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Stability and value of male care for offspring: is it worth only half the trouble?

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Models of parental investment often assume a trade-off for males between providing care and seeking additional mating opportunities. It is not obvious, however, how such additional matings should be accounted for in a consistent population model, because deserting males might increase their fertilization success at the cost of either caring males, other deserting males or both. Here, we present a game theory model that addresses all of these possibilities in a general way. In contrast to earlier work, we find that the source of deserting males' additional matings is irrelevant to the evolutionary stability of male care. We reject the claim that fitness gains through male care are intrinsically less valuable than those through desertion, and that the former must therefore be down-weighted by 1/2 when compared with the latter.

1. INTRODUCTION

The evolutionary significance of the relative parental investment of the sexes is a classic, yet still debated, theme in the study of animal mating systems (Kokko & Jennions 2003; Houston *et al.* 2005). Earlier work by Trivers (1972), Maynard Smith (1977) and others has provided a framework that has been extensively used, but has also been fundamentally questioned (Wade & Shuster 2002).

A basic challenge for parental investment theory is to explain why males in some species, but not in others, care for offspring. Maynard Smith (1977) used a game theoretical approach to address this question, focusing on a trade-off between providing care and seeking additional mating opportunities. One of his models ('model 2') has been particularly influential but also controversial. Among other findings, it predicts that a male should provide care if this increases the number of its surviving offspring more than the alternative strategy of desertion and further mate search. Although this appears straightforward, and is in agreement with some subsequent work (e.g. Werren *et al.* 1980; Queller 1997; Webb *et al.* 1999), Wade & Shuster (2002) claim that this prediction is based on a fundamental logical flaw. Intriguingly, their alternative approach yields strikingly different

results, indicating that a fitness gain from enhanced offspring survival through male care must be down-weighted by the factor 1/2 when compared with a fitness gain through additional matings.

One problem with model 2 is that it does not specify the source of additional mating opportunities accrued by deserting males (Webb *et al.* 1999). To amend this shortcoming, Wade & Shuster (2002) assumed that deserting males gain additional matings by mating with the mates of caring males. Unfortunately, as we discuss below, their approach is problematic itself, thus leaving the controversy over model 2 unresolved (see also Houston & McNamara 2005).

Here, we present a model that addresses the implications of deserting males having additional matings in a simple and general way. This will allow us to examine the value of male care when compared with the value of gaining additional matings.

2. THE MODEL

Consider a seasonally breeding species in which brood survival depends on care received from adults. We focus on the simplest case where females follow a given uniform strategy, i.e. either all females care for their young or all females desert. Thus, brood survival in our model varies only with respect to male behaviour. Deserting males may increase their fitness by mating with additional females. However, if we assume a balanced sex ratio and synchrony in pairing, then there will be no unmated females available at the time of male desertion. Consequently, deserting males can gain additional matings only in the form of extra-pair copulations (EPCs). We assume that off-spring survive with probability V_c in broods that receive full male care and with probability V_d without male care. Because a female's social partner might reduce its amount of care in response to being cuckolded (e.g. Rios-Cardenas & Webster 2005), we allow for the possibility that offspring survival is V_{EPC} when the female was involved in EPCs.

