Female choice of matings to maximize parental care

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SUMMARY

We address the question of how many males a female should mate with in the context of species in which males provide care for potential offspring. Our analysis is based on the evolutionarily stable levels of parental effort of a female and a group of males. In the case of one female and two males we give a complete analysis of how the female's preference for monogamy or polyandry depends on the fitness functions assumed in the model. We then go on to consider the question of how many males a female should mate with to receive the highest level of male care. Our results are relevant in particular to the mating system of the dunnock (*Prunella modularis*) and also to the general question of whether a species should be monogamous as opposed to polyandrous.

1. INTRODUCTION

In many species of birds, males help in caring for the young (see Clutton-Brock 1991; Davies 1991; Ketterson & Nolan 1994 for reviews). Under these circumstances, it may be advantageous for a female to mate with more than one male in order to get more help than she would obtain from just one male. Harada & Iwasa (1996) have analysed when it is better for the female to mate with two males rather than with one. Their paper is important in establishing a link between patterns of mating and patterns of care, but it is limited in that it is based on specific fitness functions; and although the effort of each male is taken to depend on the other, the effort of the female is fixed. In this paper we extend the analysis of Harada & Iwasa to the case in which the effort of each bird depends on the effort of all the other birds. We look in detail at how assumptions about the underlying fitness functions used in the model affect the predictions from the model. We establish general conditions for it to be optimal for the female to allocate all the matings to one male (thus giving him a probability of paternity equal to one) as opposed to dividing the matings between two males. We then go on to look at whether it is ever better for the female to mate with more than two males. We use our results to discuss the analysis presented by Hartley & Davies (1994) concerning why female dunnocks (*Prunella modularis*) solicit matings from two males but do not encourage a third male to mate.

The basis of our approach is the standard trade-off between current and future reproductive success (see Roff 1992; Stearns 1992 for reviews). Each parent devotes an amount of effort to the current breeding attempt. The number of female young, $B(E)$, that survive to independence from this attempt is an

increasing function of the total effort, E , of all parents. The future reproductive success, f , of each parent is a decreasing function of its effort. The details of the modelling framework are given in table 1. This sort of approach was used by Houston & Davies (1985) to look for evolutionarily stable (ES) levels of parental effort in pairs (one female and one male) or trios (one female and two males) of dunnocks. Houston & Davies took the paternity of the two males in a trio to be given and explored how the ES effort of each of the birds depended on factors such as clutch size.

2. FEMALE'S OPTIMAL CHOICE OF PATERNITY

Polyandrous trios of dunnocks consist of one female and two males, which we refer to as the alpha and beta male. Although the alpha male is dominant to the beta male (see Davies (1992) for details of the dunnock's mating system), in this paper we assume that both males are identical in all respects. Assuming that the female is able to control both males' paternity of the brood, we use the model to predict the female's optimal choice of paternity. We consider whether the amount of paternal care of the brood is greater if the female only mates with one male (monogamy) or both males (polyandry). If the female mates with both males, we ask whether it is better for her to give each male an equal share of the matings or to give one male a higher proportion than the other, even if both males are identical.

Using the model we can predict a male's optimal effort given his paternity. A numerical example of this is shown in figure 1*a*. Each male's effort is plotted against the male's paternity, p . A male will provide no

Table 1

The model:

Fitness = number of female offspring surviving to maturity from current brood + reproductive success in the future.

Then for each parent:

$$\phi = pB(E) + f(e),$$

ϕ = the parent's fitness,

e = parent's effort,

E = total effort of all parents,

p = proportion of the brood which are offspring of the parent,

B function (of total parental care) describing survival of the brood,

f function (of parent's effort) describing parent's future reproductive success.

Solution:

Each parent's optimal effort given the effort of the others is fixed is given by the solution to

$$\frac{\partial \phi}{\partial e} = pB'(E) + f'(e) = 0.$$

The ESS efforts of all parents are given by the simultaneous solution of all parent's optimal efforts (given others are fixed) (see Houston & Davies (1985) for details).

Assumptions:

All parents are equal, no difference between alpha and beta status or between female and males.

Parental care additive (no interference between parents).

All chicks receive the same parental care.

