When should cuckolded males care for extra-pair offspring?

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In socially monogamous species with bi-parental care, males suffer reduced reproductive success if their mate engages in extra-pair copulations (EPCs). One might therefore expect that males should refuse to care for a brood if they can detect that an EPC has occurred. Here, we use a game-theory model to study male brood care in the face of EPCs in a cooperatively breeding species in which offspring help to raise their (half-) siblings in their parents’ next breeding attempt. We show that under certain conditions males are selected to care even for broods completely unrelated to themselves. This counter-intuitive result arises through a form of pseudo-reciprocity, whereby surviving extra-pair offspring, when helping to rear their younger half-siblings, can more than compensate for the cost incurred by the male that raised them. We argue that similar effects may not be limited to cooperative breeders, but may arise in various contexts in which cooperation between (half-) siblings occurs.

Keywords: parental care; paternal care; paternity; game theory

1. INTRODUCTION

Parental decisions about brood care reflect a trade-off between fitness gained from raising the current brood and other aspects of fitness, such as parental survival, future breeding success and extra-pair copulations (EPCs) [1–6]. Extra-pair paternity is common in (socially) monogamous species, whereas true genetic monogamy is rare (e.g. it occurs in only 14% of investigated passerine species [7]). In mating systems where a male’s paternity share can vary across successive broods, it is an important predictor of male fitness gain from a given brood. Theory therefore predicts that males in such systems should invest less in broods in which they have low paternity, provided that they can detect that this is the case [8–10]. Empirical studies indicate that paternity perception is possible, and that it is most likely mediated by males assessing female behaviour, rather than by directly assessing genetic relatedness (reviewed by Kempenaers & Sheldon [11]). Although we agree with the general view that paternity matters for the evolution of paternal care (reviewed by Kokko & Jennions [12]), here we derive the prediction that paternity should matter less in cooperative breeders, where raising young can serve as a way to recruit helpers for future breeding attempts. In cooperative breeding systems, animals help to rear offspring that are not their own [13]. Most often such behaviour is performed by non-breeding offspring that help their parents in their next breeding attempt. The benefits for the parties involved have been studied intensely (reviewed by Hatchwell [14]). The parents commonly benefit either in terms of enhanced brood survival owing to increased total feeding amount (e.g. in white-fronted bee-eaters, Merops bullockoides), and/or they compensate for the additional food provisioning by reducing their feeding effort (e.g. in the grey-crowned babbler, Pomatorhinus temporalis; reviewed by Hatchwell [14]), thus increasing their own survival [15,16]. Helpers may benefit in multiple non-exclusive ways, such as by acquiring parenting skills [17], remaining tolerated in the territory [18], enhancing their survival or future fecundity by group augmentation [19] or gaining indirect (kin-selected) fitness benefits. EPCs tend to reduce the relatedness between helpers and brood from full siblings to half-siblings, which will reduce kin-selected benefits of helping but may not affect other benefits. Indeed, helpers have been shown to adjust their effort in response to extra-pair paternity in some studies but not in others (reviewed by Hatchwell [14]).

Here, we present a model to study the adaptive value of male care for extra-pair offspring in a socially monogamous, cooperatively breeding species. We define ‘male care’ as the care provided by the social father, and ‘sibling care’ as the care provided by siblings (of either sex). In the model, males can follow three possible strategies: ‘always care’, which provides care regardless of the occurrence of EPC; ‘conditional care’, which provides care only if no EPC has occurred during the current breeding attempt; and ‘no care’, which never provides care. By comparing lifetime reproductive success under these strategies, we identify conditions where cuckolded males are selected to raise extra-pair offspring as well as their own offspring.

