the more general one Tullock (1974) called 'the social dilemma' and captured in the pithy epigram: theft is the oldest labour-saving device. A community will produce the largest total product (maximize the mean output of the members) if all effort is devoted to production. But if nothing is put into preventing theft, anyone can earn the highest rate for his own effort by stealing from his neighbours. Where property rights are not well defined, goods production is a many-sided prisoner's dilemma.

Hirshleifer (1991) presented a simple version of the 'social dilemma' with two contestants. If the marginal gains for conflict are constant, exactly one-half of the resources on each side are dissipated in conflict at equilibrium. Even if the initial endowments of the contestants differ, as long as there is an interior solution (i.e. contestant's best initial reply is not to allocate all he has to conflict) the equilibrium result will be equal allocation to conflict and equal incomes for both contestants – the contestant who starts out with less will be motivated to fight harder. In a further exploration of these relationships Hirshleifer (1995) considers what happens with more contestants and shows that as the number increases the income to each at equilibrium decreases. A fixed aggregate total of resources gives decreasing incomes with more shares, but incomes also decrease because the equilibrium allocation to conflict rises. Even if aggregate income grows proportionately with the number of contestants, the shares decrease because the equilibrium allocation to conflict goes up with the number of contestants.

The equilibrium allocation to conflict here surprises initial intuition. So much is 'wasted' in conflict. To the extent the trade-off captures the allocation problem for males it provides a corrective to the notion that if the effects of male care on infant survival are very high, then males will do better to allocate most effort to care. Intuition underestimates the window that production opens to 'appropriation'. The more produced, the more there is to steal and so the greater the

pay-off to theft and to defence against it. Guided by this model we pose the problem in terms of evolutionary game theory to explore the effects of a few variables on the ESS.

The optimal allocation to care and mating in the absence of pair bonds

To provide a standard of comparison, we begin with a model without pair bonds. Males provide care to the offspring of all females within their social group. Females are promiscuous and equally accessible to every male in the social group. Males divide their effort between caring for offspring and 'mating effort', that is, contending with other males for mating opportunities. The paternity of the offspring produced within a local group is shared (unequally) by all group males, with the largest shares of paternity going to those males whose mating effort is largest. Since caring for offspring yields benefits that are widely shared, the ESS is one in which little care is provided by males.

Conflict over mates occurs within local groups comprising N males and N females. A male who allocates a fraction c of his effort to caring and the remaining fraction $m \equiv 1 - c$ to mating will be said to exhibit strategy (c, m). Suppose that a population is dominated by individuals of strategy (c^0, m^0). If this strategy is evolutionarily stable, then a rare mutant with strategy (c, m) will have lower fitness unless $(c, m) = (c^0, m^0)$. Thus, to find the ESS, we first identify the strategy that maximizes the mutant's fitness. If this optimal strategy equals (c^0, m^0), then we have found the ESS.

Let $B(x)$ denote the fertility of a female whose offspring receive x units of care from males, and $F(m, m^0)$ the fraction of the group's offspring sired by the mutant male. The mutant's fitness is

$$w \equiv NB(c/N + c^0[N - 1]/N)F(1 - c, m^0) \tag{1}$$

This definition is justified as follows. Each of the N females in the group receives c/N units of care from the mutant male and c^0/N units from each of the $N - 1$ non-mutant males. The mutant male sires a fraction $F(1 - c, m^0)$ of the resulting offspring.

We show in Appendix 1 that the first-order condition for an ESS is

$$\frac{B'(\hat{c})}{B(\hat{c})} = N\frac{F_1(\hat{m}, \hat{m})}{F(\hat{m}, \hat{m})} \tag{2}$$

where $(\hat{c}, \hat{m})$ is the ESS. Here and elsewhere, subscripts are used to indicate partial differentiation. Thus, $F_1(\hat{m}, \hat{m}) \equiv \partial F(m, \hat{m})/\partial m|_{m=\hat{m}}$. This equation implies that increases in group size N will require smaller values of $F_1(\hat{m}, \hat{m})/F(\hat{m}, \hat{m})$ or larger values of $B'(\hat{c})/B(\hat{c})$. If B and F increase at a decreasing rate, this requires decreasing $\hat{c}$ and increasing $\hat{m}$. Thus, as with Hirshleifer's model we should see less care and more mating effort in large groups.

To gain further insight into this system, we now introduce two specific forms of the production function B and the conflict function F. Let

$$B(c) \equiv A(C + x)^\alpha \tag{3}$$

where C is the care that each female provides to her offspring. The parameter A sets the height of the gain function for the effectiveness of care, while α determines the function's shape. B is linear when $\alpha = 1$, but exhibits decreasing marginal returns when $\alpha < 1$.