Figure 1. An example of the predictions of the model using different alpha male paternity. (a) Example of predicted male and female effort: (i) alpha male effort for paternity p , (ii) beta male effort for paternity $1-p$, (iii) total male effort which is maximal when both males share paternity of the brood equally ($p = \frac{1}{2}$), (iv) corresponding female effort which is minimal at ($p = \frac{1}{2}$). (b) Corresponding parents' fitness: (i) alpha male, (ii) beta male, (iii) female which is maximal at paternity $p = \frac{1}{2}$.

care if his paternity is below a critical value (in some cases this may be zero, in which case a male will always provide care). Above this value the amount of care provided increases as paternity increases. Figure 1a also shows the total amount of male care to the brood plotted against the alpha male's paternity, p . In this example there is a maximum total male effort when $p = \frac{1}{2}$. Figure 1b shows the corresponding fitness of each parent. The female fitness is maximal when each male has equal paternity, i.e. $p = \frac{1}{2}$, whereas each male has maximal fitness when he has full paternity of the brood (at $p = 1$ alpha has maximal fitness, at $p = 0$ beta has maximal fitness). Thus we have a conflict between the female and the males with the female preferring polyandry and each male preferring monogamy. In general the female's fitness will be maximal (minimal) at the same alpha male paternity as when the total male effort is maximal (minimal). See Appendix 1 for a proof of this. Thus in the qualitative outcomes of the model we can consider total male effort and female fitness as being equivalent.

The qualitative outcomes of the model depend on the shapes of the functions $B(E)$ and $f(x)$. Figure 2a shows four different future fitness functions, $f(x)$. These are arbitrary algebraic functions which have been chosen to satisfy $f > 0$, $f' \leq 0$ and $f'' \leq 0$ (that is a parent's future reproductive success is a convex, decreasing function of the amount of care it provides) and hence have a similar biological meaning. Figure 2b shows the corresponding predictions of female fitness when these functions are used in the model. We see that even using very similar future fitness functions we can get very different predictions from the model. For one function we find that two males having equal paternity will provide the most care ($p = \frac{1}{2}$ is a maximum). It is also possible to predict that one male having full paternity will provide the most care and that two males having equal paternity will provide the least amount of care ($p = \frac{1}{2}$ is a global minimum), and therefore it is

Figure 2. The effect on the outcomes of predicted effort with paternity using different future fitness functions, f , in the model. (a) Four different future fitness functions: (i) $f(x) = 0.6(1 - (4x + 0.002)^3)$, (ii) $f(x) = 0.6(1 - (4x + 0.002)^2)$, (iii) $f(x) = 0.6(1 - (4x + 0.002)^3)$ and (iv) $f(x) = 0.625 - 0.025(100(4x^2) + 0.1 \cos(80x))$. All four satisfy $f' < 0$, $f'' < 0$. However, f'' is increasing for function (i), constant for (ii), decreasing for (iii) and non-monotonic for (iv). (b) The corresponding predictions of total male effort with alpha male paternity using the four different $f(x)$, (i)–(iv), shown in (a).

optimal for the female to mate with only one of the males. Alternatively, as can be seen from the outcome of the model using the fourth function, it is possible that giving both the males matings, but in unequal proportions will provide the most amount of male care. In the example shown (figure 2b), if the alpha male's paternity is $p = 0.85$, then the males will provide the highest total effort. We now analyse the model in detail and consider what general conditions on the fitness functions will cause these different outcomes.

We assume that $B(E)$ satisfies $B(E) \geq 0$, $B'(E) > 0$ and $B''(E) < 0$ (that is the chick survival rate increases with total parental care at a decelerating rate). We find that if the second derivative of f , f'' , is strictly monotonic or constant then the actual details of $B(E)$ do not affect the outcome of the model and the optimal choice for the female is either to give each male equal paternity or only to mate with one male, but never to mate with both males in unequal proportions. In

particular if $E(p)$ is the total parental effort as a function of the alpha male paternity then we have:

$$f'' \text{ strictly increasing} \Rightarrow E(p) \text{ has a minimum at } p = \frac{1}{2}; \quad (1)$$

$$f'' \text{ constant} \Rightarrow E(p) \text{ is locally constant around } p = \frac{1}{2}; \quad (2)$$

$$f'' \text{ strictly decreasing} \Rightarrow E(p) \text{ has a local maximum at } p = \frac{1}{2}. \quad (3)$$

See Appendix 2 for analysis.

