REPORT

Cuckoldry and the stability of biparental care

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Abstract

In socially monogamous species, females may engage in extra-pair fertilizations to gain direct or indirect benefits not provided by the social mate, with the potential risk of a reduction in the social mate's paternal effort. I present an ESS model of cuckoldry frequencies, which considers both facultative and nonfacultative male responses to losses in paternity. Two possible equilibria exist: stable social monogamy with varying degrees of extra-pair paternity, and polygamy with little or no male care. Monogamy with limited cuckoldry can be stable only if the initial cuckoldry frequency is low, intrinsic cuckoldry benefits are not high, males can reasonably accurately detect cuckoldry, and female compensation for losses in male care is incomplete. Deviations from these assumptions lead to stronger mate acquisition in males at the expense of paternal care, and eventually to runaway evolution towards polygamy. Average female fitness is reduced in the runaway, although it is initiated by females maximizing the survival of offspring – a potential "tragedy of the commons" in breeding systems.

Keywords

Cuckoldry, ESS, extra-pair paternity, paternal care, polygamy, runaway evolution, social monogamy, sperm competition, tragedy of the commons.

INTRODUCTION

Benefits of mate choice may be direct or indirect (Kirkpatrick & Ryan 1991). Often both act together: a good example is provided by a study of great reed warbler *Acrocephalus arundinaceus*, where females prefer males that hold good territories but they also pay attention to song-repertoire size (Hasselquist 1998). This may lead to a pressure to seek extra-pair fertilizations (EPFs), since not all females may mate socially with the male who would provide the highest indirect benefits. Indeed, female great reed warblers obtain EPFs from neighbouring males with larger song repertoires than the social mate, and this leads to improved offspring survival (Hasselquist *et al.* 1996). EPFs may be advantageous for the female for more direct reasons as well: suggested benefits include fertility insurance (Sheldon 1994) and courtship provisioning of food (Wolf 1975) or nesting material (Hunter & Davis 1998), among others (reviewed in Møller 1998).

However, there is a potential cost to a female with extra-pair young in the nest: the social mate who suffers reduced paternity might become less willing to provide paternal care (Trivers 1972; Dixon *et al.* 1994; Westneat & Sargent 1996). Here, it is important to distinguish between ecological and evolutionary timescales, i.e.

between facultative and nonfacultative responses of the male (Westneat & Sherman 1993). It is not always in the male's interest to reduce paternal effort, if his paternity becomes reduced in an ecological timescale; this depends on whether he has the potential to fare better in subsequent breeding attempts (Westneat & Sherman 1993). Male responses may also be weak if cues for paternity are uncertain: males will need to balance the risk of not providing care for one's own young and of providing care for young who are not. As an evolutionary response, however, enhanced extra-pair paternity levels typically result in larger variance in male mating success (Webster *et al.* 1995). While reduced paternity in a single brood is not always expected to affect male behaviour much, reduced average levels of paternity imply larger opportunity costs of paternal care. Including these opportunity costs are essential for understanding the trade-offs that males face (Wright 1998). As an evolutionary response, consequently, males are selected to care less, and instead spend more effort on mate acquisition, when EPF frequencies increase (Møller & Birkhead 1993; Houston 1995; Kokko 1998).

In this paper, I develop a model that combines behavioural and evolutionary responses of males and the evolution of female cuckoldry strategies. Even when

facultative responses exist, the relationship between paternity and paternal care may be weak (Houston 1995). Here, I show that this does not mean that males should care (largely) regardless of paternity. Instead, too weak behavioural responses may, over evolutionary time, completely destroy the stability of biparental care. This arises from the following possibility. Females are selected to have mixed broods if there is any intrinsic benefit for doing so, and if the immediate cost of losing paternal effort is low. Over evolutionary time this may lead to overall paternity levels being low enough so that the optimal male strategy is not to care at all, but to compete for paternity in as many broods as possible. The success in the latter task again depends on the availability of extra-pair females, forming a positive feedback loop between cuckoldry frequency and reductions in male care.

Since not all species are polygamous, a model of cuckoldry must explain why such a "runaway" process does not always occur. The model thus also addresses the question of whether there are selective limits to cuckoldry despite its intrinsic benefits, or whether females are always selected to cuckold as much as possible whenever such benefits exist.

THE CUCKOLDRY GAME

Model assumptions

The model presents a game where females decide whether or not to seek extra-pair copulations, males may detect losses of paternity (and also become suspicious mistakenly), and both sexes adjust their parental effort according to their best knowledge. The following seven assumptions form the rules of the game (a list of all variables is also presented in Table 1):

1 Cuckoldry: A female has two options, (i) to seek extra-pair copulations (denoted C), or (ii) to be faithful to her social mate (no cuckoldry, denoted $\bar{C}$). The proportion of cuckolding females in the population is denoted x.