The behaviour of this function is illustrated in Fig. 1. We have provided two horizontal axes. The upper one plots B against total parental care, $C + x$. The lower one plots B against aggregate male care x, under the assumption that females devote all their effort to care so that $C = 1$. The upper axis shows that, when $\alpha < 1$, the marginal effect of care declines as $C + x$ increases. However, when $C + x > 1$ the curves are nearly linear and the marginal effect of care is therefore
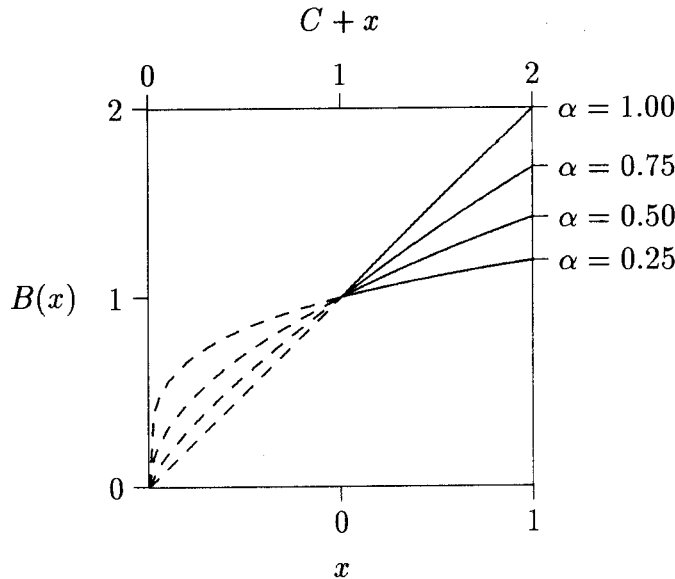
Figure 1. Reproduction function. $B(x)$ is the number of offspring produced by a female whose offspring receive x units of care from males (see Equation 3). Since A has no effect on the ESS, we have set $A = 1$ in each curve. Consequently, $B(0) = 1$ and the curves intersect where $x = 0$.

nearly constant. Henceforth, we shall assume that females devote all effort to care, so that $C = 1$. This restricts us to the region where the figure shows nearly constant marginal effects. It implies that the graph of B against x is nearly a straight line regardless of α's value.

Although the curves for different values of α do not differ much in curvature, they do differ in slope, and these slopes can be interpreted as measuring the relative efficiency of care by males compared to care by females. Male care is less efficient than female care when $\alpha < 1$, i.e. when total care from both parents shows decreasing marginal returns.

Our formulation of the conflict function,

$$F(m, m^0) \equiv \frac{(m)^\beta}{(m)^\beta + (N - 1)(m^0)^\beta} \tag{4}$$

follows Hirshleifer (1991) in assuming that the success of a contestant depends on the ratio of his effort to the effort allocated by all males in the group. The parameter β, like Hirshleifer's mass effectiveness parameter, measures the 'decisiveness' of individual differences in mating effort, m. This function is undefined when $m = m_0 = 0$, so special care is needed in the neighborhood of this value. This difficulty is unimportant because real populations (and simulations) always exhibit variation. Consequently, it does not matter much how we treat the case in which variation is absent.

The effect of β on F is illustrated in Fig. 2. If β is large, slight differences in m will yield large differences in the proportion of unguarded offspring that are sired. Gains for mating effort saturate slowly. When β is small, on the other hand, the gains for mating effort saturate quickly; large differences in m yield only small differences in the proportion sired.

We show in Appendix 2 that this formulation allows Equation 2 to be re-expressed as

$$\hat{c} = \frac{1 - (N - 1)\beta/\alpha}{1 + (N - 1)\beta/\alpha} \tag{5}$$
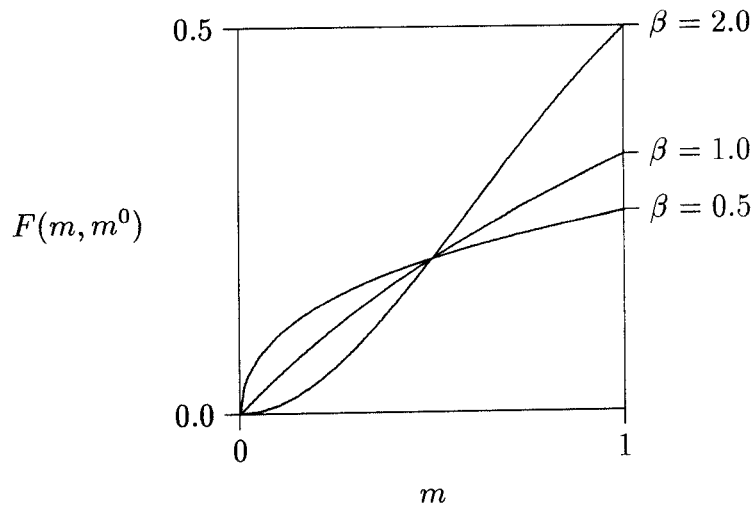
Figure 2. Mating success function. $F(m, m^0)$ is the fraction of unguarded offspring accruing to a male whose mating effort is m when all other males have mating effort m^0 (see Equation 4). Here, each group has $N = 5$ individuals, 4 of whom allocate $m^0 = 0.5$ of their effort to mating.

This equation provides a solution between zero and unity when

$$0 < \beta < \alpha/(N - 1) \tag{6}$$

Second-order conditions show that this solution is an ESS whenever $\hat{c}$ falls between 0 and 1. Inequality 6 requires that $\beta \ll \alpha$. Thus, an ESS with non-zero male care can exist only if mating effort gives decreasing marginal returns.

Inequality 6 implies that paternal care is unlikely to evolve in large groups. For example, consider the case in which $\alpha = 0.8$ and $\beta = 0.2$. Since α is a good deal greater than β, we might expect a fair amount of paternal care. Yet even with these values, the equilibrium level of paternal care exceeds zero only if $N < 5$.

This model generates very little care from males. Even more effort goes to conflict here than in Hirshleifer's model. This difference probably reflects the fact that even when males do not contribute anything to care, they still compete for the paternity of offspring raised by females alone. In the standard social dilemma there is nothing to fight over when nothing is allocated to production.

In this model, a male cannot direct his care to offspring more likely to be his. This should bias the result against male care. To see whether this is so, we now introduce a model that partitions mating effort into two parts: mate guarding and all other forms. In addition to competing with other males for paternity, it allows them to pair with particular females, guard them, and care for the offspring of the females they guard.

