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Fertility Assurance through Extrapair Fertilizations and Male Paternity Defense

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Extrapair paternity has been observed in many formally monogamous species. Male pursuit of extrapair fertilizations is explained by the advantages of having offspring that receive essential paternal care from other males. Since females are capable of exercising a degree of control over the post-copulatory sperm competition, extrapair paternity cannot persist unless it confers fitness benefits on cuckolding females. Thus, extrapair paternity involves cooperation between mated females and extrapair males. On the other hand, paired males frequently exhibit strategies that minimize their loss of paternity and/or conserve paternal investment if paternity is lost. Hence, extrapair attributes of diverse species and populations reported in the literature are particular solutions of *evolutionary games* involving gender-specific cuckolding/anti-cuckolding strategies. Here we use methods of evolutionary game theory to study the role of male paternity guarding strategies in situations where females seek extrapair fertilizations for reasons of genetic compatibility and/or in pursuit of genetic diversity for their offspring. Our results indicate that in these circumstances pursuit of extrapair fertilizations is the only evolutionary stable female strategy. Males, on the other hand, have two, mutually exclusive, evolutionary stable strategies: full time pursuit of extrapair fertilizations and a compromise strategy wherein they protect in-pair paternity during their mate's fertile periods and pursue extrapair paternity the rest of the time. The relative merits of these two strategies are determined by the efficiency of male in-pair paternity defense, breeding synchrony, fitness advantages of extrapair over in-pair offspring, and the intensity of competition for extrapair fertilizations from floater males.

1. Introduction

Advent of the molecular techniques used to assign paternity (Jeffreys *et al.*, 1985) has revealed that many socially monogamous species exhibit *extrapair paternity* (EPP), i.e. at least some of the female's young are not descendants of her social mate (cf. Burke, 1989). The incidence of EPP varies extensively. In some species, extrapair paternity is absent or occurs at very low frequencies, while in others the majority of broods contain extrapair young. Furthermore, this variation is not restricted to distantly related species with markedly different ecologies. There are also significant differences between different species of the same genus, different populations of the same species, and even within individual populations over time (Petrie & Kempenaers, 1998).

Male pursuit of extrapair fertilizations is explained by the advantages of having offspring

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that receive essential paternal care from other males. However, observations reveal that mixed paternity is often associated with active female solicitation of extrapair copulations (Kempenaers *et al.*, 1997; Currie *et al.*, 1998; Stutchbury, 1998). Furthermore there is evidence that females are more than passive recipients of sperm, and exercise at least a degree of control over post-copulatory *sperm competition* (Birkhead & Møller, 1993; Møller & Briskie, 1995; Dunn *et al.*, 1999). Thus, persistence of extrapair paternity indicates that females derive net fitness benefits from having extrapair young. These benefits fall into several distinct classes (Jennions & Petrie, 2000), and each class is associated with a distinct type of female reproductive strategies. On the other hand, paired males can benefit by evolving strategies that minimize paternity loss and/or conserve paternal investment should paternity be lost.

Consequently, extrapair paternity phenomena involves interplay among female and male inter- and intragender reproductive strategies (heritable behavioral phenotypes). In these interactions the Darwinian fitness of the involved phenotypes (and hence of the underlying genotypes) depends, among other things, on the distribution of the phenotypes in question within a population. In other words, extrapair characteristics of diverse species and populations reported in the literature are particular solutions of *evolutionary games* (cf. Weibull, 1996) involving combinations of gender-specific cuckolding and anti-cuckolding strategies. Thus, in our view, thorough understanding of the extrapair phenomena, and its place in the general framework of mating systems, depends on supplementing empirical studies with mathematical analysis using game theoretical methods.

Mating involves female pursuit of optimal *genetic* endowment for their offspring. However, in situations where raising offspring requires an extensive male parental investment, females must form a social bond in order to secure such an investment (cf. Black, 1996). *Extrapair fertilization* (EPF) may provide a viable evolutionary compromise between these two, potentially conflicting, tendencies. In particular, females that are forced to pair with inferior males can solicit extrapair fertilizations from superior males to obtain *better genes* for their offspring—reviewed by Petrie & Kempenaers (1998).

However, better genes explanation of the female pursuit of extrapair paternity implies existence of an unidimensional scale of male desirability with respect to both social mates and extrapair partners. While instances of such uniformity of female preference are well documented (cf. Møller, 1997), the situation is by no means universal. There are reports indicating that attractive males may be cuckolded by less attractive neighbors (cf. Lifjeld *et al.*, 1997), and that territorial males may be cuckolded by non-territorial *floaters* (cf. Ewen *et al.*, 1999). Thus we must conclude that better genes hypothesis cannot be the sole explanation for female pursuit of extrapair fertilizations.

Mixed paternity of the female's offspring is not unique to socially monogamous species with extrapair fertilizations. In their seminal review of mixed paternity Jennions & Petrie (2000): (i) argue that female control of fertilization precludes mixed paternity based on purely *material* benefits, and (ii) demonstrate that pursuit of superior genes is unlikely to be the only *genetic* reason for a female to mate with more than one male in a single reproductive cycle.