2 Paternity of cuckolded males: The expected paternity of the social mate drops from $p_{\bar{C}} = 1$ to $p_C < 1$ if he has been cuckolded. I include cases where all paternity is extra-pair, $p_C = 0$, but do not restrict the analysis to these. A limitation of p_C remaining larger than 0 may result from mate-guarding, from sperm competition (as the female must mate with the social mate as well), and from limited chances of finding extra-pair mates (e.g. due to low population density; Westneat *et al.* 1990; Møller & Ninni 1998).

3 Detecting cuckoldry: A male does not know his level of paternity, but he may detect cuckoldry with a certain probability. Imperfect knowledge is also assumed in that he may become mistakenly suspicious. A cuckolded male suspects (S) that he has been cuckolded with probability $P(S|C) = d$ (detection probability); a noncuckolded male may erroneously suspect that he has been cuckolded with probability $P(S|\bar{C}) = e$ (error probability). Being unsuspicious is denoted $\bar{S}$. Becoming suspicious is more likely if there is reason for it: $d > e$. Males classify female behaviour accurately if d is large and e is small.

4 Paternal and maternal effort: A male decides his paternal effort PE depending on whether or not he suspects that he has been cuckolded. These efforts are denoted PE_S and $PE_{\bar{S}}$, respectively, and they maximize the male's success according to his costs and benefits (details below). A female maximizes her effort ME depending on the father's effort PE, by trading off brood survival and her own cost (details below).

5 Benefits of care: Total care ($E = PE + ME$) brings about benefits to offspring survival, such that the value of the brood $v(E)$, interpreted as an expected number of fledged offspring, increases with E. Males cannot give care preferentially to their own offspring within the brood (as is typical in birds, Davies *et al.* 1992; Kempenaers & Sheldon 1996). Therefore, the care benefit equals $v(PE + ME)$ for the female parent, but is proportional to paternity, $p\, v(PE + ME)$, for the male parent. Since increasing PE may allow the female to reduce her ME, paternal effort PE benefits the female's fitness more than the male's; hence the sexual conflict.

6 Costs of care: Caring imposes a cost $c(ME)$ on the female, and $c(PE)$ on the male. In addition, males pay an opportunity cost of parental effort as a reduction in extra-pair success. I assume that expected extra-pair success decreases with paternal effort as $\exp(-PE)$, which leads to marginally increasing (accelerating) extra-pair gains for males that decrease their paternal effort (thus allowing for the evolution of exaggerated male ornamentation as an alternative reproductive strategy; see Kokko 1998). Extra-pair males also compete with each other, such that an individual male's extra-pair success is inversely proportional to the strength of competition in the environment [indicated by the average of $\exp(-PE)$ of all males], proportional to the availability of females seeking extra-pair copulations, x, to the fraction of offspring that will be extra-pair, $1 - p_C$, and to the expected success of the resulting mixed brood, calculated from expected care patterns in such broods. (Note that these rules do not assume that any single extra-pair male achieves the full paternity $1 - p_C$ which is "left over" from the social mate.)

7 Benefits of mixed broods: All other factors being equal (i.e. assuming unchanged care), achieving mixed paternity improves the value of the brood by a factor $b_C \geqslant 1$; no improvement arises in the borderline case $b_C = b_{\bar{C}} = 1$. Such an improvement might arise from several factors, either direct or indirect. Cuckolding females may find, on average, extra-pair mates of higher

Table 1 A list of symbols used in the model

C	Female cuckolds
$\bar{C}$	Female does not cuckold
S	Male suspects cuckoldry
$\bar{S}$	Male does not suspect cuckoldry
a	Parameter that scales the importance of maintaining high care levels (and hence determines compensatory responses)
b	Relative intrinsic value of brood that contains (b_C) or does not contain ($b_{\bar{C}} = 1$) extra-pair young; does not include effects of care (see V_M)
d	Probability that cuckolded male detects cuckoldry
e	Probability that noncuckolded male becomes mistakenly suspicious
p	Paternity of cuckolded (p_C) or noncuckolded ($p_{\bar{C}}$) males
x	Proportion of females that seek extra-pair fertilizations
PE	Paternal effort of males that are suspicious (PE_S) or not ($PE_{\bar{S}}$); optimal effort is denoted PE^*
ME	Maternal effort of female; optimal effort is denoted ME^*
E	Total parental effort of the breeding pair
$v(E)$	Number of survived offspring as a function of care
$c(ME), c(PE)$	Cost of maternal or paternal care
V_M	Expected value of mixed broods; includes effects of care
$w_F(ME, PE, b)$	Fitness of female as a function of a male's and female's care levels and the intrinsic brood value
$W_S, W_{\bar{S}}$	Expected fitness of suspicious and unsuspicious males
$W_C, W_{\bar{C}}$	Expected fitness of cuckolding and noncuckolding females

genetic quality (Møller 1988; Kempenaers *et al.* 1992; Hasselquist *et al.* 1996), or superior heterozygosity (Brown 1997), or they may benefit from enhancing genetic diversity within the brood (Williams 1975) or insuring their brood against infertility (Sheldon 1994). The value enhancement b_C is counted to benefit the female parent only, since none of these benefits apply to the cuckolded male's offspring.