2. THE MODEL

We consider an infinite population with an even sex ratio in which reproduction occurs in discrete breeding events (time steps) in socially monogamous pairs. Each female produces N offspring per time step (N = 4 in all numerical examples).
Table 1. Notation.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
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<tr>
<td>N</td>
<td>number of offspring produced per brood</td>
</tr>
<tr>
<td>n</td>
<td>number of surviving offspring per brood</td>
</tr>
<tr>
<td>V₀</td>
<td>baseline offspring survival</td>
</tr>
<tr>
<td>Vₘₐₑ</td>
<td>a caring male's contribution to offspring survival</td>
</tr>
<tr>
<td>Vₛ₁𝑏</td>
<td>a helper's contribution to offspring survival</td>
</tr>
<tr>
<td>e</td>
<td>male behaviour (e = 1 if he cares; e = 0 otherwise)</td>
</tr>
<tr>
<td>v(ċ, n)</td>
<td>offspring survival probability</td>
</tr>
<tr>
<td>Sₖₐᵅₑ , S₀</td>
<td>survival probability of a male who provides care or not</td>
</tr>
<tr>
<td>τⱼ</td>
<td>expected number of time steps spent in state j</td>
</tr>
<tr>
<td>T</td>
<td>life expectancy</td>
</tr>
<tr>
<td>α</td>
<td>probability that an extra-pair copulation occurs</td>
</tr>
<tr>
<td>β</td>
<td>paternity share of extra-pair male</td>
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Offspring survival \( v(ċ, n) \) is a function of the male's care behaviour \( ċ \), and of the number of surviving siblings from the previous brood, \( n \), which help to raise the current brood. For an overview of our notation, see table 1. Throughout this article, we use angled brackets to enclose function arguments.

We let

\[ v(ċ, n) = V₀ + nVₛ₁𝑏 + ċVₘₐₑ, \]

where \( V₀ \) is baseline survival, \( Vₛ₁𝑏 \) is the survival increment provided by each of the \( n \) helpers, \( ċ \) specifies whether the male cares \((ċ = 1)\) or not \((ċ = 0)\), and \( Vₘₐₑ \) is the survival increment due to male care. For simplicity, we assume that female behaviour is fixed, and thus is accounted for in terms of \( V₀ \).

In each time step, there is a probability \( α \) that a female engages in an EPC. If this happens, each of her offspring produced in this time step has probability \( β \) of being sired by the extra-pair male.

We consider three strategies: always care (AC), in which the male always cares for his social partner's brood (showing behaviour \( ċₑₚₑ𝑐 = 1 \) when an EPC occurred and \( ċₑₚₑ𝑐 = 1 \) otherwise); conditional care (CC), in which the male cares only if no EPC has occurred \((ċₑₚₑ𝑐 = 0; ċₑₚₑ𝑐 = 1)\); and no care (NC), in which the male never provides care \((ċₑₚₑ𝑐 = 0; ċₑₚₑ𝑐 = 0)\). Implicit in this formulation is the assumption that males can detect EPC (e.g. by monitoring the behaviour of the female) but not their genetic relatedness to the brood.

Following a game-theory approach [20], we study the possible invasion of a rare mutant strategy \((ċₑₚₑ𝑐; ċₑₚₑ𝑐)\) in a population where almost all males use the same (‘resident’) strategy \((ċₑₚₑ𝑐; ċₑₚₑ𝑐)\).

Providing care in a given time step reduces a male’s probability to survive until the next time step from \( S₀ \) to \( Sₖₐᵅₑ \). Thus, for each strategy, male survival when cuckolded or not is given by \((Sₑₚₑ𝑐 = Sₖₐᵅₑ; Sₑₚₑ𝑐 = Sₖₐᵅₑ)\) for AC; \((Sₑₚₑ𝑐 = S₀; Sₑₚₑ𝑐 = Sₖₐᵅₑ)\) for CC and \((Sₑₚₑ𝑐 = S₀; Sₑₚₑ𝑐 = S₀)\) for NC.