Briefly: Better genes explanation applies only when all females in a population benefit by mating with certain males. However, there are at least two reasons why such situations cannot be universal.

1.1. FERTILITY ASSURANCE

Since genetic incompatibility leads to infertility, there may be variation in what constitutes an ideal genetic partner for individual females. Hence, females may evolve to mate polyandrously and use *in copula* and/or *post-copulatory* mechanisms to ensure preferential fertilization by sperm that increase genetic benefits to their offspring (Zeh & Zeh, 1996, 1997).

1.2. BET HEDGING

Since environments vary in unpredictable ways, variable genotypic offspring offer a better chance of winning—or at least not loosing completely—in the "evolutionary lottery".

Hence, multiple mating may be selected because it increases genetic diversity among the progeny —reviewed by Seger & Brockmann (1987).

Jennions & Petrie (2000) do not base these particular conclusions on the studies of extrapair paternity. However, some recent reports (Strohbach *et al*., 1998; Krokene *et al*., 1998; Kempenaers *et al*., 1999) describe populations where female choice of extrapair partners is more consistent with pursuit of fertility assurance and/or genetic diversity than a pursuit of better genes.

Female extrapair success depends, among other things, on the efficiency of the anti-cuckolding strategies exercised by their mates. Male anti-cuckolding strategies fall into two categories.

1.3. PATERNITY DEFENSE STRATEGIES

The most straightforward paternity defense strategy is *mate guarding*—males maintain close guard over their fertile mates (cf. Wagner *et al*., 1996; Chuang-Dobbs *et al*., 2001). In populations where ecological constraints compel separation between social mates during female's fertile periods, males exhibit an alternative strategy of trying to swamp out possible competitors' sperm through *frequent copulation* (cf. Hunter *et al*., 1992; Komdeur *et al*., 1999). The principal male cost of the paternity assurance strategies is the loss of the EPP opportunities. That is, due to time constraints in mate guarding, and sperm depletion in frequent copulation—protection of in-pair paternity and pursuit of extrapair paternity activities are mutually exclusive (Birkhead & Møller, 1992; Chuang-Dobbs *et al*., 2001). Hence, males have been known to adopt a compromise strategy of protecting in-pair paternity during their mate's fertile periods and pursuing extrapair paternity for the remainder of the breeding season (cf. Currie *et al*., 1998).

1.4. PATERNAL EFFORT CONSERVING STRATEGIES

If paternity defense fails, males face the possibility of investing paternal care in unrelated young. One possible male response is to deny parental care to offspring whose paternity is uncertain. However, extrapair paternity is associated with situations where males are incapable of distinguishing between their own and extrapair young (Kempenaers & Sheldon, 1996). Hence, when paternity is uncertain, males can only respond by withdrawing, or at least reducing, parental care to all of female's offspring (cf. Dixon *et al*., 1994; Cézilly & Nager, 1995; Sheldon *et al*., 1997). The principal cost of this anti-cuckolding strategy is that reduction in paternal care injures male's own, as well as the extrapair offspring.

In this paper we formulate and analyse an evolutionary game addressing situations where female reasons for pursuit of extrapair fertilizations are fertility assurance and/or bet hedging, and male strategies involve choices between the protection of their in-pair paternity and the pursuit of extrapair paternity.

2. Formulation of the Game

Following commonly used approaches in evolutionary game theory (e.g. Maynard Smith, 1982), we consider the evolution of genetic strategies in a simplified uniform population in which all individuals are of the same quality (i.e. we formulate the game in terms of population averages). This implies, for example, that we will consider only the average values of parameters like mate guarding efficiency or breeding synchrony, while in fact we know that these parameters are different for a particular high-quality individual who is very efficient in mate guarding and breeds very early. This commonly used simplification does not allow therefore to explore the role of individual variation in quality in generating variable strategies within populations (e.g. Fishman *et al*., 2001). Yet, it is highly useful in the initial exploration of how variation in strategies across populations (or species) can be explained as different solutions of evolutionary games played under different ecological or genetical parameters.

Because, in the current context, mate guarding and frequent copulation strategies have the same analytical description, we shall not make a distinction between the two. That is, in the present model, we address the properties of a generic *paternity-preserving* male strategy.

For the sake of simplicity in this, initial exploration of a very complex subject, we shall assume that the modeled species are socially monogamous. Hence, the numbers (densities) of mated males and females are equal, and therefore frequencies of the gender-specific reproductive strategies can be used in lieu of the numbers of individuals exhibiting these strategies. We shall further postulate that reproduction requires possession of a nesting site and/or foraging territory. Thus, the modeled population is divided into territorial, *resident* pairs and non-territorial *floaters*. We start by considering the gender-specific strategies of the resident individuals.

