

# Extra-pair paternity as the result of reproductive transactions between paired mates

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Transactional ('optimal skew' or concessions') models of social evolution emphasize that dominant members of society can be favoured for donating parcels of reproduction to same-sexed subordinates in return for cooperation by the latter. We developed a mathematically similar model in which extra-pair paternity in broods receiving biparental care is viewed as emerging from a reproductive transaction between the paired mates. The model quantitatively predicted the maximum paternity that a male mate can demand before its female mate is favoured to break the pair bond and caring solitarily for a brood sired entirely by a neighbouring male. The model predicts that extra-pair paternity results when the neighbouring male is of sufficiently higher quality than the male mate. In such cases, the exact amount of extra-pair paternity will vary directly with the difference in quality between the two males and inversely with the value (fitness impact) of the male mate's parental care. Importantly, the transactional model provided a unified explanation for experimental and observational evidence that extra-pair paternity rises with decreasing quality of the male mate, increasing genetic variability among breeding males, increasing breeding density, increasing availability of food and decreasing involvement of the male mate in parental care.

**Keywords:** cooperation; monogamy; parental care; reproductive skew

## 1. INTRODUCTION

Transactional models of skew in reproduction attempt to explain the degree of reproductive dominance (skew) within animal societies by predicting the extent to which potential breeders differing in competitive power should reproductively pay each other to stay in the group and cooperate peacefully (Vehrencamp 1979, 1983; Emlen 1982; Reeve 1991; Reeve & Ratnieks 1993; Johnstone 2000). These models, both the classic transactional model and its recent variants (Reeve 1998; Johnstone *et al.* 1999), have received some striking empirical support (Bourke & Heinze 1994; Reeve *et al.* 1998, 2000; Reeve & Keller 2001) and appear promising in integrating our understanding of multiple features of animal societies (Reeve & Ratnieks 1993; Keller & Reeve 1994; Johnstone 2000).

By a similar logic, extra-pair paternity in broods cared for by pair-bonded, cooperating mates can be viewed as arising from a reproductive transaction between these mates. We begin by considering the reproductive options for a paired male and female in a population exhibiting biparental care. The female mate is paired with a male with genetic quality  $q$ , the latter variable measuring the viability, fecundity or fertility of this male mate's offspring. The female has a fraction  $p$  of her brood sired by her male mate, with the remaining fraction  $1-p$  being sired by a neighbouring male who has a genetic quality  $q'$  and who is paired with another female. The female has the option of remaining with her paired mate, in which case her (standardized) expected offspring output is equal to  $k[pq + (1-p)q']$ , where  $k$  is the ratio of the expected total brood success with the paired male's care to the expected total brood success without the male's care. The parameter  $k$  (which can be directly quantified from field experiments) thus measures the value of the male mate's

parental care, which may depend on both the quality of and need for his care. If the female breaks the pair bond with her mate, her brood is sired completely by the neighbouring male. However, she receives no parental care from this already paired male, so her (standardized) expected offspring output is just  $q'$ .

If the female's mate is of higher quality than the neighbouring male (i.e.  $q > q'$ ), then the female has no incentive for obtaining extra-pair fertilizations and her mate will enjoy complete paternity ( $p = 1$ ). In contrast, if the neighbouring male is of higher quality ( $q' > q$ ), then the female would fare best if all the brood were sired by the neighbouring male, but her male mate continued to provide parental care. Of course, the male mate will resist such cuckoldry and attempt to maximize his paternity of the tended brood. However, if the male mate demands too much paternity  $p$  in exchange for his parental care, then the female may be favoured to break the pair bond and have her single-parent brood sired entirely by the neighbouring male. We show that this game (transaction) between paired mates can result in partial paternity for the paired male (i.e. extra-pair paternity) as an evolutionarily stable outcome.

Thus, the central question addressed by our model is the following: what is the maximum paternity  $p$  that the paired male can demand before it pays the female to break the pair bond (assuming that the paired male has a lower quality than the neighbouring male)? Our model predicts this maximum paternity  $p^*$  ( $0 < p^* \leq 1$ ) as a function of (i) the ratio of the quality of the neighbouring male to that of the male mate, i.e.  $q'/q$ , and (ii) the value of the male mate's parental care, i.e.  $k$ .