Mate guarding

By guarding a mate, a male can increase his own paternity among her offspring. To model this effect, we (following a suggestion by Hirshleifer, 1991), imagine that the offspring of each female are divided into two fractions, one invulnerable to theft by other males and the other vulnerable. Effort devoted by a male to mate guarding will increase the invulnerable fraction of his female partner's offspring.

A male with strategy (c, g, m) spends a fraction c of his effort caring for eggs or infants of his mate, a fraction g guarding her against other males, and a fraction m contending with other males for mating opportunities. We assume that these activities are mutually exclusive so that $c + g + m = 1$. The female partner of a male with strategy (c, g, m) will produce $B(c)$ offspring. Now, however, a fraction g of these are guaranteed to have been sired by her social partner. The remaining fraction $1 - g$ of this female's offspring are 'unguarded,' and many have been sired by some other male. This formulation assumes that guarding is 100% effective and that it gives constant marginal gains, a restriction that we relax below. Paternity of unguarded offspring is distributed as before, according to the (non-guarding) mating effort of the males within the group.

Intuition suggests that this amendment to the model might lead to an ESS at which males provide much more care. But it does not. The ESS allocation is all to the two forms of mating effort. When the gains for conflict saturate quickly, exhibiting decreasing returns to scale, the ESS requires that males devote all or nearly all of their effort to mate guarding. When conflict saturates slowly, marginal gains increasing with scale, the ESS requires that males devote all their effort to conflict.

Computer simulations

We have explored this model by computer simulations as well as analytically. Since we are modelling the decisions of one sex only, our simulations assume haploid reproduction. The results reported here all assume populations of 100 groups, with each group containing five males.

Let m^i denote the mating effort of the ith male and let $\mathbf{m} \equiv (m^1, m^2, ..., m^N)$ the vector of individual mating effort values. The fitness of the ith male in a group is

$$w^i = B(c^i)g^i + F^i(\mathbf{m}) \sum_j B(c^j)(1 - g^j) \tag{7}$$

where (c^i, g^i, m^i) is the strategy of male i and the summation is over all $N - 1$ males in the group except male i. The first term on the right is the number of guarded offspring produced by the ith male's female partner and the second term adds the unguarded offspring that are sired by male i. The function $B(c)$ is defined as in Equation 3 and measures the offspring produced by the female partner of a male who devotes effort c to care. $F^i(\mathbf{m})$ is analogous to the function $F(m)$ of the previous model and measures the fraction of the unguarded offspring that are sired by male i. It is defined as

$$F^i(\mathbf{m}) \equiv \begin{cases} 1/N & \text{if } \sum m^i = 0 \\ \dfrac{(m^i)^\beta}{\sum_j (m^j)^\beta} & \text{otherwise} \end{cases} \tag{8}$$

where the summations are across all males within a group. This definition implies that when no male devotes any effort to conflict, each male has an equal chance of siring each unguarded offspring. As we noted above, this definition has little effect on results because simulated populations almost always contain variation, so it is almost never true that $\sum m^i = 0$. Details concerning the simulation are relegated to Appendix 3.

Figure 3 shows the distribution of a simulated population after 10 000 generations of natural selection. In this simulation, $\alpha = 0.5$ (so that males are less efficient at child care than females; see Fig. 1) and $\beta = 0.5$ (so that mating shows decreasing returns to scale; see Fig. 2). Points are plotted on the triangle so that g is the distance up from the horizontal line, c the distance
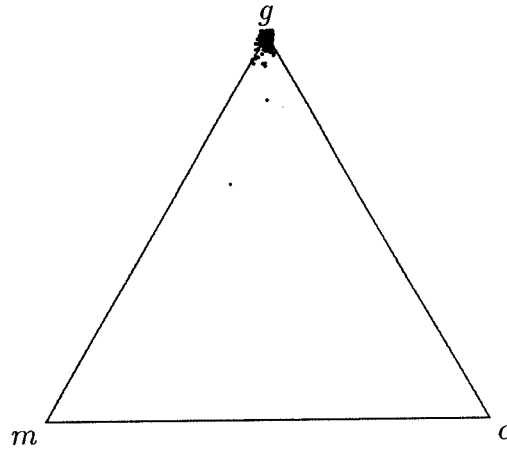
Figure 3. A population in which males are less efficient at child care than females and mating conflict gives diminishing returns. This is the distribution after 10 000 generations of a population of 100 groups with parameters $(\alpha, \beta, N) = (0.5, 0.5, 5)$. In the plot, points are 'jittered' by adding a small random amount both to the horizontal and the vertical positions.
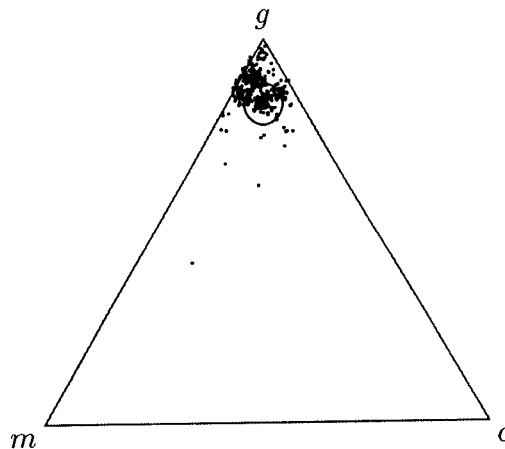

Figure 4. A population in which males are as efficient as females at caring, and mating conflict gives diminishing returns. This is the distribution after 10 000 generations of a population of 100 groups with parameters $(\alpha, \beta, N) = (1, 0.5, 5)$. The means $(\bar{c}, \bar{g}, \bar{m}) = (0.06, 0.86, 0.08)$, are close to the predicted ESS $(\hat{c}, \hat{g}, \hat{m}) = (0.08, 0.83, 0.08)$, which is shown as an open circle on the graph.