2.1. GENDER-SPECIFIC STRATEGIES

2.1.1. *Female Strategies*

As discussed above, female pursuit of fertility assurance and/or genetic diversity is tantamount to the absence of pre-copulatory preferences in selecting either social or extrapair mates. Because only territorial males can provide material benefits that are essential for reproduction, all females will try to pair with such males. Moreover, we have no reason to assume any specific association between the types of resident males' strategies considered in this paper and control of resources. Thus, since control of resources is a sole criterion of a male's desirability as a social mate in the current context, we do not expect any specific correlation between resident males' strategies and female mating preferences. Finally, resident females that seek extrapair fertilizations should pursue diversity in extrapair copulations, and use *in copula* and/or *post-copulatory* mechanisms to select optimal genetic partners (Zeh & Zeh, 1997).

Thus we have to consider two female strategies: (resident) females that seek extrapair fertilizations, $\mathbf{F}_E$; and females that do not seek extrapair fertilizations, $\mathbf{F}_N$. As we shall see below, under the assumptions of our model (in particular, that seeking EPF is cost free), the advantage of $\mathbf{F}_E$ over $\mathbf{F}_N$ is quite intuitive, which may allow to discard the later strategy and to simplify the model. We chose, however, to consider both strategies in the model in order to illustrate this point formally, and to facilitate future exploration of the model under different assumptions (see the discussion).

2.1.2. *Male Strategies*

As discussed in the introduction, paternity guarding and EPF seeking activities are mutually exclusive. Thus, there are two possible strategies for resident males.

- Individuals who pursue opportunities for extrapair fertilizations while neglecting protection of their in-pair paternity, $\mathbf{M}_{EE}$. Here the first (subscript) E represents pursuit of EPFs at the expense of protecting in-pair paternity, and the second represents pursuit of EPFs when this activity does not conflict with protecting in-pair paternity.
- Individuals who adopt a compromise strategy of protecting in-pair paternity during their mate's fertile periods and pursuing extrapair paternity opportunities the rest of the time, $\mathbf{M}_{GE}$. Thus $\mathbf{M}_{GE}$ players gain a higher measure of reproductive success within their own nests at the expense of loosing a fraction p of extrapair reproductive opportunities. The magnitude of p depends on the breeding synchrony within a population. For example, in the hypothetical case of a completely asynchronous breeding (i.e. there is no overlap in the fertile periods of the resident females) the value of p would be equal to zero. At the other extreme, what of complete synchronization (i.e. a complete overlap in the fertile periods among the resident females), the value of p would be unity. Quite apart from observational evidence to the contrary (cf. Currie *et al.*, 1998), elementary probability theory (cf. Hoel *et al.*, 1971) indicates that a complete absence of overlap in the fertile periods of the resident females is highly unlikely. Thus, for the remainder of this paper, $0<p\leqslant 1$. Note that in contrast with earlier models in which breeding synchrony constrains male infidelity (cf. Maynard Smith, 1977; Knowlton, 1979), in the present case of seeking EPF through a quick sexual encounter, no such constraints need to be considered. $\mathbf{M}_{EE}$ males can easily seek EPFs during their in-mate fertile period, and the number of other females available at this period

is actually higher when breeding synchrony is high (see Stutchbury & Morton, 1995).

Let us define the frequency of the $\mathbf{F}_E$ players by $0 \leqslant x \leqslant 1$, and the frequency of the $\mathbf{M}_{EE}$ players by $0 \leqslant y \leqslant 1$. In these terms the gender-specific strategy sets are given by

$$X = \left\{(x, 1-x)^{\mathrm{t}} | 0 \leqslant x \leqslant 1\right\},$$

and

$$Y = \left\{(y, 1-y)^{\mathrm{t}} | 0 \leqslant y \leqslant 1\right\}. \tag{1}$$

Remark 1. To recollect, strategies such as $\mathbf{F}_E$ through $\mathbf{M}_{EE}$: which are represented by the integer values zero and one of x and y in the current model, are known as *pure strategies*. Whereas strategies for which either x or y take fractional values—in effect "mixing" the pure strategies—are known as *mixed strategies*. There are two types of real word situations that give raise to mixed strategies.

- *Population level polymorphism* wherein each individual exhibits a specific pure strategy, but there is more than one pure strategy present on the population level.
- Alternatively, individuals may exhibit behavior corresponding to different pure strategies at different times. In such situations, it is useful to think of pure strategies as extreme cases, delimiting the range of the possible individual behavior.

Remark 2. For logical completeness we should have added two more male pure strategies. (a) Individuals who protect their in-pair paternity but do not seek extrapair fertilizations, $\mathbf{M}_{GN}$. (b) Individuals who are neither paternity guarding, nor EPF seeking, $\mathbf{M}_{NN}$. However, it is easy to see that $\mathbf{M}_{GN}$ strategy is indistinguishable from $\mathbf{M}_{GE}$ strategy when extrapair fertilizations are not available and inferior to $\mathbf{M}_{GE}$ otherwise. Analogously, $\mathbf{M}_{NN}$ strategy is undistinguishable from $\mathbf{M}_{EE}$ strategy whenever extrapair fertilizations are not available and inferior to the $\mathbf{M}_{EE}$ otherwise.