Cuckoldry probabilities for suspicious and unsuspicious males

To solve the game, one first needs to solve the probabilities that a suspicious versus unsuspicious male indeed suffers from cuckoldry. This follows Bayes' theorem applied to signal detection theory (e.g. Bradbury & Vehrencamp 1998, pp. 402–403). When a fraction x of females seek extra-pair copulations, the proportion of suspicious males in the population becomes

$$P(S) = xd + (1-x)e. \qquad (1)$$

The proportion of cuckolded males in the population is, by definition, $P(C) = x$. The probability that a suspicious male has indeed been cuckolded then equals, by Bayes' theorem,

$$P(C|S) = \frac{P(C)P(S|C)}{P(S)} = \frac{xd}{xd + (1-x)e} \qquad (2)$$

The probability that an unsuspicious male is cuckolded is

$$P(C|\bar{S}) = \frac{P(C)P(C|\bar{S})}{P(\bar{S})} = \frac{x(1-d)}{x(1-d) + (1-x)(1-e)}.$$

$$(3)$$

Naturally, we also have $P(\bar{C}|S) = 1 - P(C|S)$ as the probability of erroneous suspicion, and $P(\bar{C}|\bar{S}) = 1 - P(C|\bar{S})$ as the probability of correctly believing in full paternity. Since it is assumed that there is generally reason in suspicion, $d > e$, the cuckoldry probability is greater if the male is suspicious: $P(C|S) > P(C|\bar{S})$.

Optimal female care levels

Assume that the brood has an intrinsic value b, and the social mate cares with effort PE. The female's optimal maternal effort ME maximizes her fitness, which is given by

$$w_F(ME, PE, b) = bv(ME + PE) - c(ME). \qquad (4a)$$

In all examples, I assume accelerating costs of care, $c(E) = E^2$, and brood value $v(E) = \arctan[a(E-1/2)] - \arctan(-a/2)$. This function is designed to give no chances of survival if neither the male nor the female cares. It incorporates a parameter a that scales the importance of maintaining high care levels (Fig. 1A). Substituting the above cost and benefit functions into equation (4a) and differentiating with respect to ME gives the condition for the optimum ME^*:

$$\frac{ab}{1 + a^2(ME^* + PE - \frac{1}{2})^2} - 2ME^* = 0. \qquad (4b)$$
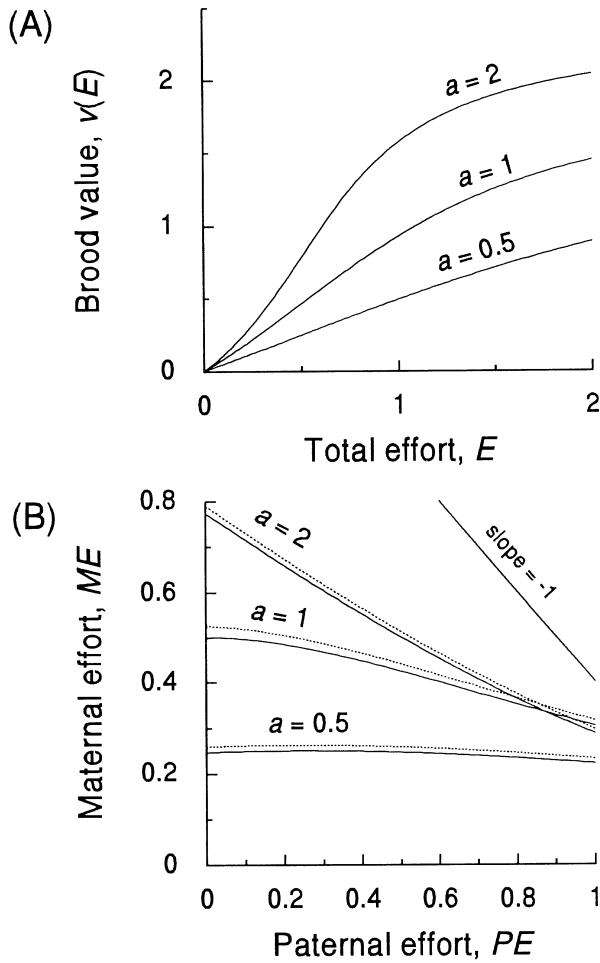
(A)

(B)

Figure 1 (A) Possible relationships between total care $E = ME + PE$ provided by the mother and the social father, and brood value (expected number of fledged offspring), exemplified with three different parameter values a. (B) The dependency of the brood value on care leads to varying degrees of compensation by the female; compensation becomes stronger with increasing a. Complete compensation would have a slope −1. Solid lines show a faithful female's responses to male care, whereas dotted lines show a slight increase in an unfaithful female's care levels, based on an improvement in the brood value by a factor $b_C = 1.05$.