'southeast' from the triangle's left edge and m the distance 'southwest' from the triangle's right edge. Thus, the concentration of points near the triangle's apex means that all males in this population are devoting all or nearly all of their effort to mate guarding. Intuition suggests that if male care were more efficient, more care would be provided. The simulation in Fig. 4 verifies this intuition, but also shows that the effect is not pronounced. Even with males and females of equal efficiency ($\alpha = 1$), the ESS is near $g = 1$.

These results are all the more surprising since they assume a value of β that is probably unrealistically low. If a few males get most of the unguarded matings, then mating effort would

show increasing rather than decreasing returns to scale. Thus, it is probably reasonable to assume that $\beta > 1$. Simulations indicate that changing this one parameter leads to an ESS at which males spend all their effort mating.

These simulations are remarkable: even when males are able to protect a portion of the paternity of the offspring produced by their female partners, evolution still leads to equilibria with very little male care. To show why, we turn next to an analytical treatment of the model.

Analytical results

To find the ESS, we consider a rare mutant with strategy (c, g, m) within a population dominated by 'wild type' individuals of strategy (c^o, g^o, m^o). Since the mutant is rare, its $N - 1$ neighbours all exhibit the wild type strateyg and the mutant's fitness is

$$w \approx B(c)g + [B(c)(1 - g) + (N - 1)B(c^0)(1 - g^0)]F(m, m^0) \tag{9}$$

where F is as defined in Equation 4.

In such a model, several types of equilibria are possible. There may be (1) 'interior equilibria' at which all three behaviours are present, (2) equilibria along 'edges', where one behaviour is absent and the other two present and (3) equilibria at 'corners', where only a single behaviour is present. We investigate these possibilities in Appendix 4 and find that some parameter values lead to interior equilibria, others to equilibria at corners. There are no equilibria along edges. These results are summarized in Table 1.

If an interior equilibrium exists, then

$$\hat{c} = (1 - \beta)(1 - \hat{g}) \tag{10}$$

$$\hat{m} = \beta(1 - \hat{g}) \tag{11}$$

$$1 - \hat{g} = \frac{\alpha\frac{N}{N-1} - 1}{1 - \beta + \alpha} \tag{12}$$

where $(\hat{c}, \hat{g}, \hat{m})$ is the ESS. These results are consistent with simulations, as illustrated by the large open circle in Fig. 4.

Equations 10 and 12 help explain why so little care is provided in the simulations. A high level of care would require both that $\beta \ll 1$ and that $\alpha \gg (N - 1)/N$. The first condition is unlikely if we are correct in assuming that conflict exhibits increasing returns to scale. If male care is indeed less efficient than female care – i.e. if total parental care $(C + c)$ cannot exhibit increasing returns to scale – then the second condition is unlikely and impossible when N is large. These observations account for the low level of care in interior solutions, but what of the other equilibria?

As Table 1 summarizes, there are two additional equilibria: (1) the ESS is at $g = 1$ when $\beta < 1$

Table 1. Equilibria in model with care, guarding and mating

ĉ	ĝ	m̂	Requirements	
(10)	(12)	(11)	$1 > \beta$	$1 < \alpha N/(N - 1)$
0	1	0	$1 > \beta$	$1 > \alpha N/(N - 1)$
0	0	1	$1 < \beta$	$N\beta > \alpha N/(N - 1)$

Requirements for $g = 1$ are necessary but may not be sufficient.

and $\alpha < (N - 1)/N$ and (2) the ESS is at $m = 1$ when $\beta > 1$. These conditions are both necessary and sufficient in the latter case, but we were only able to establish necessity in the former case. Computer simulations, however, suggest that both conditions are sufficient as well as necessary. In neither case do males provide any care at all. These results are consistent with our simulations and amplify their central point: the addition of mate guarding produces a model in which males devote even less effort to care for eggs or infants.

When the marginal benefits of guarding decrease with scale

How can we reconcile the models with observations of male care? We expected that making guarding 100% effective, no matter the number or strategy of competitors, would increase the allocation to care. Those assumptions assured that some paternity could be protected from the male's dilemma. To further reduce the fraction of paternity open to competition we introduce a scaling parameter to change the shape of the gain function for guarding, previously assumed to be linear. If the marginal gains for guarding are not constant but instead saturate quickly, so that a small investment in guarding assures a male of most of his partner's conceptions, then optimal allocations might include more care. As the gains for guarding diminish, effort might be better spent elsewhere. But the marginal gains for mating conflict would also decline as the pool of unguarded conceptions shrank, leaving less paternity open to competition. Marginal gains for caring, on the other hand, should go up. The more a male is assured the paternity of his partner's offspring, the more any increases in their numbers or survival would add to his protected 'private' income instead of the common pool.

To investigate these effects, we assume that a male who allocates g units of effort to guarding can be sure of a fraction $G(g)$ of the paternity of his female partner's offspring, where G is a function with decreasing marginal returns. The fitness function of our simulation (Equation 7) becomes

$$w^i = B(c^i)G(g^i) + F^i(\mathbf{m})\sum_j B(c^j)(1 - G(g^j))$$

We define the guarding function by

$$G(g) = g^\gamma \tag{13}$$

where γ determines the function's shape, as shown in Fig. 5. If $\gamma = 1$, then $G(g) = g$ as before. Guarding exhibits decreasing marginal returns when $\gamma < 1$.