If f satisfies condition (1) then the female always does best if she gives exclusive matings to one male. If f satisfies condition (3) then she does better if she shares matings equally between the two males (unless the effects of a male providing no care at low paternity cause her fitness to be higher if she gives matings exclusively to one male). If f satisfies condition (2) and $f'(0) = 0$, then $E(p)$ will be globally constant and the female's fitness will be unaffected by the males' paternity. If f satisfies condition (2) and $f'(0) \neq 0$ then a male will provide no care when his paternity is low and this will cause the female's fitness to be greatest at $p = 0$ or 1. The female will do best by mating with only one male.

If f does not satisfy any of the above conditions (i.e. f'' is not strictly monotonic or constant) then the details of the function $B(E)$ affect the predictions of the model. It is possible that the female's fitness is maximized at some paternity $\tilde{p} \neq 0, \frac{1}{2}, 1$ even though both males are identical (see example in figure 2). Then it would be optimal for the female to split the matings unequally between the males (e.g. give 85 % of matings to the alpha male and 15 % to the beta male). If this is the case then the actual value of the optimal paternity will depend on both the functions B and f .

Given biological data on the detrimental effect of parental care on a parent's future reproductive success we may be able to determine conditions for f and f' . However, it is highly unlikely that we would ever be able to say whether the second derivative of f satisfies one of the above conditions.

Harada & Iwasa (1996) consider the case in which the future fitness function is a power function, $f(x) \propto x^k$, $k > 1$. They show that as long as B satisfies $B' > 0$, $B'' \leq 0$ then the details of B are irrelevant and the criterion which determines whether the female prefers polyandry or monogamy is whether the power, k , is greater or less than two. We have shown that this result generalizes to a condition for any function f satisfying $f \geq 0$, $f' \leq 0$ and $f'' \leq 0$. If the second derivative of f is monotonic and B satisfies $B' > 0$, $B'' \leq 0$, then the details of B are irrelevant. The criterion as to whether $p = \frac{1}{2}$ is a local maximum or minimum of total male effort is whether the second derivative of f is increasing or decreasing (as long as the effect of the males dropping out at low paternities is not great this is also the criterion separating the female's preference for monogamy or polyandry). We have also shown that if the second derivative of f is not monotonic then the details of B do matter and we can get more complicated predictions of total male effort with maximums

(minimums) at a paternity other than 0, 1 or $\frac{1}{2}$. Using a power function, Harada & Iwasa also predict that even if the males are unequal in terms of their future fitness, then whether the power is less than or greater than two will imply monogamy or polyandry. It is not so clear for more general functions. Even if polyandry is optimal for the female with two identical males, when the males are not identical the effect of them dropping out at low paternities can cause monogamy to be the preferred mating system.

3. OPTIMAL NUMBER OF MALES

In polyandrous trios of dunnocks, although the female dunnock tries to escape the alpha male and mate with the beta male she will tend to reject matings from a third male (Hartley & Davies 1994). Hartley & Davies suggest that the female is actively limiting the number of males in the polyandrous group to two, and that this may be because two males provide more care than three or more. We now extend the model to allow any number of males in the group. A simple way to do this is to assume that all males have equal paternity. So, if there are n males in the system then we will assume that each male has paternity $1/n$. Consequently each male will provide the same amount of care and the model reduces to two equations:

$$\phi_f = B(\hat{x}(n) + n\hat{y}(n)) + f(\hat{x}(n)),$$

$$\phi_m = \frac{1}{n}B(\hat{x}(n) + n\hat{y}(n)) + f(\hat{y}(n)),$$

where ϕ_m is a male's fitness and $\hat{x}(n)$ and $\hat{y}(n)$ are the female's effort and the male's effort as functions of the number, n , of males in the model. We then solve the model to predict the total amount of male care in a group of n males. Using a similar argument to that in Appendix 1, it can be shown that the female's fitness is maximal (minimal) when the total male effort is maximal (minimal). Hence the predicted total male effort is qualitatively equivalent to the predicted female fitness. Figure 3a shows four different future fitness functions, f , and figure 3b shows the corresponding outcomes when these functions are used in the model. Using function (iii) the model predicts that the total male effort will always increase as we add more males. Using function (ii) it predicts that the total male effort will remain constant however many males we add to the group. Function (iv) predicts that the total male effort will always decrease as we add more males. Function (i) predicts that the optimal number of males is two and if we add more males beyond this number the amount of male effort will decrease. Given the differences in these results we then ask what conditions on the fitness functions are necessary for there to exist an optimal number of males and what does this number depend on?