The solution of ME^* (not shown because of its excessive length) predicts that females partially compensate for losses in paternal care (more strongly with larger a), and also slightly adjust their effort according to whether or not the brood has mixed paternity (Fig. 1B). The latter adjustment being slight means that males cannot effectively use a female's parenting behaviour as a means to deduce their paternity.

Optimal male care levels for suspicious and unsuspicious males

Males pay opportunity costs from parental care, but these depend on how successfully extra-pair activities lead to young produced. The expected value of mixed broods, denoted V_M, depends on how often other cuckolded males respond by becoming suspicious, and it is thus one factor scaling the expected success of an extra-pair fertilization. It is calculated using the population-wide strategies PE_S and $ME^*(PE_S, b_C)$ of suspicious, cuckolded males and their mates (the relative frequency of which is $P(S|C) = d$), and the strategies $PE_{\bar{S}}$ and $ME(PE_{\bar{S}}, b_C)$ of unsuspicious but cuckolded males and their mates (of relative frequency $P(\bar{S}|C) = 1 - d$):

$$V_M = d\, v\,[ME^*(PE_S, b_C) + PE_S] \\ + (1 - d)\, v[ME^*(PE_{\bar{S}}, b_C) + PE_{\bar{S}}] \qquad (5)$$

A suspicious male's fitness sums the expected benefit from his own care, the direct cost from care, and his expected extra-pair success. With a cuckolded male's paternity being p_C, the benefit equals $p_C\, v(E) = p_C v[ME^*(PE, b_C) + PE]$ if cuckoldry indeed happened [probability $P(C|S)$], but $v[ME^*(PE, 1) + PE]$ if it did not [probability $P(\bar{C}|S)$]. The direct cost of care is simply $c(PE)$, whereas the expected extra-pair is a product of the male's success e^{-PE} relative to that of other males [average $P(S)\, e^{-PE_S} + P(\bar{S})e^{-PE_{\bar{S}}}$], of the availability of extra-pair females x, of the proportion $(1 - p_C)$ of extra-pair young in their broods, and of the expected value of mixed broods, V_M. Thus, the expected fitness of a suspicious male becomes

$$W_S(PE) = P(C|S)\, p_C\, v[ME^*(PE, b_C) + PE]$$

$$+ P(\bar{C}|S)\, v[ME^*(PE,1) + PE]$$

$$-c(PE) + \frac{e^{-PE}}{P(S)e^{PE_S} + P(\bar{S})e^{-PE_{\bar{S}}}}\, x\,(1 - p_C)V_M.$$

$$(6\ a)$$

By similar reasoning, an unsuspicious male's expected fitness equals

$$W_{\bar{S}}(PE) = P(C|\bar{S})\, p_C v[ME^*(PE, b_C) + PE]$$

$$+ P(\bar{C}|\bar{S})\, v[ME^*(PE, 1) + PE]$$

$$-c(PE) + \frac{e^{-PE}}{P(S)e^{PE_S} + P(\bar{S})e^{-PE_{\bar{S}}}}\, x\,(1 - p_C)V_M$$

$$(6\ b)$$

In these equations, PE is the strategy used by an invading mutant, and the population-typical care strategies PE_S and $PE_{\bar{S}}$ affect the male's fitness both by setting up the competitive environment and through V_M. The less

other males care, the more competition there is for EPFs, and the smaller is the success of extra-pair young since they are expected to receive less care. The overall cuckoldry frequency x also affects the strategies, as it determines both expected within-pair paternity and the availability of females for extra-pair matings.

The stable effort levels $PE_S^*(x)$ and $PE_{\bar{S}}^*(x)$ for suspicious and unsuspicious males are solved by seeking the population-level strategies PE_S and $PE_{\bar{S}}$ that allow no improvement in fitness (Eqs. 6) for any alternative choice. In practice, these values are found numerically by computing the best responses of suspicious and unsuspicious males (i.e. PE values that maximize expressions 6a and 6b for each combination of population-wide values of PE_S and $PE_{\bar{S}}$). Unlike in some previous analyses (see Westneat & Sherman 1993 for a review), a suspecting male should reduce his paternal effort in this game, as cuckoldry reduces the payoff from his current brood but is not assumed to directly reduce its costs: a cuckolded male would still stand a chance of getting extra-pair matings, if he spent enough effort to do so (although the chances diminish as more males join the pool of hopeful extra-pair sires).