Figure 6 shows the result of simulations in which $\gamma < 1$. The three rows of figures show the effect of varying γ; the two columns show that of varying β. In both columns, increasing values of γ yield increasing levels of care. However, the two columns accomplish this change in very different ways. When $\beta < 1$ (as in the left column), the ESS moves steadily away from the corner where $g = 1$ and closer to that at which $c = 1$. But when $\beta > 1$ (as in the right column) decreasing γ leads to a polymorphic ESS. One morph specializes in mating, while the other divides its effort between child care and mate guarding. Decreasing γ increases the amount of effort allocated by this latter morph to care.

Although this model does yield more care, it still does not yield very much. Even where marginal returns from guarding saturate very rapidly (e.g. where $\gamma = 0.2$ in the bottom row of Fig. 6), the average male still devotes only about 30–40% of his effort to care.

Discussion

Posed as the problem of allocating effort between the struggle for paternity and caring for babies, the male's dilemma is another version of familiar sex allocation problems (Charnov, 1982). Fisher
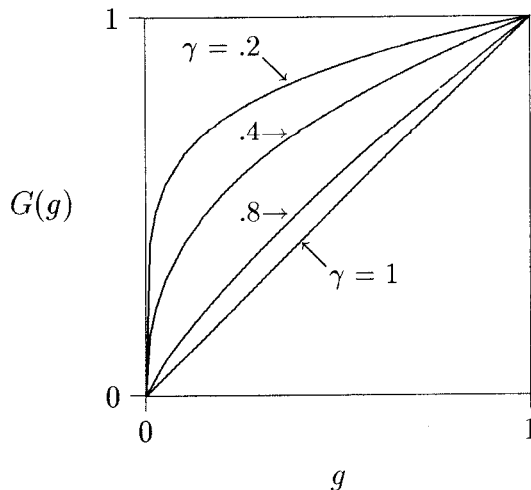
Figure 5. Guarding function.

(1930) first noted the powerful evolutionary consequences of frequency-dependent pay-offs in both sex allocation and sexual selection. The models here highlight the parallels. As in sex allocation, the pay-offs to one of the alternatives (sons or male function) is frequency dependent in a way the other (daughters or female function) is not. Sex ratios evolve increasing allocation to competing sons at the expense of productive daughters as groups get larger with local mate competition (Hamilton, 1967), and more of a male's allocation goes to non-productive effort as the number of competitors increases.

The models show the powerful effects of the male's dilemma. But male care is sometimes observed. In simulations, care increases when gains for guarding saturate quickly, leaving less paternity open to competition. The simulations showed, however, that even when gains for guarding saturate quickly, the male's dilemma still has surprisingly large effects and the overall amount of male care is not high (Fig. 6). Only quite extreme values give substantial amounts of care. Further explorations of the role of this parameter and varying assumptions about the effectiveness of guarding are clearly in order.

Other directions for further inquiry into the evolution of male care, in light of the models, include consideration of untallied pay-offs. The models consider only the fitness gains for caring that accrue through the increases in offspring raised by a male and his partner. Could some of the observed 'care' be only incidentally that, while the carer primarily gains from guarding? Could females preferentially choose caring males for extra-pair copulations and in-pair fidelity? Recent data from monogamous birds has already pointed toward the role of mating competition in shaping activities once readily classed as paternal investment (e.g. Birkhead and Moller, 1992; Davies, 1992; Moller, 1994). Similar questions have been raised about non-human primates (e.g. Smuts, 1985; Whitten, 1986; Smuts and Gubernick, 1992) and about men's hunting among people who forage for a living (Hawkes, 1990, 1993). The models add independent reasons to consider the overwhelming effects of mating competition on male strategies.

The models, of course, capture only a few aspects of the complex problems males must solve. They ignore the necessarily powerful effects of female choice. They depend on the assumption that effort in mating competition and in offspring production are mutually exclusive, an unrealistic simplification, useful in clarifying the relative importance of these fitness components. The models also ignore temporal constraints. Gains for conflict and production will often not be
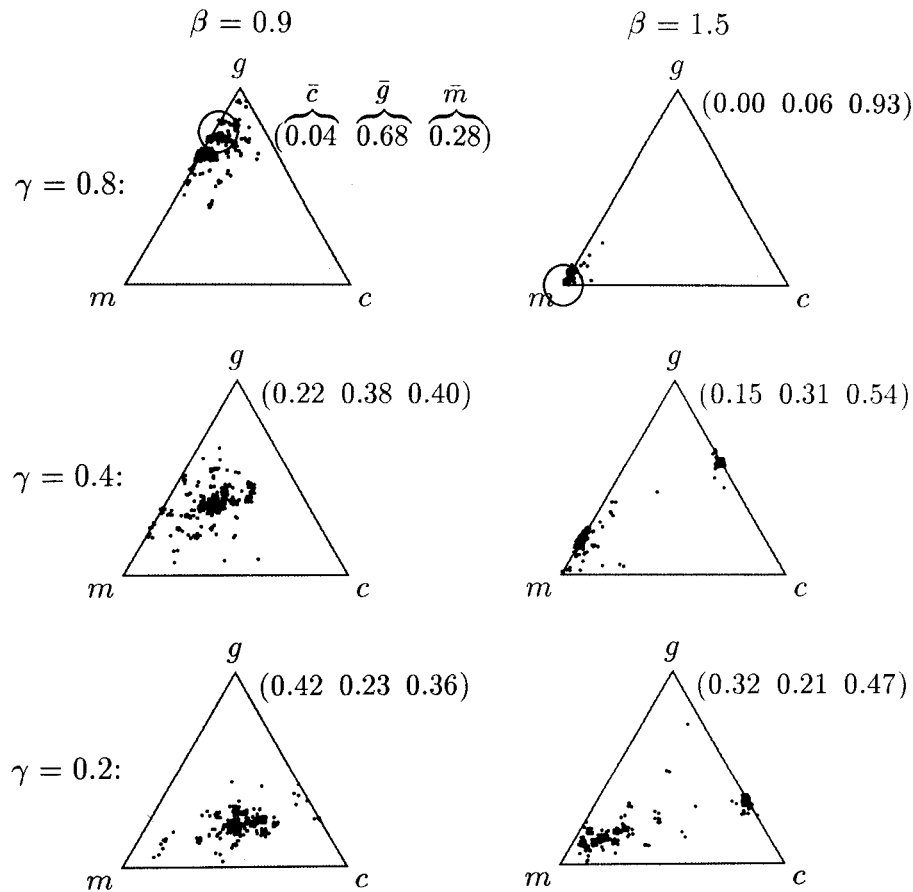
Figure 6. Effect of diminishing marginal returns from guarding. Marginal returns from guarding diminish rapidly when $\gamma \ll 1$; they are constant when $\gamma = 1$. In all plots, $\alpha = 1$ and $N = 5$. Open circles indicate the position of the theoretical ESS when $\gamma = 1$. Note that the results are not very different from the simulation with $\gamma = 0.8$. Each plot shows a jittered distribution in the 10 000th generation, and the mean strategy in that generation is given to the right of each plot.