From the analysis in Appendix 3 we see that if $f'(0) = 0$ and $f'' > 0$, then the total male effort increases as the number of males increases. Thus the more males the better. However, this is unrealistic biologically because we have ignored effects such as

Figure 3. The effect on the outcomes of predicted effort with number of males in the group using different future fitness functions, f , in the model. (a) Four different future fitness functions: (i) $f(x) = 0.8(1 - \exp(-2.4(1 - 4x)))$, (ii) $f(x) = 0.6(1 - (4x)^3)$, (iii) $f(x) = 0.6(1 - (4x)^2)$, (iv) $f(x) = 0.6(1 - (4x)^{\frac{3}{2}})$. (b) The corresponding predictions of total male effort against number of males from the model using the four functions (i)–(iv) in (a).

interference between the males. If $f'(0) = 0$ and $f'' < 0$ then the total male effort decreases as the number of males increases (i.e. one male is optimal). If $f'(0) < 0$ and $f'' > 0$ then there exists an optimal number of males $\tilde{n}$. The actual value of $\tilde{n}$ for which the total male effort is highest will also depend on the details of the function B .

4. HARTLEY & DAVIES (1994)

Hartley & Davies (1994) show a relationship between male effort and paternity from data obtained from groups of one female with two males. They then use this relationship to predict how total male effort will change as more males are added to the group. Unlike our model they assume that the amount of care a male will provide depends only on his paternity and not on the efforts of any of the other parents. They use this to predict that the total male care will decrease (or stay the same) as more males are added to the system,

Figure 4. Male effort predicted from two different methods: using the model with n males present or using predicted data from the model with two males to extrapolate to n males. (a) The change in the shape of the alpha male effort when an increasing number of males are in the group. (i) Alpha and beta, (ii) alpha plus two others, (iii) alpha plus four others, (iv) alpha plus 10 others. (b) Total male effort in groups of n males: (i) using the model with two males to extrapolate to an n male system, (ii) predicting from the model with n males, predicting a smaller optimal number of males than by the method in (i).

and hence two males will provide the most care. Is it reasonable to extrapolate data to a three- (or more) male system from data from a two-male system? Figure 4a shows a numerical example of how a male's level of care, given his paternity, may vary as the number of males is increased. Figure 4b shows two predictions of total male effort in groups consisting of n males. The first prediction is obtained by using results of the model with two males to extrapolate to n males. The second prediction uses data from solving the model with n males. Numerical results suggest that extrapolating data from a two-male system will predict the same or a greater optimal number of males than predicting from the n male system. For example, suppose the model with n males predicts that three males is optimal. Then using results from the model with two males to extrapolate to n males would predict either three or four or more males is optimal. Thus, if using a two male system to extrapolate to any number of males, we predict that two males is optimal; then from taking the model with n males we would also predict that two males is optimal.

The prediction of Hartley & Davies that two males is optimal for the female relies very much on the relationship of male effort against paternity which they fit to their data. They use a quadratic curve to relate the amount of feeds to the brood per hour by the alpha male to his paternity but use a linear fit to relate the beta male's care to his paternity. If slightly different curves are fitted to the data then we may get very different predictions. To see this let us assume that a male's effort depends only on his status (alpha or beta) and his paternity. Let $\alpha(p)$ be the alpha male's effort, given his paternity is p , and $\beta(p)$ be a beta male's effort given his paternity is p . If we have two males, then total male effort = $\alpha(p) + \beta(1-p)$, and this is maximized at $\tilde{p}$, where $\alpha'(\tilde{p}) - \beta'(1-\tilde{p}) = 0$. If $\beta(p)$ is linear (as Hartley and Davies assume), say $\beta(p) = bp$, then the female's optimal choice of paternity $\tilde{p}$ satisfies $\alpha'(\tilde{p}) = b$ (i.e. $\tilde{p}$ is the point where the functions of the alpha and beta male efforts have the same gradient). In general this will not be at $p = \frac{1}{2}$.