When deserting males have EPCs, they may have these with either the mates of caring males, the mates of deserting males or both. In any case, consistency requires that paternity gains through EPCs inflict a corresponding paternity reduction on the males that are cuckolded (Queller 1997; Houston & McNamara 2002; Houston *et al.* 2005). We allow the extent of paternity exchange through EPCs to depend on the frequency ρ of deserting males. Let $\alpha(\rho)$ and $\beta(\rho)$ be the functions describing the paternity that a deserting male can expect through EPCs with the mates of caring males and deserting males, respectively. For example, $\alpha(\rho) = 0.1$ could mean that each deserting male sires 10% of the offspring of just one female whose social partner is a caring male; it could also mean that each deserting male has a 10% chance of siring all offspring of such a female, or that each deserting male sires 5% of the offspring of each of two females that have a caring male as their social partner. The general formulation in terms of $\alpha(\rho)$ and $\beta(\rho)$ can accommodate various patterns of paternity exchange among males. For example, both male types may be equally susceptible to paternity loss, or caring males may have a superior ability to defend their paternity (Kvarnemo 2006) or, as assumed by
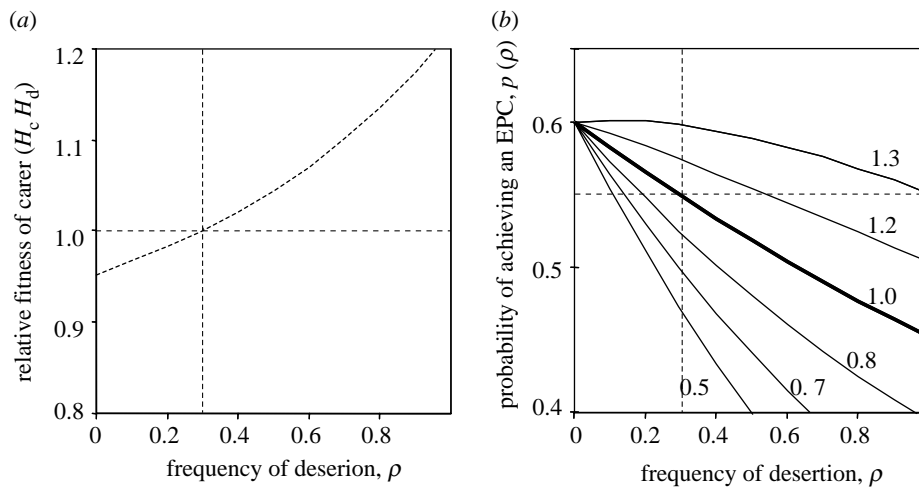
Figure 1. The case where an intermediate frequency of desertion (broken vertical line at $\rho=0.29$) is evolutionarily stable. (a) Relative fitness of caring males as a function of ρ. (b) Probability $p(\rho)$ of achieving an EPC as a function of ρ. Assumptions regarding the allocation of EPCs are indicated by index values adjacent to each line. Deserting males may be biased towards either cuckolding caring males (index values above 1), deserting males (below 1) or neither. In the latter case, the equilibrium occurs where $p(\rho)$ (bold line) equals s (broken horizontal line), the survival advantage associated with care. Parameter settings: $n=1$; $x=1$; $V_c=1$; $V_{EPC}=1$; $V_d=0.45$; $P_A=0.6$; index values are P_A/P_B (see appendix II of the electronic supplementary material for details).

Wade & Shuster (2002), deserting males may have EPCs exclusively with the mates of caring males, $\alpha(\rho)>\beta(\rho)=0$. Although the latter assumption is problematic (see §3), we stress that it is within the scope of our model.

We define N as the total number of broods in the population, w as the brood size prior to mortality and $\gamma(\rho)$ as the fraction of caring males' broods in which EPCs occur. Then, caring males obtain $V_c w$ surviving offspring from each of $N(1-\rho)(1-\gamma(\rho))$ broods in which no EPCs occur. Now, consider the $N(1-\rho)\gamma(\rho)$ broods of caring males in which EPCs do occur. Each of these broods contains $V_{EPC}w$ surviving offspring. However, because there are $N\rho$ deserting males, each of which can expect paternity $\alpha(\rho)$ with caring males' mates, these broods also include a total number of $N\rho\alpha(\rho)V_{EPC}w$ extra-pair offspring that do not contribute to the fitness of caring males. Hence, caring males collectively produce $V_c w N(1-\rho)(1-\gamma(\rho))+V_{EPC}wN(1-\rho)\gamma(\rho)-N\rho\alpha(\rho)V_{EPC}w$ offspring. If we divide this by the number of caring males, $N(1-\rho)$, we obtain H_c, the fitness per caring male,

$$H_c = \frac{V_c wN(1-\rho)(1-\gamma(\rho))+V_{EPC}wN(1-\rho)\gamma(\rho)-N\rho\alpha(\rho)V_{EPC}w}{N(1-\rho)},$$

which simplifies to

$$H_c = w\left(V_c(1-\gamma(\rho))+V_{EPC}\gamma(\rho)-\frac{\rho\alpha(\rho)V_{EPC}}{1-\rho}\right). \tag{2.1}$$

Deserting males, on the other hand, gain $V_d w$ offspring in their own brood, as well as $\alpha(\rho)V_{EPC}w$ extra-pair offspring through EPCs with caring males' mates. They also gain $\beta(\rho)V_d w$ extra-pair offspring through EPCs with deserting males' mates, but this has no effect on their net fitness as they, on average, lose the same amount of paternity in their own brood. Hence, the fitness of a deserting male is

$$H_d = V_d w + \alpha(\rho)V_{EPC}w. \tag{2.2}$$

Males are selected to care if $H_c>H_d$. Substituting equations (2.1) and (2.2), we obtain

$$V_c(1-\gamma(\rho))+V_{EPC}\gamma(\rho)-\frac{\rho\alpha(\rho)V_{EPC}}{1-\rho}>V_d+\alpha(\rho)V_{EPC}, \tag{2.3}$$

as the condition for males to care.

Now, let us use condition (2.3) to address two scenarios that have been discussed in the literature. Both scenarios assume that deserting males have probability p of achieving a single EPC, which then results in full paternity to the deserting male; this implies that a deserting male's expected EPC paternity is equivalent to p. In terms of our model, p can be expressed as $p(\rho)=\alpha(\rho)+\beta(\rho)$, which makes explicit that it should also depend on ρ.