Stable cuckoldry probabilities

The payoffs for unfaithful and faithful females depend on the responses of suspicious and unsuspicious males, and on the accuracies d and e with which males can classify the female's behaviour. For faithful females, this is derived by substituting the stable paternal effort of suspicious or unsuspicious males [$PE_{\bar{S}}^*(x)$ or $PE_S^*(x)$] and the resulting compensation of the female, $ME^*[PE_S^*(x), 1]$ or $ME^*[PE_{\bar{S}}^*(x), 1]$, into eqn 4a, and weighing the results with the probabilities that her mate becomes suspicious (e) or not ($1-e$):

$$W_{\bar{C}}(x) = e\, w_F[ME^*(PE_S^*(x), 1), PE_S^*(x), 1] \\ + (1-e)\, w_F[ME^*(PE_{\bar{S}}^*(x), 1), PE_{\bar{S}}^*(x), 1] \quad (7a)$$

For the unfaithful female, the derivation is similar, but the intrinsic value of the brood has improved from $b_C = 1$ to b_C, and the probability of her mate becoming suspicious is d rather than e:

$$W_C(x) = d\, w_F[ME^*(PE_S^*(x), b_C), PE_S^*(x), b_C] \\ + (1-d)\, w_F[ME^*(PE_{\bar{S}}^*(x), b_C), PE_{\bar{S}}^*(x), b_C]. \quad (7b)$$

The cuckoldry proportion x will increase whenever $W_C(x) > W_{\bar{C}}(x)$. Stable equilibria may arise in three cases:

(i) Strict monogamy is stable if $W_{\bar{C}}(0) > W_C(0)$.
(ii) Complete cuckoldry is stable if $W_C(1) > W_{\bar{C}}(1)$.
(iii) Intermediate equilibria x^* exist if $W_C(x^*) = W_{\bar{C}}(x^*)$ and $d[W_C(x) - W_{\bar{C}}(x)]/dx < 0$ at $x = x^*$.

The criteria in (iii) specify the conditions for a mixed ESS: both cuckolding and noncuckolding females have equal fitness, but increasing the frequency of cuckolders would lead to cuckoldry being selected against (and vice versa).

RESULTS

Assuming that cuckoldry has positive fitness consequences to the female ($b_C > 1$) leads to the suspected possibility of a "runaway", where females are always selected to increase the cuckoldry proportion x, and males are selected to reduce their paternal effort and instead focus more on the increasing importance of competition for additional matings, until, at equilibrium, males do not care for offspring at all (Fig. 2A). This process leads to an overall reduction in female fitness: females pay costs as they compensate for reduced male care, while brood survival still deteriorates. However, at any cuckoldry frequency x, there is a relative, "selfish" advantage to a cuckolding female over the faithful one. This is an example of the "tragedy of the commons" (Hardin 1968): females would, as a group, do better if they decided to remain faithful, but any single female is not sufficiently threatened by a male's facultative responses, that she would do worse by choosing to engage in extra-pair activities.

However, improving the ability of males to detect reduced paternity, e.g. through mate guarding, may stop this process. With sufficient detection accuracy (large d and small e), parenting strategies of suspicious and unsuspicious males can become different enough to balance the female's expected cuckoldry benefit b_C and the cost of a reduction of the social mate's paternal effort. This leads to an intermediate, nonzero equilibrium of the frequency of cuckoldry (Fig. 2B). Interestingly, there are often two possible equilibria. If the initial cuckoldry frequency is low to moderately high, the breeding system will converge to this intermediate equilibrium where females use a mixed strategy of shared paternity, males spend some of their effort in the pursuit of extra-pair matings, but both sexes care for the offspring. If the initial frequency is high, however, even unsuspecting males care so little that females are not stopped by the threat of losses in paternal effort. The proportion of cuckolding females then increases to 1, and females remain the only caring sex (Fig. 2B).