Remark 3. Recent evidence (cf. Saino *et al.*, 1999) suggests that males do not control the timing of their mates' fertile periods. Thus, $\mathbf{M}_{GE}$ strategy is predicated on male ability to detect fertility in their mates. Since $\mathbf{M}_{GE}$ strategy is defined on the basis of actual observations (Currie *et al.*, 1998), we know that—at least in some bird species—males do posses the ability to detect fertility in females. However, for the sake of logical completeness, we have to address the issue of male–female interplay in, hypothetical, populations where males lack an ability to detect fertility in females. Clearly, in such situations males have the choice of either giving up any attempts to protect their in-pair paternity, or giving up any attempts to seek extrapair paternity. That is, analytically, this situation is identical to the populations with male fertility detection and complete breeding synchrony represented in the current model as the specific instance $p = 1$.

Remark 4. Until recently it was thought that floaters do not reproduce (cf. Alcock, 1993). However, recent reports show that floater males can gain limited reproduction success via extrapair fertilization of resident females (Barber & Robertson, 1999; Ewen *et al.*, 1999; Peer *et al.*, 2000). As discussed above, when fertility assurance or bet hedging is the female reason for the pursuit of extrapair fertilizations, we would expect females to seek copulations with as diverse a set of males as possible. In particular, we would expect some extrapair fertilizations to be effected by floater males (Kempenaers *et al.*, 1999). Thus, extrapair fertilization of resident females by floater males is an integral feature of the present model.

Remark 5. An increase in the frequency of $\mathbf{M}_{EE}$ males increases the frequency of $\mathbf{F}_E$ females that are free to compete for extrapair fertilizations. However, since male reproductive potential is higher than female reproductive potential (i.e. a male can fertilize several females) the increase in the frequency of $\mathbf{M}_{EE}$ males should lead to net increase in the *per capita* reproductive opportunities for EPF seeking females.

2.2. FEMALE PAYOFFS

In birds, eggs are produced and fertilized individually. Let us denote an average *per* female number of eggs produced during a breeding season by "n". Hence, at least to a first approximation, it is reasonable to model female pursuit of extrapair fertilizations during the breeding season as a sequence of n independent repetitions of a success/failure random experiment—a *binomial distribution*.

To define the probability of success for an individual trial (gaining extrapair fertilization for an individual egg), we reason as follows. Let us start with an unguarded female. As discussed above, the probability that this female can gain extrapair fertilization increases with the increase in the numbers of the EPF seeking males, and decreases with the increase in the numbers of EPF seeking females. To recollect, we have defined the frequency of the $\mathbf{F}_E$ players by $0 \leqslant x \leqslant 1$, and the frequency of the $\mathbf{M}_{EE}$ players by $0 \leqslant y \leqslant 1$. Thus the sought probability can be written as a function of x and y: $\phi(x,y)$, with the following properties:

(a) Since $\phi(x,y)$ represents probability, $0 \leqslant \phi(x,y) \leqslant 1$ for $0 \leqslant x,y \leqslant 1$.

(b) $\phi(x,y)$ is monotone decreasing in x and monotone increasing in y, for $0 \leqslant x,y \leqslant 1$.

(c) Finally, because resident females can gain extrapair fertilizations from floater and $\mathbf{M}_{GE}$ males, as well as $\mathbf{M}_{EE}$ males, we must have: $\phi(x,0) > 0$ for $0 \leqslant x \leqslant 1$. Thus, by (b), $\phi(x,y) > 0$ for $0 \leqslant x,y \leqslant 1$.

To define the corresponding probability for a female mated to a paternity guarding male we reason as follows. While social mate's paternity guarding may reduce female's ability to gain extrapair fertilizations (cf. Komdeur *et al.*, 1999), this reduction is unlikely to be complete because such a situation will tend to favor the evolution of counter-adaptations by females and their extrapair partners (cf. Johnsen *et al.*, 1998). Consequently, we shall represent male success in protecting in-pair paternity by a parameter $0 < s < 1$, i.e. the *per* egg probability of an $\mathbf{F}_E$ female mated to a $\mathbf{M}_{GE}$ male to gain an extrapair fertilization is given by $(1-s)\phi(x,y)$.

Now we can proceed to defining female payoffs.

Let an (average) payoff for having an egg fertilized by the social mate be denoted by $a > 0$. In defining the payoff for extrapair fertilization we reason as follows. We are modeling situations where female pursuit of EPF is motivated by fertility assurance and/or bet hedging.

- Given fertility assurance as motivation, the fact that females exercise a degree control over the post-copulatory *sperm competition* (Møller & Briskie, 1995) means that an extrapair male gains fertilization (as distinct from copulation) only when this male is superior (as a genetic partner for that specific female) to the social mate. That is, on the average, extrapair offspring are more valuable than in-pair offspring.
- When females seek extrapair fertilizations to achieve genetic diversity in their offspring we can assume that they pursue fertilization by as diverse a set of males as possible, rather than extrapair fertilizations *per se*. Thus the extent of the clutch's genetic diversity, and hence its total (fitness) value, increases with the increase in the extent of extrapair paternity in that clutch. Which, in an analytical formulation, is analogous to extrapair offspring being more valuable.