simultaneously possible (e.g. Westneat *et al.*, 1990). However, the selective attention of the models allows them to show how large a problem mating competition is likely to be for males and indicates some promise in rethinking its effects.

Acknowledgements

References

Alexander, R.D., Hoogland, J.L., Howard, R.D., Noonan, K.M. and Sherman, P.W., (1979) Sexual dimorphisms and breeding systems in pinnepeds, ungulates, primates, and humans. In *Evolutionary biology and human social behavior: an anthropological perspective* (N. Chagnon and W. Irons, eds) pp. 402–35. Duxbury Press, North Scituate, MA.

Birkhead, T.R. and Moller, A.P. (1992) *Sperm Competition in Birds: Evolutionary Causes and Consequences.* Academic Press, London.

Charnov, E.L. (1982) *The Theory of Sex Allocation.* Princeton University Press, Princeton.

Davies, N.B. (1991) Mating systems. In *Behavioural ecology: an evolutionary approach,* third edition, (J. Krebs and N. Davies, eds) pp. 263–94. Blackwell Scientific Publications, Oxford.

Davies, N.B. (1992) *Dunnock Behaviour and Social Evolution.* Oxford University Press, Oxford.

Fisher, R.A. (1930) *The Genetical Theory of Natural Selection.* Clarendon Press, Oxford. Reprinted 1958, Dover, New York.

Hamilton, W.D. (1967) Extraordinary sex ratios. *Science* **156,** 477–88.

Hawkes, K. (1990) Why do men hunt? Some benefits for risky strategies. In *Risk and uncertainty* (E. Cashdan, ed.) pp. 145–66. Westview Press, Boulder.

Hawkes, K. (1993) Why hunter–gatherers work: an ancient version of the problem of public goods. *Curr. Anthropol.* **34,** 341–61.

Hirshleifer, J. (1991) The paradox of power. *Econ. Politics* **3,** 177–200.

Hirshleifer, J. (1995) Anarchy and its Breakdown. *Journal of Political Economy* **103,** 26–52.

Kleirman, D.G. (1977) Monogamy in mammals. *Q. Rev. Biol.* **52,** 39–69.

Lack, D. (1968) *Ecological Adaptations for Breeding in Birds.* Metheun, London.

Lancaster, J. and Lancaster, C. (1983) Parental investment: the hominid adaptation. In *How humans adapt: a biocultural odyssey* (D. Ortner, ed.) pp. 33–65. Smithsonian Institution Press, Washington, DC.

Lovejoy, C.O. (1981) The origin of man. *Science* **211,** 341–50.

Moller, A.P. (1994) *Sexual Selection and the Barn Swallow.* Oxford University Press, Oxford.

Orians, G.H. (1969) On the evolution of mating systems in birds and mammals. *Am. Nat.* **103,** 589–603.

Smuts, B.B. (1985) *Sex and Friendship in Baboons.* Aldine, New York.

Smuts, B.B. and Gubernick, D.J. (1992) Male–infant relationships in nonhuman primates: paternal investment or mating effort? In *Father–Child relations: cultural and biosocial contexts* (B. Hewlett, ed.) pp. 1–29. Aldine de Gruyter, New York.

Tullock, G. (1974) *The Social Dilemma: The Economics of War and Revolution.* The Center for the Study of Public Choice, Blacksburg, VA.

Washburn, S.L. and Lancaster, C. (1968) The evolution of hunting. In *Man the hunter* (R. Lee and I. DeVore, ed.) pp. 293–303. Aldine, Chicago.

Westneat, D.F. and Sherman, P.W. (1993) Parentage and the evolution of parental behavior. *Behav. Ecol.* **4,** 66–77.

Westneat, D.F., Sherman, P.W. and Morton, M.L. (1990) The ecology and evolution of extra-pair copulations in birds. In *Current ornithology* (D. Power, ed.) **7,** pp. 331–69. Plenum, New York.

Whitten, P.L. (1986) Infants and adult males. In *Primate societies* (B. Smuts, D. Cheyney, R. Seyfarth, R. Wrangham and T. Struhsaker, eds) pp. 343–57. University of Chicago Press, Chicago.