Which type of solution is found depends on the magnitude of benefits b_C, on the detection and misdetection probabilities d and e, on female compensatory responses, and on the degree that losses of paternity for mates of unfaithful females will be limited by factors such as mate guarding, or environmental constraints. Non-zero cuckoldry is an ESS whenever mixed broods bring any benefits to the female (i.e. $b_C > 1$, Fig. 3A). Stable
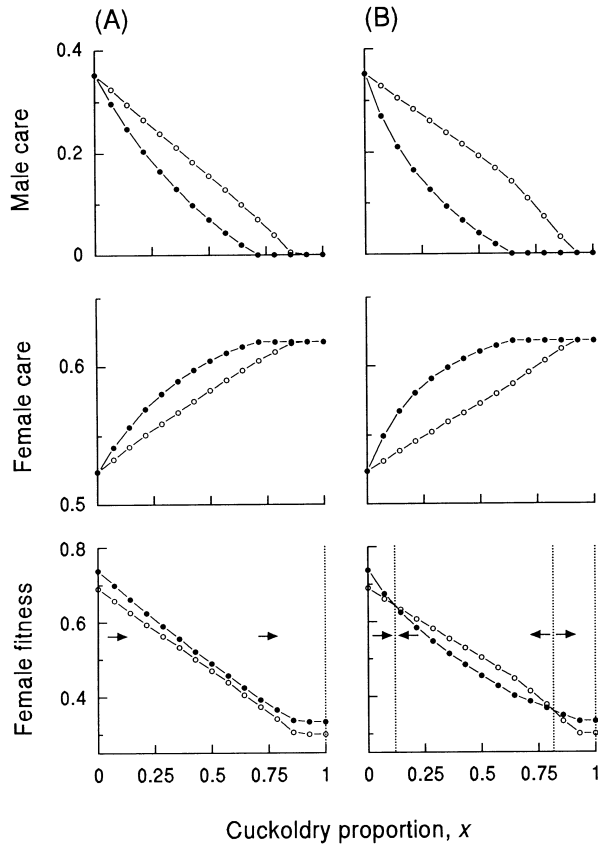
Figure 2 Examples of male care, female care, and the fitness of a cuckolding or noncuckolding female, showing the emergence of different equilibria. Upper row, optimal responses of male parental effort $PE*(x)$ to a population-wide frequency of cuckoldry x; black dots give effort for a suspicious male, open dots for an unsuspicious male. The difference between the two levels of care is a behavioural response, while changes with x represent evolutionary responses. Middle row, optimal maternal effort of unfaithful females whose mate is suspicious (black dots) or unsuspicious (open dots). Lowest row, fitness of unfaithful (black dots) and cuckolding (open dots) females. The arrows point to the direction in which cuckoldry frequency x is evolving: if the fitness of unfaithful females exceeds that of faithful ones, x will increase, and decrease otherwise. In all examples, unfaithful females enjoy a 5% advantage in the values of their broods ($b_C = 1.05$). In (A), males are not very efficient in detecting cuckoldry ($d = 0.3$, $e = 0.1$), and the difference between optimal parental effort of suspicious and unsuspicious males is not very large. Females are hence not much threatened by male behavioural responses, and a "tragedy of the commons" evolution towards promiscuity and no male care stops only when $x = 1$. Other parameters: $a = 1.2$, $p_C = 0.3$. (B) is as (A), but males detect cuckoldry with 70% probability ($d = 0.7$, $e = 0.1$). A stronger behavioural response from males leads to the existence of an intermediate equilibrium with 12% cuckoldry frequency. However, the "tragedy of the commons" solution also exists and evolution towards it starts if the initial cuckoldry frequency exceeds 81%.

cuckoldry frequencies increase if its benefits b_C increase (Fig. 3A), if males have difficulties in categorizing the female's behaviour correctly (i.e. at small d and/or relatively large e, Fig. 3B–C), or if females compensate strongly for reduced male care (Fig. 3D). Somewhat counterintuitively, stable cuckoldry levels also increase if the female achieves the same benefit b_C with a smaller extra-pair fraction $1 - p_C$ of offspring (Fig. 3E: cuckoldry x increases with p_C). The last effect appears because the care levels of suspecting and unsuspecting males differ less if their paternity is similar; hence a female is less affected by the loss of male care and can "afford" to be less faithful.

Increasing stable cuckoldry levels usually leads to reductions in care levels provided by both suspicious and unsuspicious males (Fig. 3). However, a few exceptions exist: suspicious males may be selected to care more, if their risk of being erroneously suspicious is increased from 0 to a small value, even though this leads to an increase in overall cuckoldry levels (Fig. 3C). Also, increasing compensatory responses in females may in some cases make it beneficial for males to care more as well, if brood survival can thus be brought to a much better level — even though this again allows females to cuckold more (Fig. 3D).

Evolution towards complete cuckoldry $x = 1$, usually accompanied by a breakdown of biparental care, always exists as the alternative equilibrium if there are the slightest benefits of cuckoldry (i.e. at any $b_C > 1$). Any difference in care provided by suspicious and unsuspicious males must vanish when x approaches 1. Therefore, the benefit b_C will, at sufficiently high cuckoldry frequencies, always exceed any losses of paternal care. If benefits of cuckoldry are small, reaching this alternative requires that the initial fraction of cuckolding females is high (Fig. 3A). However, changing any of the factors listed in Fig. 3 may lead to a situation where an intermediate, stable cuckoldry frequency becomes suddenly replaced with complete cuckoldry $x = 1$ that evolves from *any* initial proportion of cuckolding females (Fig. 3 with large b_C, e, a, or p_C, or with small d).

The equilibrium of complete cuckoldry usually leads to no male care (Fig. 3). However, when promiscuity is limited such that a single social mate obtains large enough paternity p_C, some degree of male care can remain stable even if all females cuckold (Fig. 3E, dashed line); especially so if females compensate little for losses in paternal care (Fig. 3D, dashed line with small a).