We now consider predicting total male care for n males. Following Hartley & Davies, we assume that we have one alpha male and $n-1$ beta males, with all males having equal paternity. Then:

$$\text{total male effort} = \alpha\left(\frac{1}{n}\right) + (n-1)\beta\left(\frac{1}{n}\right),$$

which will be maximized at $\tilde{n}$ where $\tilde{n}$ satisfies

$$-\frac{1}{\tilde{n}^2}\alpha'\left(\frac{1}{\tilde{n}}\right) - \frac{(\tilde{n}-1)}{\tilde{n}^2}\beta'\left(\frac{1}{\tilde{n}}\right) + \beta\left(\frac{1}{\tilde{n}}\right) = 0.$$

If, again, $\beta(p) = bp$ then the optimal number of males, $\tilde{n}$, satisfies $\alpha'(1/\tilde{n}) = b$. Thus $\tilde{n} = 2$ only if $\tilde{p} = \frac{1}{2}$ which will not be the case in general. Alternatively if we fix the alpha male's paternity at say q , and assume that the beta males share the remaining paternity equally, then

$$\begin{aligned} \text{total male effort} &= \alpha(q) + (n-1)\beta\left(\frac{1-q}{n-1}\right) \\ &= \alpha(q) + b(1-q) \quad \text{if } \beta \text{ is linear.} \end{aligned}$$

This is constant for any given q . Thus the total male effort will not change as more males are added.

If the beta effort is not predicted to increase linearly with paternity then we may get different results. For instance, if both alpha and beta are predicted to react identically, $\alpha(p) = \beta(p)$, then the optimal paternity is at $p = \frac{1}{2}$ and

$$\begin{aligned} \frac{\partial}{\partial n}[\text{total male effort}] &= \frac{\partial}{\partial n}\left[n\alpha\left(\frac{1}{n}\right)\right] \\ &= -\frac{1}{n}\alpha'\left(\frac{1}{n}\right) + \alpha\left(\frac{1}{n}\right). \end{aligned}$$

If $\alpha(p)$ is a smooth, convex curve with $\alpha(0) = 0$, then $\partial/\partial n[\text{total male effort}] > 0$ for all n . This predicts that the more males there are the greater the total male effort is. So if a quadratic fit is made to both alpha and beta males' efforts then it is predicted that total male effort increases as more males are added.

5. DISCUSSION

Using a simple game theoretical model to predict levels of parental care, and hence female fitness, we have shown that subtle differences in the shape of the fitness functions assumed in the model produce very different predictions. We have kept the model simple; we assume that all the parents are identical in terms of their future reproductive success and that the efforts of all parents contribute additively to chick care with no interference between parents. In dunnoek groups the alpha male is dominant to, and often older than, the beta male (Davies 1992). Therefore differences in terms of future reproductive success between the males are likely. If the efforts of the parents are not simply added to give total care to the chick, for instance if we assume that the beta male is less efficient at providing care, then we have further complications. In this paper we have restricted attention to how the fitness functions affect the underlying model without these added complications and have been able to establish general analytic results for this case.

There is evidence that the dunnoek mating system involves conflict between the males (who each want full paternity of the brood) and the female who wants both males to provide care (and therefore must mate with both of them) (Davies & Houston 1986; Davies 1990, 1992). In the examples in this paper when the female fitness is maximal at $p = \frac{1}{2}$, then each male's fitness is maximal when he has full paternity, and thus this conflict is predicted. But not all cases will produce this conflict. Results show that in some cases a male's fitness will be maximal at a paternity less than one and therefore the alpha male will want the beta male to obtain some of the matings and there will be less conflict between the males. It is hard to establish general results on whether a male's fitness will be maximal at $p = 1$ or whether it will be maximal at $p < 1$.

By assuming different functions in the model it is possible to predict that the female will do best by mating with only one male, by mating equally with both males, or by mating with both males in unequal proportions (even though both males are identical).