Appendix 1: derivation of Equation 2

To find the value of c that maximizes w, we set

$$0 = \frac{d \ln w}{dc} = \frac{B'(c/N + [1 - 1/N]c^0)}{N\, B(c/N + [1 - 1/N]c^0)} - \frac{F_1(1 - c, m^0)}{F(1 - c, m^0)}$$

If (c^0, m^0) is an interior ESS – one at which neither c^0 nor m^0 equal zero – then we can find the ESS by setting $(c, m) = (c^0, m^0)$. This substitution produces Equation 2.

Appendix 2: derivation of Equation 5

Equations 3 and 4 imply that

$$B'(c) = B(c)\frac{\alpha}{1 + c} \tag{14}$$

$$F_1(m, m^0) = \frac{\beta}{m}[F(m, m^0) - (F(m, m^0))^2]$$

$$= \frac{\beta}{m}\left(\frac{1}{N} - \frac{1}{N^2}\right) \tag{15}$$

where the last line follows because $F(m, m^0) = 1/N$ whenever all N individuals in a group exhibit the same value of m, as they must at any monomorphic equilibrium. Substituting these results into Equation 2 yields Equation 5.

Appendix 3: simulation details

At the beginning of each generation, three individuals are chosen to be affected by mutation. With probability $1/100$ the mutant is assigned to a random 'corner', i.e. to one of the strategies $(1,0,0)$, $(0,1,0)$ or $(0,0,1)$. With probability $99/100$ he is given a new strategy by perturbing his old strategy in a random direction on the *c-g* plane, by a random distance (drawn from an exponential distribution with mean 0.2). If the new strategy lies outside the triangle shown in Fig. 3, then the perturbation's magnitude is halved as many times are necessary to bring it back inside.

Before reproduction, fitnesses were rescaled to ensure that enough offspring would be produced to populate all local groups. It was also necessary to convert each individual's fitness to an integer. This might have been done by drawing from some distribution such as the Poisson. However, we used the following 'lottery' algorithm in order to minimize the effect of genetic drift. First, we set $w^i = k + x$, where k is an integer and $0 \le x < 1$. We then generated a random variate, u, from a distribution uniform on the interval $[0, 1)$. If $u < x$ then the individual produced $k + 1$ offspring; otherwise it produced k. This algorithm introduces little variance, thereby minimizing genetic drift. To begin the next generation, offspring were randomly allocated into groups.

Appendix 4: analysis of model with care, guarding and mating

First-order conditions for equilibria depend on the three partial derivatives, which we record here for future reference:

$$w_c = B'(c)g + B'(c)(1 - g)F(m, m^0)$$

$$w_g = B(c)(1 - F(m, m^0))$$

$$w_m = [B(c)(1 - g) + (N - 1)B(c^0)(1 - g^0)]F_1(m, m^0)$$

Interior equilibria

An interior ESS is one at which all three behaviours are exhibited at non-zero frequencies. At any such equilibrium, the partial derivatives of w with respect to c, g and m must all be equal. To derive the first condition, set $w_c = w_m$, substitute Equations 14 and 15, set $(c, g, m) = (c^0, g^0, m^0)$ and set $F(m, m^0) = 1/N$. This produces

$$\frac{m}{1 - g} = \beta \tag{16}$$

Next, set $w_g = w_m$, make the same substitutions as above and simplify the result by substituting for w_c. This gives

$$\alpha \cdot (N/(N - 1) - m/\beta) = 1 + c$$

Since $c + g + m = 1$, Equation 16 also implies that $m = c\beta/(1 - \beta)$. Putting this into the expression above gives Equation 10 and (using Equation 16 once again) Equation 11. Finally, summing Equations 10 and 11 gives Equation 12.

These equations provide a necessary condition for an interior ESS. Second order conditions were explored numerically and indicate that Equations 10–12 describe an ESS whenever they yield an interior solution. This requires that $\beta < 1$ and that $\alpha > (N - 1)/N$.

Equilibria along edges

We consider here the possibility of equilibria along 'edges', where one of the variables c, g, and m equals zero and the other two take non-zero values. Such equilibria require three conditions. First, the marginal derivatives of fitness with respect to the two non-zero variables must be equal. For example, if $g = 0$ then w_c) must equal w_m. Second, the entry of the selection gradient that corresponds to the zero variable must be negative. Third, the ESS must satisfy the usual second-order conditions for a maximum. This last requirement turns out not to be binding in any of the cases below and will not be discussed further.

The selection gradient is a vector pointing in the direction that selection tends to move the system. The component of this vector corresponding to c is negative if $w_c < (w_g + w_m)/2$. But since $w_g = w_m$ at any ESS along the edge where $c = 0$, the requirement for an ESS along this edge becomes $w_c < w_g = w_m$. Analogous conditions are required for the other edges.

Absence of care. Along this edge, any ESS must satisfy $w_c < w_g = w_m$, after making the same substitutions as above and setting $c = c^0 = 0$. The equality between w_g and w_m reduces to $\beta = 1$. No ESS can exist unless β is exactly equal to 1. An equilibrium that requires a parameter to take a specific value is unlikely to occur in nature, since there is no reason to suppose that the parameter often takes this value. Such equilibria are said to be 'structurally unstable'. The result shows that there can be no structurally stable ESS along the edge where $c = 0$.

Absence of guarding. Along this edge, an ESS must satisfy.

$$w_g < w_c = w_m \tag{17}$$

after making the usual substitutions and setting $g = g^0 = 0$. The equality in Condition 17 leads to Equation 2, just as in the model where guarding was not allowed. This implies that Equation 5 gives the ESS solution along this edge, provided that such an ESS exists.