## 2. THE MODEL

In order to find the maximum paternity at which the female is favoured for breaking the pair bond, we equate

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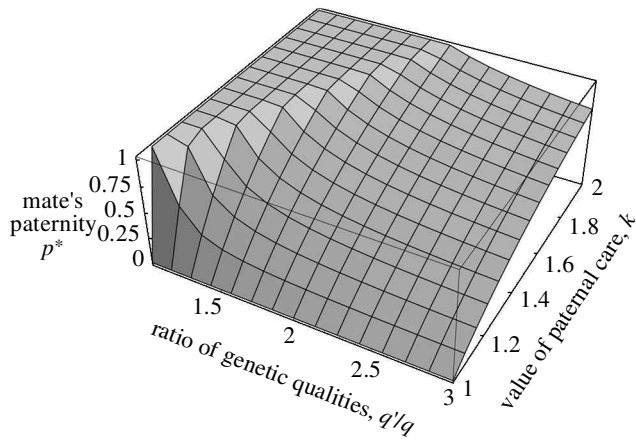


Figure 1. Male mate's paternity  $p^*$  as a function of the ratio of the neighbouring male's quality to the male mate's paternity  $q'/q$  and of the fitness value of the male mate's parental care,  $k$ .

the expected offspring outputs for the female if she stays, i.e.  $k[pq + (1-p)q']$ , versus those if she leaves, i.e.  $q'$  and solve for the male mate's paternity  $p$ . We then obtain

$$p^* = q'(k-1)/k(q'-q) \quad (1)$$

for the maximal paternity.

Thus, the level of extra-pair paternity is equal to  $1-p^*$  and is exactly analogous to the 'staying incentive' that dominants give to same-sexed subordinates in transactional models of reproductive skew (Vehrencamp 1979, 1983; Emlen 1982; Reeve 1991, 1998; Reeve & Ratnieks 1993; Johnstone *et al.* 1999; Johnstone 2000).

We must then ask under what conditions will the paired male benefit from being paired with paternity  $p^*$  versus abandoning its mate and seeking other females. If the male stays, his standardized offspring output is  $p^*kq$  whereas, if he leaves, he receives some pay-off  $x_q$ , where  $x_q$  is some increasing function of his own genetic quality  $q$ . Thus, the male will remain paired even with partial paternity if  $p^*k > x_q$ , which, after substitution of equation (1), becomes

$$x_q < q'(k-1)/(q'-q). \quad (2)$$

Thus, the male will stay paired, even with partial paternity, if his pay-off for seeking other females, i.e.  $x_q$  is sufficiently low.

The above model predicts the precise level of paternity in a stable pair. If the paired male is of lower quality than the neighbouring male then, according to equation (1), the paired male will still achieve complete paternity if  $q'/q < k$ , i.e. if the ratio of the genetic qualities of the two males is less than the value of parental care  $k$  (which is seen by solving  $p^* = 1$ ). Thus, we do not expect to see significant extra-pair paternity when the value of parental care  $k$  is sufficiently large. For cases of partial paternity, the level of paternity will decrease with increases in the neighbouring male's quality (because  $\partial p^*/\partial q' = -q(k-1)/k(q'-q)^2 < 0$ ), with decreases in the paired male's quality (because  $\partial p^*/\partial q = q'(k-1)/k(q'-q)^2 > 0$ ) (note that this also will be true if  $k$  varies directly with  $q$ ) and with decreases in the value of parental care (because  $\partial p^*/\partial k = q'/[k^2(q'-q)] > 0$ ). Thus, extra-pair paternity should increase as the ratio of the

males' qualities  $q'/q$  increases and as the value of parental care  $k$  decreases (figure 1).

### 3. DISCUSSION

The transactional model of extra-pair paternity provides a remarkably unified explanation for all of the major empirically observed predictors of the level of extra-pair paternity in birds providing biparental care.