We summarize these facts by denoting a payoff for an extrapair fertilization by $a + b$, where $b > 0$.

In these terms the expected payoff to an $\mathbf{F}_E$ female mated to an $\mathbf{M}_{EE}$ male, when the frequencies of these strategies in a population are $0 \leqslant x,y \leqslant 1$, respectively, is given by

$$\sum_{k=0}^{n} \binom{n}{k} [\phi(x,y)]^k [1-\phi(x,y)]^{n-k} [k(a+b) + (n-k)a] = na + n\phi(x,y)b \equiv A + \phi(x,y)B. \tag{2}$$

As usual when calculating expected values, by definition we must consider the probabilities of all scenarios and thus eqn. (2) sums over all possible values of k, the number of potential extrapair eggs, in a clutch of size n.

Hence, the corresponding expression for a $\mathbf{F}_E$ female mated to an $\mathbf{M}_{GE}$ male is given by

$$A + (1-s)\phi(x,y)B. \tag{3}$$

Finally, the expected payoff to an $\mathbf{F}_N$ female is always A.

2.3. MALE PAYOFFS

Resident males' payoffs fall into two categories: *in-pair* and *extrapair*:

- To define in-pair payoffs we reason as follows. Let the expected male benefit of fertilizing a single egg of the social mate be denoted by $c > 0$. Thus a male mated to an $\mathbf{F}_N$ female gains the average payoff of nc in its own nest. An $\mathbf{M}_{EE}$ male mated to a $\mathbf{F}_E$ female gains the average payoff of $n[1-\phi(x,y)]c$ in its own nest, and the corresponding payoff to an $\mathbf{M}_{GE}$ male is given by $n[1-(1-s)\phi(x,y)]c$.
- To define extrapair payoffs for $\mathbf{M}_{EE}$ males, we reason as follows. Extrapair payoffs depend on the availability of extrapair fertilizations, and competition from other males. The expected number of extrapair fertilizations for a $\mathbf{F}_E$ mated to an $\mathbf{M}_{EE}$ is $n\phi(x,y)$, and the corresponding value for an $\mathbf{F}_E$ mated to an $\mathbf{M}_{GE}$ is $n(1-s)\phi(x,y)$. Thus, the total number of available extrapair fertilizations is proportional to

$$\begin{aligned} &n\phi(x,y)x[y+(1-s)(1-y)] \\ &= n\phi(x,y)x(1-s+sy). \end{aligned} \tag{4}$$

To derive the average number of extrapair fertilizations *per* an $\mathbf{M}_{EE}$ male we just divide the number of the available extrapair fertilizations by the *effective* number of males competing for these fertilizations. Hence, the expected extrapair payoff for a $\mathbf{M}_{EE}$ male is proportional to

$$\frac{n\phi(x,y)x(1-s+sy)}{\theta+y+(1-p)(1-y)} = n\phi(x,y)xg(y), \tag{5}$$

where θ represents the competition from floater males, and $(1-p)(1-y)$ represents the competition from $\mathbf{M}_{GE}$ males. The corresponding expression for $\mathbf{M}_{GE}$ males is simply $(1-p)n\phi(x,y)xg(y)$. As discussed, males benefit by having offspring that receive paternal care from other males. Moreover, in discussing female payoffs we have detailed an argument that, on the average, an extrapair offspring is more valuable than an in-pair offspring. Similar argument can be made for males. We express these facts by denoting male payoff for an extrapair fertilization by $c+d$, where $d>0$. Finally, for analytical convenience, we define $C=nc$ and $D=nd$.

3. Evolutionary Stability Analysis

We can summarize the results of section—1 as female (P_F) and male (P_M) *payoff matrixes* here $\psi(x,y) = \phi(x,y)xg(y)(C+D/C) = \phi(x,y)xg(y)(1+\delta)$

$$P_F = \begin{array}{c|cc} & \mathbf{M}_{EE} & \mathbf{M}_{GE} \\ \mathbf{F}_E & A+\phi(x,y)B & A+(1-s)\phi(x,y)B \\ \mathbf{F}_N & A & A \end{array},$$

$$P_M = \begin{array}{c|cc} & \mathbf{F}_E & \mathbf{F}_N \\ \mathbf{M}_{EE} & [1-\phi(x,y)+\psi(x,y)]C & [1+\psi(x,y)]C \\ \mathbf{M}_{GE} & [1-(1-s)\phi(x,y)+(1-p)\psi(x,y)]C & [1+(1-p)\psi(x,y)]C \end{array}, \tag{6}$$

Note: $\delta = D/C = d/c$ is the difference between male benefits of the extrapair vs. in-pair fertilization relative to the benefits of the in-pair fertilization. That is, δ is the *relative male advantage of an extrapair over an in-pair offspring*.