Assuming the function relating the total parental care to the fitness gain from the current brood, B , is an increasing function with a decreasing slope ($B \geq 0$, $B'' < 0$), we have found general conditions on f which produce various outcomes of total male effort from the model. The slope of the second derivative of f is critical in determining whether two males provide more care than one. Given that this is the case, then whether $f'(0) = 0$, or not, is crucial to whether the model predicts that there exists an optimal number of males which provide the most paternal care.

We realize that it is difficult to obtain information on the relationship between parental effort and future reproductive success, f , and on f' in any particular system, and even harder to obtain information on f'' . We do not, however, think that this reduces the relevance of our results. One of the goals of theory is to establish general patterns. We have given a complete characterization of how the underlying fitness functions

affect the outcomes of our model. If crucial information about the relationship between parental care and future reproductive success cannot be obtained, then our results show that sweeping statements about how many males it is optimal for a female to mate with cannot be made.

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APPENDIX 1

Result

Maximizing total male effort with respect to p is equivalent to maximizing female fitness with respect to p , assuming $B' > 0$.

Proof

Let the optimal total male effort as a function of p be $E_m(p)$ and the female's optimal effort be $\hat{x}(p)$. Then the female's fitness is given by $\phi_f = B(\hat{x}(p) + E_m(p)) + f(\hat{x}(p))$. Differentiating with respect to p gives

$$\begin{aligned} \frac{d\phi_f}{dp} &= B'(\hat{x}(p) + E_m(p)) \left\{ \frac{d\hat{x}}{dp} + \frac{dE_m}{dp} \right\} + f'(\hat{x}(p)) \frac{d\hat{x}}{dp} \\ &= \{B'(\hat{x}(p) + E_m(p)) + f'(\hat{x}(p))\} \frac{d\hat{x}}{dp} \\ &\quad + B'(\hat{x}(p) + E_m(p)) \frac{dE_m}{dp}. \end{aligned}$$

But $B'(\hat{x}(p) + E_m(p)) + f'(\hat{x}(p)) = 0$ since the female's effort is optimal. So

$$\frac{d\phi_f}{dp} = B'(\hat{x}(p) + E_m(p)) \frac{dE_m}{dp}.$$

Assuming that $B' > 0$, then $B'(\hat{x}(p) + E_m(p)) > 0$, and we have

$$\frac{dE_m}{dp} < 0 \Rightarrow \frac{d\phi_f}{dp} < 0, \quad \frac{dE_m}{dp} > 0 \Rightarrow \frac{d\phi_f}{dp} > 0$$

$$\text{and } \frac{dE_m}{dp} = 0 \Rightarrow \frac{d\phi_f}{dp} = 0.$$

APPENDIX 2

The fitness of each parent is given by

$$\phi_f = B(E) + f(x),$$

$$\phi_\alpha = pB(E) + f(y_\alpha),$$

$$\phi_\beta = (1-p)B(E) + f(y_\beta),$$

where ϕ_f , ϕ_α , ϕ_β , x , y_α , y_β are the female's, alpha and beta male's fitness and efforts respectively, and total effort $E = x + y_\alpha + y_\beta$.

Let $\hat{x}(p)$ and $\hat{y}(p)$ be the female's optimal effort and a male's optimal effort as functions of the alpha male paternity, p (males are assumed to be identical). Let $\hat{E}(p) = \hat{x}(p) + \hat{y}(p) + \hat{y}(1-p)$ be the total parental effort as a function of p .

Then these optimal efforts of each parent satisfy

$$0 = B'(\hat{E}(p)) + f'(\hat{x}(p)),$$

$$0 = pB'(\hat{E}(p)) + f'(\hat{y}(p)),$$

$$0 = (1-p)B'(\hat{E}(p)) + f'(\hat{y}(1-p)).$$

Let $g = (-f')^{-1}$ and $k(p) = B'(\hat{E}(p))$, then $\hat{x}(p) = g(k)$ and $\hat{y}(p) = g(pk)$. $k(p) = B'(g(k) + g(pk) + g((1-p)k))$ and differentiating with respect to p gives:

$$k'(p) = B''(\theta) \{g'(k)k' + g'(pk)[k + pk'] + g'((1-p)k)[-k + (1-p)k']\},$$

where

$$\theta = g(k) + g(pk) + g((1-p)k).$$

So

$$k'\{1 - B''(\theta)[g'(k) + pg'(pk) + (1-p)g'((1-p)k)]\} = B''(\theta)\{k[g'(pk) - g'((1-p)k)]\}. \quad (1)$$