DISCUSSION

The model shows how two different equilibria may exist in breeding systems: an intermediate equilibrium of social monogamy, where a fraction of broods contain extra-pair
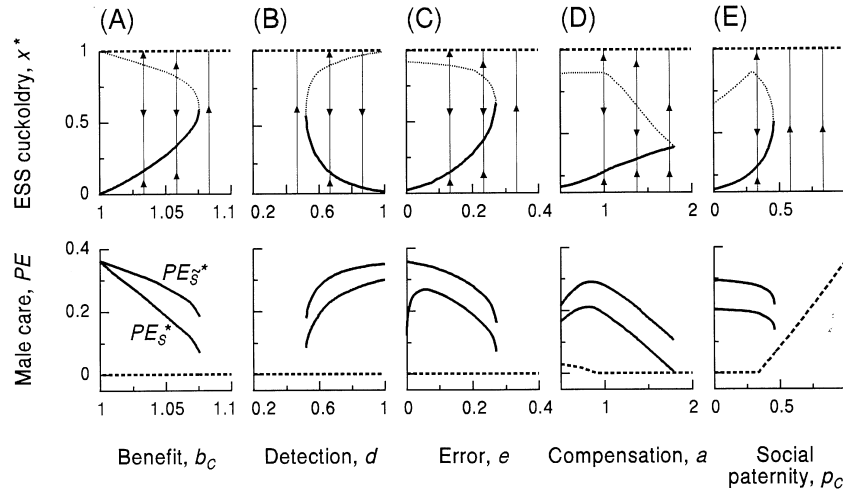
Figure 3 The stable cuckoldry frequency $x*$ (upper row) and male care strategies (lower row) depend on (A) the extra-pair benefit b_C, (B) the probability d that a male detects a female's extra-pair activity, (C) the probability e that the male becomes erroneously suspicious of extra-pair activity, (D) the parameter a that determines how strongly females will compensate for losses in paternal care, and (E) the paternity p_C of a cuckolded social mate. Parameter values are $b_C = 1.05$, $d = 0.6$, $e = 0.2$, $a = 1$, and $p_C = 0.3$, where not specifically varied. Bold lines (either dashed or solid) show stable cuckoldry strategies in the upper row, and corresponding male care strategies in the lower row. The dotted line (upper row only) indicates unstable equilibria, i.e. it separates regions in which cuckoldry increases or decreases (shown with arrows). Bold solid lines indicate solutions with incomplete cuckoldry. In these cases, suspicious males care less (PE_S) than unsuspicious males ($PE_{\bar{S}}$). The bold dashed line shows that complete cuckoldry $x = 1$ exists as an alternative ESS, and it always leads to equal care levels (usually 0) in both suspicious and unsuspicious social mates. Evolution towards complete cuckoldry requires very high initial cuckoldry frequencies if benefits b_C are small or detection probability d is large. At no benefit to cuckoldry, $b_C = 1$, this equilibrium becomes unstable.

young, and an alternative equilibrium with complete cuckoldry, which is associated with reduced male care (usually no male care at all). When cuckoldry is complete and males do not care, social mates can hardly be said to exist. Instead, several females are then free to mate with the same male (e.g. to obtain best genes) or to mate promiscuously (e.g. to guarantee fertility), and males devote their energy to mate acquisition. This alternative equilibrium can therefore be equalled with polygamy (with or without female promiscuity). Benefits of extra-pair fertilizations may therefore lead to evolution towards polygamy with female-only care. Although initiated by females, average female fitness and offspring survival decrease in this process; hence, it can be described as a "tragedy of the commons".

The model assumes variable paternity in different breeding attempts of a male and ignores any cost reductions; hence it is designed to bring about strong behavioural responses in males (see Westneat & Sherman 1993 for comparisons of cuckoldry models). Nevertheless, these responses are not always strong enough to prevent the females' "tragedy of the commons". Where they are, social monogamy with a certain degree of extra-pair paternity can remain a stable option. If behavioural responses of males are strong enough, cuckoldry is selected against once

it becomes relatively common, but not yet so common that male care is already very much diminished. Therefore, social monogamy can be inherently stable, and not just a consequence of external constraints such as low population density or lack of intrinsic benefits of extra-pair paternity.

The model predicts that a large variety of cuckoldry frequencies may exist in nature, with a continuum from males that devote all their energy to paternal care and very little to mate acquisition, to high extra-pair levels where males allocate much more into sexual advertisement. In good agreement with the model, extra-pair paternity in birds correlates negatively with paternal care (Møller & Birkhead 1993) and positively with plumage brightness (Møller & Birkhead 1994). In the model, even very high (> 50%) cuckoldry frequencies can be stable and still result in significant male care, at least if males cannot reliably assess a female's faithfulness; but stable cuckoldry frequencies should more commonly lie below 50%, where there is a wide safe margin between stable cuckoldry and the runaway towards polygamy. Data on extra-pair paternity frequencies in birds fit this prediction well (Petrie & Kempenaers 1998).