If each of the \( N \) offspring in a brood survives with independent probability \( v_j \), the probability that exactly \( n \) of them survive is given by a binomial distribution as

\[ \binom{N}{n} v^n (1 - v)^{N - n}. \]

When a male has to make the decision of whether or not to care for the first brood of his life, he can be in one of two possible states: either he has 0 helpers and an EPC has occurred, or he has 0 helpers and no EPC has occurred. In subsequent time steps, if he is still alive, he may be in any of \( 2(N + 1) \) possible states, representing all combinations of helper number (between 0 and \( N \)) and EPC occurrence. The transition probabilities between states define a Markov chain (table 2) for which we can calculate \((\text{using first-step analysis})\) the expected durations \( τⱼ \) that a male spends in each state \( j \). These durations add up to a male’s life expectancy as

\[ T = \sum_j τⱼ. \]

Assuming that all males alive at a given time have the same probability of siring extra-pair offspring, males can expect to sire

\[ \bar{γ} = αβ \sum_{i=0}^{N} \frac{1}{N} \cdot \binom{N}{i} (n; N, v(ċₑₚₑ𝑐, i)) \]

extra-pair offspring per time step, where

\[ \hat{p}_i = \frac{1}{T} \sum_j \binom{i}{N} \]

is the probability that \( i \) helpers are present at a randomly chosen resident brood. (Equivalently, \( \hat{p}_i \) is the probability that \( i \) offspring survive in a randomly chosen resident brood.) Here, the index \( j \) runs over all possible states, \( τⱼ/T \) is the probability that a randomly chosen resident brood is in state \( j \), and \( \bar{γ} \) is the offspring survival probability corresponding to state \( j \) in resident broods.

The expected number of surviving within-pair offspring produced per time step by a male in state \( j \) is given by

\[ f(j) = (1 - β) \sum_{i=1}^{N} \binom{i}{N} \]

for broods in which an EPC has occurred, and by

\[ f(j) = \sum_{i=1}^{N} \binom{i}{N} \]

for broods in which no EPC has occurred.

Lifetime reproductive success of a mutant strategy in a population dominated by a given resident strategy is given by

\[ \bar{w}_{\text{mutant, resident}} = \sum_j τ_j (f_j + \bar{γ}). \]

where \( τ_j \) and \( f_j \) depend on the mutant strategy and \( \bar{γ} \) depends on the resident strategy. The evolutionary stability conditions for each strategy are as follows:

- AC is an evolutionarily stable strategy (ESS) if \( w_{AC,AC} > w_{CC,AC} \) and \( w_{AC,AC} > w_{NC,AC} \).
- CC is an ESS if \( w_{CC,CC} > w_{AC,CC} \) and \( w_{CC,CC} > w_{NC,CC} \).
- NC is an ESS if \( w_{NC,NC} > w_{AC,NC} \) and \( w_{NC,NC} > w_{NC,NC} \).
helpers, no EPC

S

to offspring survival; 

stakes in the brood (figures 1 and 2). This counterintuitive result arises because surviving extra-pair offspring can mutually invade each other so that no pure strategy can be an ESS even if extra-pair sires achieve full paternity in their broods (cf. electronic supplementary material, figures S1 and S2 versus figures 1–3). This can be explained by a combination of two arguments. First, delayed benefits from caring for unrelated offspring become relatively less important in the face of immediate benefits. On the other hand, high baseline offspring survival \( V_0 \) disfavours AC, by making offspring less dependent on male care. Similarly, high \( V_0 \) also makes offspring less dependent on sibling care, explaining why \( V_{slb} \) most strongly affects AC at low levels of \( V_0 \) (figures 1 and 2). High prevalence of EPCs (a) disfavours AC (compare figure 2 with figure 1), because a male’s fitness gains from caring become more diluted as an increasing proportion of the recipients are unrelated to him. Higher male baseline survival \( S_0 \) favours AC under some conditions (cf. electronic supplementary material, figures S1 and S2 versus figures 1 and 2), presumably because longevity predicts a male’s probability to recoup any delayed benefits (in terms of pseudo-reciprocity) of his actions. However, this effect of \( S_0 \) on AC is reversed if cuckolded males retain partial paternity in their broods (cf. electronic supplementary material, figure S3 versus figure 3). This can be explained by a combination of two arguments. First, delayed benefits from caring for unrelated offspring become relatively less important in the face of immediate benefits from caring for genetic offspring. Thus, second, we need to consider how \( S_0 \) affects male care for intra-pair offspring. Because first broods (which never have helpers)

3. RESULTS AND DISCUSSION

Each of the considered male strategies has an area of parameter space where it is evolutionarily stable (figures 1–3). We never found more than one ESS for given parameter values, but under some conditions two strategies can mutually invade each other so that no pure strategy is an ESS (figures 1–3). Of particular theoretical interest is the strategy AC, which provides care for extra-pair offspring as a side-effect [22]. The results are affected by parameter settings as follows.