In the first scenario, featured in Maynard Smith's (1977) model 2, it is assumed that the cuckolded male does not care for the resulting brood, nor does the deserting male (i.e. $V_{EPC}=V_d$). Thus, by appendix I of the electronic supplementary material,

$$V_c>V_d(1+p(0)) \tag{2.4}$$

is the condition where male care is an evolutionarily stable strategy (ESS); this is equivalent to the condition derived by Maynard Smith (1977). We note that although Maynard Smith (1977) did not explicitly account for the exchange of paternity among males in his model, he nevertheless arrived at the correct ESS condition given his assumptions.

Alternatively, following the scenario considered by Wade & Shuster (2002), we assume that cuckolded males fully care for the brood, i.e. $V_{EPC}=V_c$. To match the notation used by Wade & Shuster (2002), we set $V_d=V_c(1-s)$, where s can be thought of as the survival advantage associated with male care. Thus, by appendix I of the electronic supplementary material,

$$s>p(0), \tag{2.5}$$

is the ESS condition for male care. In contrast to Wade & Shuster's (2002) analysis, the value of care

here is not devalued by the factor 1/2. It is worth noting, however, that we can obtain the factor 1/2 from our model if we consider the special case where EPCs occur exclusively with caring males' mates while both male types are equally frequent (see appendix I of the electronic supplementary material).

Our model is not limited to the case where desertion is rare, but applies at any value of ρ. Given additional assumptions about behaviour that specify how $\alpha(\rho)$, $\beta(\rho)$ and $\gamma(\rho)$ change with ρ (see appendix II of the electronic supplementary material), we can even find stable equilibria where both male types coexist (figure 1*a*). Note that at such an equilibrium, $p(\rho)$ may be either greater or smaller than s, depending on assumptions regarding the allocation of EPCs (figure 1*b*). Note also that values of $p(\rho)$ in figure 1*b* converge for small ρ, which makes the underlying assumptions regarding the allocation of EPCs irrelevant when modelling invasion of desertion.

3. DISCUSSION

Specifying the source of deserting males' additional matings does not change the ESS condition for male care in our analysis when compared with Maynard Smith's (1977) model 2. This result rests on the recognition that whatever fitness reduction an individual caring male may suffer as a consequence of a deserting male's behaviour, the impact of this effect on the mean fitness of caring males depends critically on the relative frequencies of male types. The standard method for deriving an ESS condition is to consider a large population in which a mutant phenotype occurs at near zero frequency (Maynard Smith 1982). In the context of our model, this means that a rare deserting mutant in a population dominated by caring males has a negligible effect on caring males' mean fitness.

How, then, did Wade & Shuster (2002) arrive at the factor 1/2? The answer is that their analysis does not take into account the relative frequencies of male types (see their expressions (5)–(8)), which in effect amounts to the implicit, though unintended, assumption that both male types occur with equal frequency (see appendix I of the electronic supplementary material). In this special case, any fitness gain accrued to deserters through remating inflicts an exactly corresponding fitness decrement on carers, and thus has a double impact on relative fitness of male types. This impact can be balanced only if the benefit of male care is twice as high as would be the case otherwise. It is worth stressing that, even if male types do occur with equal frequency, the factor 1/2 as in Wade & Shuster's analysis arises only if deserting males are maximally biased towards cuckolding caring males rather than other deserting males (see appendix I of the electronic supplementary material)—an assumption that appears hard to justify biologically, especially since caring males may often be in a better position to defend their paternity (Kvarnemo 2006). If the latter proposition is true, then male care actually provides a twofold advantage and can be maintained despite high probabilities that deserting males achieve an EPC (figure 1).

Our results are consistent with previous studies (Werren *et al.* 1980; Queller 1997; Webb *et al.* 1999), which have not regarded fitness gains through care as intrinsically less valuable than those through desertion. Queller (1997) provides an excellent discussion of the benefits of providing care for either sex, concluding that paternity uncertainty will tend to make the evolution of care less probable in males. In our model, alternative male behaviour can coexist at a mixed ESS (figure 1)—a pattern that has previously been shown to be possible in a context of parental care (Webb *et al.* 1999).

In conclusion, we have shown that Maynard Smith (1977), despite failing to specify the source of deserting males' additional matings, nevertheless arrived at a correct ESS condition for male care. We have rejected an 'interpretation [that] stands parental investment theory on its head' (Wade & Shuster 2002), namely the view that a fitness gain achieved through male care is generally worth less than an alternative fitness gain through remating. The latter point is critical to the interpretation of past and future studies of parental care, sexual selection and the evolution of mating systems.

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