Stable extra-pair fertilization frequencies are predicted to be higher if intrinsic benefits of cuckoldry are large, if it is easy (or rather, optimal) for females to compensate for losses

in male paternal care, and if males cannot very accurately assess female behaviour. These are the same factors which, if strong enough, lead to polygamy. The first and second of these prerequisites have been found to correlate with degrees of extra-pair paternity (Petrie *et al.* 1998; Møller, unpublished work). To my knowledge, no study has attempted to relate the likelihood and strength of male behavioural responses to the observed degree of extra-pair paternity.

The model also generates the possibility of some degree of stable male care, even if male behavioural responses do not suffice to limit the unfaithfulness of females. This happens if females willing to cuckold rarely actually find extra-pair partners, or if the paternity of the social mate (p_C) remains high for some other reason even if he has been cuckolded. In such cases, female fitness should appear to increase with her realized EPF success, whereas the alternative of balanced selection predicts equal fitness for females that have or don't have extra-pair young.

The paternity and classification parameters p_C, d, and e were constant in the model; in reality, they too are likely to evolve through processes such as sperm competition and mate guarding. If males can push these values in their favourable direction, payoffs from male care will increase, possibly also accompanied by a decrease in ESS cuckoldry frequencies. This leads to the surprising conclusion that in the sexual conflict over paternity, male strategies may have a predominantly stabilizing effect on biparental care, whereas female strategies may threaten it. A very central assumption behind this conclusion is that extra-pair fertilizations only occur when solicited by females; the model does not apply to cases where forced copulations are successful. In birds, however, unforced EPCs seem most common (Birkhead & Møller 1998).

The above conclusion is in sharp contrast to several models that have considered female strategies that maximize male care (Houston & Davies 1985; Harada & Iwasa 1996; Houston *et al.* 1997; Iwasa & Harada 1998). These models assume that several males may receive high enough paternity from a single female, to be classified as social mates. This possibility is not considered in the current model, where extra-pair males are either fixed to their own social mates or (in case they do not care at all) devote all their energy to seeking as many extra-pair partners as possible. Allowing for polyandry where multiple males provide for a single nest may render female strategies actually enhancing social monogamy, rather than threatening it (Iwasa & Harada 1998). These polyandry models, however, consider paternal care as the only currency of mate choice for the female, and thus ignore any intrinsic benefits that mixed broods have. They also do not explicitly formulate opportunity costs of males. It would be necessary to combine both direct and indirect benefits of mate choice to the studies of polyandrous mating strategies,

to see if the polygamous "tragedy of the commons" is restricted to cases with maximally one social mate.

Another assumption of the current model that may not be true for all species is the existence of opportunity costs, i.e. that extra-pair success of males decreases with paternal effort. This trade-off does not necessarily exist if breeding is synchronous, resulting in a minor time overlap between paternal care and extra-pair activities. It turns out, however, that predictions of the model remain valid even if this assumption is removed (by replacing all e^{-PE} terms in equations 6a–b with 1). Cuckolded males still gain from reducing their paternal effort as long as paternal care has direct costs, such as reduced survival to future breeding attempts (which are potentially better with respect to paternity). A more complicated factor that the current model ignores is quality-dependence in male mating strategies. It is not immediately obvious how this would affect overall care strategies. Large heritable variation in male quality would enhance the benefits b_C that a female obtains from EPFs, hence quality variation would threaten the stability of biparental care (as in Petrie & Lipsitch 1994). However, with large quality variation in males, opportunity costs would be reduced for low-quality males who know their meagre chances as extra-pair sires. This would enhance the relative payoffs that low-quality males gain from caring for their offspring, and might therefore stabilize a "differential allocations" care pattern (Burley 1986; Kokko 1998).

Females are selected to find the best genetic mate (or to mate promiscuously to ensure fertility), rather than give high paternity to one social mate, if male care is of little importance (Petrie & Lipsitch 1994; Møller, unpublished manuscript); males, in turn, are selected to care little if they can potentially fertilize many females (Clutton-Brock 1991; Houston 1995; Kokko 1998). The circular nature of this statement makes it an "chicken and egg" problem in evolutionary ecology, but the model suggests that circularity might indicate a positive feedback loop rather than faulty logic. It may be compared to the apparent circularity of the Fisher process of sexual selection, where females are selected to mate with attractive males, because females (of the next generation) mate with attractive mates. Both Fisherian sexual selection and the cuckoldry game can lead to enhanced promiscuous mating strategies of males, and a reduction in offspring survival. In the case of cuckoldry, this result can quite paradoxically originate from individual females being continually selected to improve the survival of their offspring.

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BIOSKETCH

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