(a) Always care
The strategy AC is favoured if male brood care provides high benefits (in terms of enhanced offspring survival, \( V_{male} \)) at low costs (in terms of male survival, \( S_{care} \); figures 1–3). High benefits of sibling care (\( V_{slb} \)) favour AC because they magnify the return investments obtained by caring males through pseudo-reciprocity. On the other hand, high baseline offspring survival \( V_0 \) disfavours AC, by making offspring less dependent on male care. Similarly, high \( V_0 \) also makes offspring less dependent on sibling care, explaining why \( V_{slb} \) most strongly affects AC at low levels of \( V_0 \) (figures 1 and 2). High prevalence of EPCs (a) disfavours AC (compare figure 2 with figure 1), because a male’s fitness gains from caring become more diluted as an increasing proportion of the recipients are unrelated to him. Higher male baseline survival \( S_0 \) favours AC under some conditions (cf. electronic supplementary material, figures S1 and S2 versus figures 1 and 2), presumably because longevity predicts a male’s probability to recoup any delayed benefits (in terms of pseudo-reciprocity) of his actions. However, this effect of \( S_0 \) on AC is reversed if cuckolded males retain partial paternity in their broods (cf. electronic supplementary material, figure S3 versus figure 3). This can be explained by a combination of two arguments. First, delayed benefits from caring for unrelated offspring become relatively less important in the face of immediate benefits from caring for genetic offspring. Thus, second, we need to consider how \( S_0 \) affects male care for intra-pair offspring. Because first broods (which never have helpers)

Table 2. Transition probabilities between consecutive states during a male’s life.

<table>
<thead>
<tr>
<th>current state</th>
<th>next state</th>
<th>y helpers, EPC occurred</th>
<th>y helpers, no EPC</th>
</tr>
</thead>
<tbody>
<tr>
<td>x helpers, EPC occurred</td>
<td>( S_{epc} \cdot \text{bin}(y; N, v(\epsilon_{epc}, \hat{x})) )</td>
<td>( S_{epc}(1 - \alpha)\text{bin}(y; N, v(\epsilon_{epc}, \hat{x})) )</td>
<td></td>
</tr>
<tr>
<td>x helpers, no EPC</td>
<td>( S_{noepc} \cdot \text{bin}(y; N, v(\epsilon_{noepc}, \hat{x})) )</td>
<td>( S_{noepc}(1 - \alpha)\text{bin}(y; N, v(\epsilon_{noepc}, \hat{x})) )</td>
<td></td>
</tr>
</tbody>
</table>

Figure 1. Evolutionary stable strategies in a short-lived species (\( S_0 = 0.5 \)) where EPCs occur with probability \( \alpha = 0.2 \), resulting in paternity \( \beta = 1 \) to the extra-pair male. White, AC; light grey, AC and CC can mutually invade each other; dark grey, CC; black, NC. \( V_0 \), baseline offspring survival; \( V_{male} \), a caring male’s contribution to offspring survival; \( V_{slb} \), a helper’s contribution to offspring survival; \( S_{care} \), survival probability of a caring male.

Table 2. Transition probabilities between consecutive states during a male’s life.
make up a smaller proportion of all broods in long-lived than in short-lived species, a longer lifespan in our model implies a higher prevalence of helpers. High helper prevalence in turn reduces the relative importance of male care for offspring survival, rendering male care less worthwhile. Taken together, these arguments explain why a long lifespan ($S_0$) can shift the evolutionarily stable outcome away from AC (electronic supplementary material, figure S3), while having a consistently positive effect on NC (electronic supplementary material, figures S1–S3). It is worth noting that a previous theoretical study of non-cooperative breeders predicted that males should be more tolerant of reduced paternity in short-lived than in long-lived species [23].