As discussed in Section 2: $\phi(x,y) > 0$ for every $0 \leqslant x,y \leqslant 1$, $0<s<1$, and $B>0$. Thus, we see that a payoff to an $\mathbf{F}_E$ female is always greater than the payoff to an $\mathbf{F}_N$ female mated to the same type of male. That is, the payoff for playing $\mathbf{F}_E$ strategy is always greater than the payoff for playing $\mathbf{F}_N$ strategy. Since payoffs represent (Darwinian) fitness, female pursuit of extrapair fertilizations displaces the alternative behavioral phenotype over the evolutionary time periods. Formally, $\mathbf{F}_N$

strategy is *strictly dominated* by the $\mathbf{F}_E$ strategy and can be excluded (cf. Section 5.6.1 in Weibull, 1996). That is, all the *evolutionary stable strategy* (ESS) solutions of system (6) have the form $(\mathbf{F}_E, \mathbf{M}^*)$, where $\mathbf{M}^*$ is an ESS solution of the reduced system

$$\begin{array}{c} \\ \mathbf{M}_{EE} \\ \mathbf{M}_{GE} \end{array} \begin{pmatrix} \mathbf{F}_E \\ [1-\phi(1,y)+\psi(1,y)]C \\ [1-(1-s)\phi(1,y)+(1-p)\psi(1,y)]C \end{pmatrix} = \begin{array}{c} \\ \mathbf{M}_{EE} \\ \mathbf{M}_{GE} \end{array} \begin{pmatrix} \mathbf{F}_E \\ \pi_{EE}(y) \\ \pi_{GE}(y) \end{pmatrix}. \qquad (7)$$

Since evolutionary stability depends on relative fitness, we can subtract $\pi_{GE}(y)$ from $\pi_{EE}(y)$ to obtain the difference

$$\Delta\pi(y) = \pi_{\mathrm{EE}}(y) - \pi_{\mathrm{GE}}(y) = \frac{C\phi(1,y)h(y)}{\theta+1-p(1-y)},$$

where

$$h(y) = ps\delta y + p(1+\delta) - s(\theta+1+p\delta). \qquad (8)$$

Since $C>0$, whereas $\phi(1,y)>0$ and $\theta+1>p(1-y)$ for every $0\leqslant y\leqslant 1$, fitness of $\mathbf{M}_{EE}$ strategists is greater than the fitness of $\mathbf{M}_{GE}$ strategists whenever $h(y)>0$ and vice versa. Because $h(y)$ is continuous and monotone increasing in y, we have the following possibilities:

(a) If $h(1)<0$, then $h(y)<0$ for every $0\leqslant y\leqslant 1$. That is, fitness of $\mathbf{M}_{GE}$ strategists is always greater than the fitness of $\mathbf{M}_{EE}$ strategists. Hence $\mathbf{M}_{GE}$ is the unique ESS solution of system (7).

(b) If $h(0)<0<h(1)$, exists a unique $0<\xi<1$: such that: $h(y)<0$ when $0\leqslant y<\xi$, $h(\xi)=0$, and $h(y)>0$ when $\xi<y\leqslant 1$. That is, $\mathbf{M}_{GE}$ strategy is superior on the interval $0\leqslant y<\xi$ and $\mathbf{M}_{EE}$ strategy is superior on the interval $\xi<y\leqslant 1$. Hence, given the fact that local superiority is equivalent to evolutionary stability (cf. Hofbauer & Sigmund, 1988), both $\mathbf{M}_{GE}$ and $\mathbf{M}_{EE}$ are ESS solutions of system (7).

(c) Finally, if $0<h(0)$, then $h(y)>0$ for every y such that $0\leqslant y\leqslant 1$. Hence, $\mathbf{M}_{EE}$ is the unique ESS solution of system (7).

Thus, as discussed in connection with eqn (7), system (6) has two ESS solutions.

- Strategy profile $(\mathbf{F}_E, \mathbf{M}_{GE})$ i.e. all females seek extrapair fertilizations and all males pursue EPF opportunities whenever this pursuit does not conflicts with the defense of in-pair paternity, is an ESS whenever $h(0)<0$.
- Strategy profile $(\mathbf{F}_E, \mathbf{M}_{EE})$, i.e. all females seek extrapair fertilizations and all males pursue EPF opportunities while neglecting defense of their in-pair paternity, is an ESS whenever $h(1)>0$.

Now, by eqn (8),

$$h(0) = (\theta+1+p\delta)(\sigma_1 - s)$$

where

$$\sigma_1 = \frac{p(1+\delta)}{\theta+1+p\delta},$$

and

$$h(1) = (\theta+1)(\sigma_2 - s)$$

where

$$\sigma_2 = \frac{p(1+\delta)}{\theta+1}. \qquad (9)$$

Thus, $h(0)<0$, if and only if, (*iff*) $\sigma_1<s<1$ and $h(1)>0$ iff $s<\sigma_2$. Since $0<p\leqslant 1$ and δ, $\theta>0$, $\sigma_1<1$. However,

$$\sigma_2<1 \text{ iff } \begin{array}{c} \delta<\theta \\ \text{or} \\ \delta>\theta \text{ and } p<\pi = \dfrac{\theta+1}{\delta+1}. \end{array} \qquad (10)$$

Thus, the global properties of system (6) fall into two distinct categories.