If we assume that $f > 0$, $f' < 0$ (which implies $g > 0$), and $f'' < 0$ ($\Rightarrow g' > 0$), and that $B \geq 0$, $B' \leq 0$, and $B'' < 0$, then the left hand side of equation (1) is positive, and

$$k'(p) \begin{cases} < 0 & \text{if } g'(pk) - g'((1-p)k) > 0 \\ = 0 & \text{if } g'(pk) - g'((1-p)k) = 0 \\ > 0 & \text{if } g'(pk) - g'((1-p)k) < 0. \end{cases}$$

If g' is strictly monotonic (equivalently f'' is strictly monotonic), then the only solution to $k'(p) = 0$ (and hence $\hat{E}'(p) = 0$) is $p = \frac{1}{2}$. In particular:

$$f'' > 0 \Rightarrow g'' > 0 \Rightarrow k(\frac{1}{2}) \text{ is a maximum}$$

$$\Rightarrow E(\frac{1}{2}) \text{ is a minimum,}$$

$$f'' < 0 \Rightarrow g'' < 0 \Rightarrow k(\frac{1}{2}) \text{ is a minimum}$$

$$\Rightarrow E(\frac{1}{2}) \text{ is a maximum.}$$

If f'' is not monotonic then it is possible that there exists $\tilde{p} \neq \frac{1}{2}$ such that $\hat{E}'(\tilde{p}) = 0$ and hence the female's fitness is maximized (or minimized) at $\tilde{p}$.

APPENDIX 3

Let $g = (-f')^{-1}$. Assuming the following conditions on the functions B and f :

$$B > 0, B' > 0, B'' < 0,$$

$$f > 0, f' < 0, f'' < 0 \text{ (which implies that } g > 0 \text{ and } g' > 0).$$

Let $\hat{x}(n)$ and $\hat{y}(n)$ be the functions giving the optimal female and male efforts when n males are present, all having equal paternity $p = 1/n$.

Let $k(n) = B'(\hat{x}(n) + n\hat{y}(n))$. Then $\hat{x}(n) = g(k(n))$ and

$$\hat{y}(n) = g\left(\frac{1}{n}k(n)\right).$$

So

$$k(n) = B'\left(g(k) + ng\left(\frac{1}{n}k\right)\right),$$

and

$$k'(n) = B''(\theta) \left\{ g'(k)k' + ng'\left(\frac{k}{n}\right) \left[\frac{1}{n}k' - \frac{1}{n^2}k \right] + g\left(\frac{k}{n}\right) \right\},$$

$$k' \left[1 - B''(\theta)g'(k) - B''(\theta)g'\left(\frac{k}{n}\right) \right] = B''(\theta) \left\{ g\left(\frac{k}{n}\right) - \frac{k}{n}g'\left(\frac{k}{n}\right) \right\},$$

where

$$\theta = g(k) + ng\left(\frac{1}{n}k\right).$$

Now $g' > 0$ and $B'' > 0$ (because of the conditions on f and B) hence:

$$k'(n) \begin{cases} < 0 & \text{if } g\left(\frac{k}{n}\right) - \frac{k}{n}g'\left(\frac{k}{n}\right) > 0 \\ = 0 & \text{if } g\left(\frac{k}{n}\right) - \frac{k}{n}g'\left(\frac{k}{n}\right) = 0 \\ > 0 & \text{if } g\left(\frac{k}{n}\right) - \frac{k}{n}g'\left(\frac{k}{n}\right) < 0. \end{cases}$$

Now $g(x) - xg'(x) = 0$ has a solution if $g(\tilde{x}) = 0$ for some $\tilde{x} \neq 0$ and $g' > 0$ and $g'' < 0$. So

$$\exists \frac{k(n)}{n} \text{ such that } g\left(\frac{k(n)}{n}\right) - \frac{k(n)}{n}g'\left(\frac{k(n)}{n}\right) = 0$$

$$\Leftrightarrow f'(0) \neq 0 \text{ and } g'' < 0 \text{ (i.e. } f'' < 0).$$