Although the total number of extra-pair offspring (calculated as $\alpha \cdot \beta$) is the same in figure 1 as in figure 3, it makes a big difference how these are distributed across broods: if there are relatively few EPC broods,
each containing a high proportion of extra-pair offspring ($\alpha = 0.2; \beta = 1$), caring cuckolded males can benefit only in terms of pseudo-reciprocity, limiting the success of AC (figure 2). By contrast, if there are more EPC broods, each containing fewer extra-pair offspring ($\alpha = 0.4; \beta = 0.5$), caring cuckolded males gain immediate benefits (in terms of intra-pair offspring survival) as well as pseudo-reciprocity benefits, resulting in a larger ESS area of AC (figure 3).

(b) No care
To explain why NC (oppositely to AC) is favoured by high values of $V_c$ and low values of $V_{male}$ and $S_{care}$ (figures 1–3), the same intuitive arguments given above can be used in reverse. On the other hand, the parameters specifying the prevalence and extent of extra-pair paternity ($\alpha$, $\beta$) have little effect on the ESS conditions of NC (figures 1–3). This is because the strategies NC and CC behave identically towards EPC broods. Finally, NC is favoured by long lifespan ($S_0$) and high benefits of sibling care ($V_{abs}$). This is because these parameters increase the likelihood and extent of sibling help, thus reducing the relative importance of male care for offspring survival.

It is worth noting that the presence of helpers may reduce the importance of male care also from the perspective of the female, which may lead to interesting feedbacks that are beyond the scope of our present model. For example, helpers may indirectly enable female promiscuity by limiting a female’s cost of being deserted by her mate [24]. This may destabilize the system by making brood care less worthwhile for both the male (see effect of $\alpha$, $\beta$; also see [6]) and the helpers themselves [25].

To provide a clear example of the possible consequences of sibling help for the evolution of male care, we have made a number of simplifying assumptions that necessarily limit the realism of our model. For example, while we have assumed that offspring survival is an additive function of the contributing care efforts, non-additive effects may commonly occur in nature (e.g. owing to synergistic interactions between brood carers, or because offspring benefit more from obtaining food when hungry than when satiated). If offspring survival is a strongly saturating function of brood care effort, caring strategies should probably be more flexible than envisaged in our model, allowing effort to be contingent on the number of helpers present. Nevertheless, we would then still expect that males can benefit from raising helpers (including non-related helpers) whose presence, albeit not greatly affecting offspring survival, would lighten the males’ future workload. Other complications not included in our model are the coevolutionary dynamics between the brood care efforts of all family members [1], and the interplay between behavioural and evolutionary time scales in producing observed care efforts [26]. Despite these simplifications, we believe that our model captures the essence of a biological mechanism likely to be relevant in natural systems in which a key assumption holds; namely, that cuckolded males care for unrelated offspring which later help their (half-)sibling, including the focal male’s own offspring. This principle may not be limited to cooperative breeders, but may apply in various vertebrate systems in which cooperation between (half-)siblings occurs (for reviews on cooperation, see [27,28]).

The main prediction from our model, then, is that the existence of cooperation between (half-)siblings in a species should reduce the extent to which male brood care is contingent on paternity certainty. Moreover, in addition to selecting for male brood care for unrelated offspring, the principle envisaged in our model may also select for the suppression of harmful behaviours (e.g. infanticide) towards such offspring. This may lead to less infanticide in species where helping between half-siblings is common, and to sex-biased infanticide in species where one sex is more helpful than the other. These predictions could be tested in comparative studies across species. We conclude by noting that in complex social systems, help provided by extra-pair offspring towards a caring cuckold’s wider family might endow him with additional inclusive fitness benefits.

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REFERENCES