I. If the magnitudes of p, δ and θ are such that $0<\sigma_1<\sigma_2<1$, then the magnitude of s prescribes three qualitatively different outcomes of the game.

(a) If s is small ($s<\sigma_1$), then $(\mathbf{F}_E, \mathbf{M}_{EE})$ is the only ESS solution of system (6).

(b) If s is intermediate ($\sigma_1 < s < \sigma_2$), then system (6) has two ESS solutions $(\mathbf{F}_E, \mathbf{M}_{EE})$ and $(\mathbf{F}_E, \mathbf{M}_{GE})$. That is, the long-term distribution of the resident males' strategies in such populations depends on the history of that population. To wit, on whether or not the initial frequency of $\mathbf{M}_{EE}$ strategists in that population, $y(0)$, exceeded the critical threshold value $\xi = (\theta + 1 + p\delta)(s - \sigma_1)/p/s/\delta$. Barring major perturbations: (i) $y(0) > \xi$ implies convergence to $(\mathbf{F}_E, \mathbf{M}_{EE})$, whereas (ii) $y(0) < \xi$ implies convergence to $(\mathbf{F}_E, \mathbf{M}_{GE})$.

(c) Finally, if s is large ($s > \sigma_2$), $(\mathbf{F}_E, \mathbf{M}_{GE})$ is the only ESS solution of system (6).

II. If the magnitudes of p, δ and θ are such that $0 < \sigma_1 < 1 < \sigma_2$, then s is always less than σ_2, and therefore the possible values of s are restricted to "small" and "intermediate" domains.

We summarize these results in Fig. 1.

We see that male "choice" between $\mathbf{M}_{GE}$ and $\mathbf{M}_{EE}$ strategies depends on the magnitude of s (degree of success of paternity defense) relative to the thresholds σ_1 and σ_2. And the magnitudes of σ_1 and σ_2 are determined by (a) breeding synchrony, (b) fitness advantages of extrapair over in-pair offspring and (c) the intensity of competition for extrapair fertilizations from floater males. More precisely:

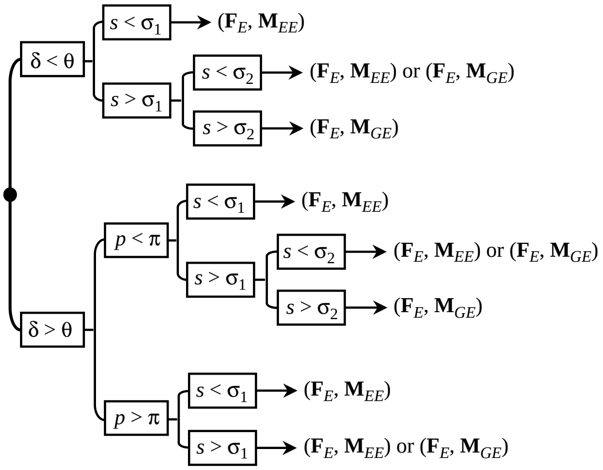

FIG. 1. Here the conditions for the evolutionary stability of the strategy profile at the terminus (→) are represented by the inequalities on the path from the origin (●) to that strategy profile. Recall that male's degree of success of paternity defense is represented by s, breeding synchrony by p, relative advantage of extrapair fertilization over in-pair fertilization by δ, and the intensity of competition for EPFs from male floaters by θ. Here σ_1, σ_2 and π are threshold values defined in eqns 9 and 10.

(a) *Breeding synchrony* is represented by the parameter p. Formally, p is the fraction of extrapair reproductive opportunities that $\mathbf{M}_{GE}$ males lose by abandoning the pursuit of extrapair fertilizations in favor of the in-pair paternity defense. Thus the magnitude of p increases with the increase in the breeding synchrony (overlap in the fertile periods of the resident females) within a population. Since both σ_1 and σ_2 increase with p, we see that an increase in breeding synchrony favors the ESS solution $(\mathbf{F}_E, \mathbf{M}_{EE})$, over its alternative $(\mathbf{F}_E, \mathbf{M}_{GE})$.

(b) Relative advantage of the extrapair fertilization over in-pair fertilization is represented by the parameter δ. Formally, $\delta = d/c$ where c represents the (average) value of an in-pair offspring, and the sum $c + d$ represents the value of an extrapair offspring. For example, δ increases with an increase in the male parental investment. Non-surprisingly an increase in δ favors pursuit of extrapair fertilizations at the expense of the protection of in-pair paternity.

(c) The relative merits of the pursuit of EPF opportunities vs. defense of in-pair paternity are influenced by the intensity of competition for extrapair fertilizations from floater males—represented by the parameter θ. As we would expect, an increase in competition from floater males favors defense of in-pair paternity over the pursuit of extrapair fertilizations.