Substituting Equation 10 into the inequality in Condition 17 leads to

$$\frac{\alpha}{N - 1} > 2 - \beta$$

Meanwhile, Inequality 6 shows that c is between 0 and 1 only if

$$\frac{\alpha}{N - 1} > \beta$$

To find out which parameter values will satisfy both inequalities, define a quantity δ such that $\beta = \alpha/(N - 1) - \delta$. The second inequality implies that $\delta > 0$. Now substitute into the first

inequality to find that $\alpha > (N - 1)(1 + \delta/2)$. Since $\delta > 0$, this implies that $\alpha > N - 1$, contrary to our assumption that $\alpha < 1$.

There can therefore be no ESS along the edge where $g = 0$.

Absence of mating. This edge is tricky because of the singularity in F. $F(m, 0)$ is undefined when $m = 0$, but equals 1 when m is ever so slightly greater than 0. Consequently, the derivative of F is undefined at the corner. Yet in real populations (as in simulations) there is always variation, so that some individuals will have values of m that exceed zero. A mutant with $m > 0$ will therefore not sire all the unguarded offspring. To avoid the singularity, we consider a population in which m_0 is very close to 0 but does not equal 0. A mutation increasing m can invade if w_m is large compared with w_c and w_g. This condition is easy to satisfy, since w_m is proportional to F_1, which is proportional to $1/m_0$. We can make w_m arbitrarily large by moving m_0 closer and closer to 0. Consequently, there can therefore be no ESS along the edge where $m = 0$.

Equilibria at corners

Having dispensed with the edges, it remains to consider 'corners', where only one type of behaviour is exhibited. There are three corners to consider, corresponding to the cases of care only ($c = 1$), guarding only ($g = 1$) and mating only ($m = 1$). In each case, the analysis proceeds from the equation

$$w - w^0 = w_c dc + w_g dg + w_m dm \tag{18}$$

where w^0 is the fitness of normal individuals, who play (c^0, g^0, m^0). To deal with the three corners, we will allow the normal strategy to take values close to $(1, 0, 0)$, $(0, 1, 0)$ or $(0, 0, 1)$. As usual, w is the fitness of a rare mutant who plays strategy $(c, g, m) = (c^0 + dc, g^0 + dg, m^0 + dm)$. Thus, dc, dg and dm are the additive effects of the mutation and are assumed to be small. Note that $dc + dg + dm = 0$, since $c + g + m = 1$. A corner is an ESS only if $w - w^0 < 0$ for all choices of (dc, dg, dm).

Care only. Rewrite Equation 18 as

$$w - w^0 = dg(w_g - w_c) + dm(w_m - w_c)$$

where dg and dm are both positive. To avoid the singularity in F, we assume as before that m^0 is slightly greater than 0 and consider mutations for which dg and dm are positive. This corner can be an ESS only if $w - w^0 < 0$ for all choices of dg and dm, including the case in which $dm = 0$. In that case, the condition for an ESS becomes $w_g < w_c$. When $(c, g, m) = (c^0, g^0, m^0)$ and $g^0 \approx m^0 \approx 0$, this inequality becomes $\alpha > 2(N - 1)$, which can never be satisfied if care provides decreasing returns to scale. Thus, there can be no pure ESS at the corner where $c = 1$.

Guarding only. Rewrite Equation 18 as

$$w - w^0 = dc(w_c - w_g) + dm(w_m - w_g)$$

where dc and dm are both positive. This corner is an ESS only if $w_c < w_g$ and $w_m < w_g$ when $(c, g, m) = (c^0, g^0, m^0) = (0, 1, 0)$.

In analysis of this corner we must deal once again with the singularity in F. As before, we suppose that normal individuals have m_0 slightly greater than 0 and that mutations move us away from the corner so that dc and dm are non-negative. Now, $F(m, m_0) \rightarrow 1/N$ smoothly as $m \rightarrow m_0$. The requirement that $w_c < w_g$ becomes

$$\alpha < (N - 1)/N \tag{19}$$

and places only a mild constraint on α. The requirement that $w_m < w_g$ becomes

$$\frac{m}{c + m} > \beta \qquad (20)$$

The corner at which $g = 1$ can be an ESS only if the right-hand side is positive. Hence, it is necessary that $\beta < 1$. For any positive β, however, inequality 20 will fail if m/c is sufficiently small. Consequently, the corner where $g = 1$ cannot be an ESS.

What, then, of the simulations? The answer appears to lie in the dynamic behaviour of the system. When $g \approx 1$, the population can be invaded by mutants with $c > 0$. But when $m \approx 0$ and $c > 0$ there is strong selection for increased m. (This follows from the fact that the partial derivative of fighting success F is proportional to $1/m$ (see Equation 15).) Thus, an increase in c apparently leads to rapid evolution towards the domain in which Inequality 20 is satisfied. This process clearly requires that $\beta < 1$, for otherwise Inequality 20 is never satisfied. We are unable to prove that Inequalities 19 and 20 are sufficient as well as necessary, but simulations suggest that they are.

Mating only. Rewrite Equation 18 as

$$w - w^0 = dc(w_c - w_m) + dg(w_g - w_m)$$

where dc and dg are both positive. This corner is an ESS if $w_c < w_m$ and $w_g < w_m$, when $(c, g, m) = (c^0, g^0, m^0) = (0, 0, 1)$. The first inequality implies that $\beta > 1$ and the second that $\alpha < (N - 1)\beta$. Since $\alpha < 1$ whenever male care is not as efficient as female care, the second condition is easily satisfied. Pure mating will be an ESS whenever $\beta > 1$.