4. Discussion

An individual that fails to pass on its genes is an evolutionary failure. Thus, reproduction is the central theme of evolutionary biology, and behavioral aspects of reproduction are the central topic in the study of behavioral adaptations, *behavioral ecology*. We know that there are conflicts of interest between the sexes in courtship and mating (Davies, 1991). Males and females cooperate because both pass their genes to the shared progeny. However, individuals tend to maximize their own reproductive success by exploiting their partners' parental investment (Trivers, 1972).

In particular, when raising offspring requires an extensive male parental investment, females must form a social bond in order to secure male cooperation. However, females that secure both paternal care and superior *genetic* endowment for their offspring have higher fitness than females that only secure paternal care. That is, a female mated to a male who is not an optimal genetic partner can benefit by obtaining fertilizations from extrapair males. These later cooperate because males benefit by having offspring that receive paternal care from other males, and may also benefit by finding an extrapair partner more genetically compatible than their social mate. On the other hand, paired males frequently exhibit strategies that minimize their loss of paternity and/or conserve paternal investment if paternity is lost. Thus, extrapair attributes of diverse species and populations reported in the literature are particular solutions of evolutionary games (cf. Weibull, 1996) involving gender-specific cuckolding and anti-cuckolding strategies.

At present the complexities of the extrapair phenomena are not well understood. In our view this is due, at least in part, to the following facts. (a) Female benefits of extrapair fertilizations fall into several distinct categories—and it is reasonable to believe that distinct categories of female EPF benefits give rise to distinct female reproductive strategies. Moreover, we cannot rule out a combination of different types of female EPF benefits within a single population. (b) There are at least two distinct categories of male anti-cuckolding strategies. Consequently, there are a large number of possible combinations of gender-specific reproductive strategies pertinent to extrapair paternity. In particular, the extreme variability in the reported incidence of EPP among species and populations—a variation not explainable by purely ecological factors (cf. Petrie & Kempenaers, 1998)—may be due to the fact that different populations are "playing" different evolutionary games.

In this paper we analyse the interplay between female reproductive strategies that obtain when the female benefit of EPF is fertility assurance, and male strategic choices are between in-pair paternity protection and pursuit of extrapair paternity. Our analysis shows that in such circumstances pursuit of extrapair fertilizations is the only female ESS. Males, on the other hand, have two mutually exclusive evolutionary stable strategies. Both involve pursuit of extrapair paternity, and only differ in whether or not males pursue extrapair fertilizations to the extent of neglecting defense of their in-pair paternity. The choice between these two strategies is determined by the degree of success of the male in-pair paternity defense, breeding synchrony, fitness advantages of extrapair over in-pair offspring, and the intensity of competition for extrapair fertilizations from floater males.

These results have a rather simple interpretation:

(a) When female pursuit of extrapair fertilizations is motivated by fertility assurance, a precopulatory selection of an optimal genetic partner is impossible. That is, females have to mate promiscuously and use *in copula* and/or *post-copulatory* selection mechanisms to ensure fertilization by sperm that increases genetic benefits to their offspring (Zeh & Zeh, 1996, 1997). Hence, in the absence of male anti-cuckolding strategies that specifically penalize EPF seeking females (cf. Kokko, 1999), the fitness of females who seek extrapair fertilizations is greater than the fitness of the (genetically) monogamous females. That is, pursuit of extrapair fertilizations is the only female ESS under the circumstances addressed in the current model. Further research is needed to explore the far more complicated situation in which guarding males penalize EPF seeking females, or where female costs for obtaining EPFs exceed the possible benefits.

(b) When all females pursue extrapair fertilizations, male strategies involving pursuit of extrapair fertilizations are superior to male strategies that forgo such pursuits: see Section 2 for details. Thus, the only male choice is between pursuing EPP "full time", and pursuing EPP only when this does not interferes with the defense of their in-pair paternity. Breeding synchrony determines what fraction of EPP opportunities is lost to males who do not neglect defense of their in-pair paternity. Whereas the magnitude of the fitness advantages of the extrapair over in-pair offspring vs. the intensity of the competition for extrapair fertilizations from floater males, determine the value of these lost EPP opportunities. Finally, the degree of success in paternity defense determines the relative value of that behavioral alternative. In simple terms, our analysis predicts that, everything else being equal, mate guarding by males is expected to be more common in populations where (i) it can be more effective, (ii) breeding synchrony is relatively low, (iii) male genetic benefits from EPF are relatively low, and (iv) competition for EPF by floater males is relatively high.

This paper illustrates our chosen approach to the study of extrapair paternity. As discussed above, EPP involves numerous possible combinations of gender-specific reproductive strategies. Thus, we start by modeling relatively simple combinations of particular female reproductive strategies—defined by the type of the female extrapair benefits, and particular male cuckolding/anti-cuckolding strategies. Once we gain a thorough understanding of such fundamental interactions, we shall proceed to the analysis of the more complicated situations involving mixtures of the different types of female benefits and male cuckolding/anti-cuckolding strategies.

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