- (i) Higher quality males, as measured indirectly by their degree of development of secondary sexual characters, degree of social dominance, body condition and/or level of sexual signalling, typically exhibit higher paternity (Bjørnstad & Lifjeld 1997; Lens *et al.* 1997; Møller & Tegelström 1997; Yezerinac & Weatherhead 1997; Møller & Ninni 1998; Otter *et al.* 1998) and male mates whose apparent quality is experimentally reduced suffer greater extra-pair paternity than do unmanipulated males (Johnsen *et al.* 1998). An underlying assumption in this interpretation is that males with greater development of secondary sexual characters (and higher paternity) also have higher genetic quality, which has received empirical support (Kempnaers *et al.* 1992; Hasselquist *et al.* 1996). However, some studies (e.g. Lubjuhn *et al.* 1999) have not found an effect of male quality on the frequency of extra-pair paternity and our model predicts that the value of male parental care ( $k$ ) will be relatively high in these populations (a higher  $k$  weakens the association between male genetic quality and paternity because an increasing fraction of males will have complete paternity regardless of their genetic quality). Interestingly, the transactional model can also explain the extreme statistical skewness and even bimodality commonly seen in the frequency distribution of extra-pair paternity, with many nests containing a high frequency of extra-pair offspring (cases where  $q < q'/k$ ) and many others containing 100% offspring of male mates (cases where  $q > q'/k$ ) (Bjørnstad & Lifjeld 1997; Møller & Tegelström 1997). We conducted a numerical simulation in which the genetic qualities of neighbouring males were independently drawn as pairs from a normal distribution of male quality and then the paternity of each male determined from our transactional model. The resulting frequency distributions of paternity looked strikingly like those obtained from field data, exhibiting high skewness and bimodality in the case of moderate to low values of parental care value  $k$  (figures 2 and 3).
- (ii) The comparative finding that levels of extra-pair paternity are generally lower in species where males have a relatively greater role in brood care (Dixon *et al.* 1994; Negro *et al.* 1996; Møller & Ninni 1998; Møller & Thornhill 1998; Pierce & Lifjeld 1998; Møller 2000) strongly supports the transactional model prediction that extra-pair paternity should be greater when the value of male parental care is reduced (figures 1 and 2). The finding that extra-pair paternity is significantly higher when more food is available (Hoi *et al.* 1999), which is also when male brood-feeding rates are lower, also

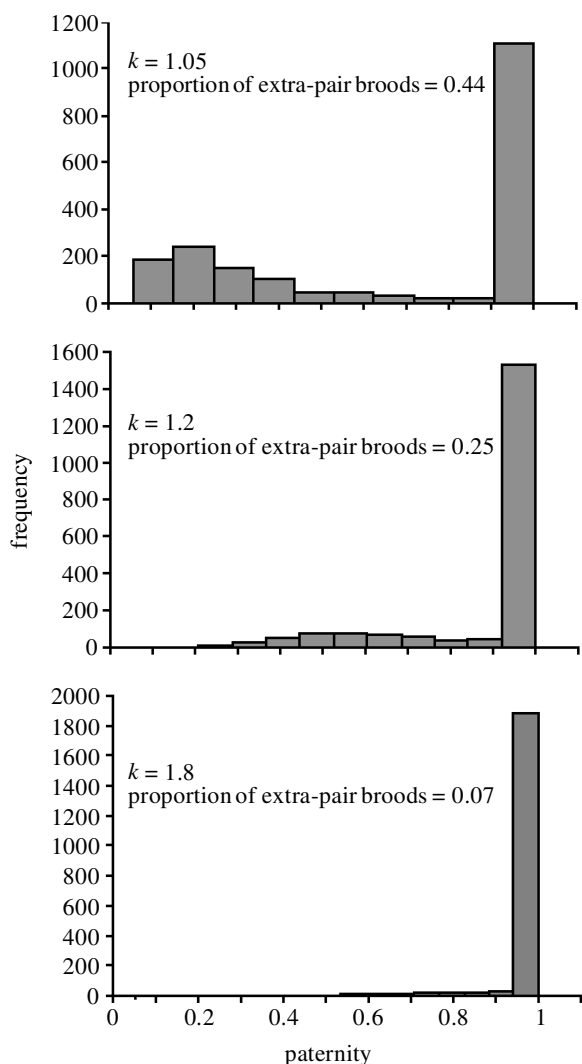


Figure 2. Numerical simulation of the frequency distribution of paternities within broods under the transactional model demonstrating the effect of male parental care value. Genetic qualities of neighbouring males were drawn independently from a normal distribution with a mean of 100 and standard deviation of 20 for a total of 2000 males (the mean of the distribution is arbitrary, since only the ratio of male genetic qualities matters). The frequency distributions of paternity for three values of parental care  $k$  are shown. A lower  $k$  leads to lower mean paternity and enhanced bimodality in the distribution of paternities.

supports this prediction. Increased extra-pair paternity in polygynously paired, female house wrens relative to monogamously paired females (Soukup & Thompson 1997) may reflect the lesser degree of male care in the former. Broods of secondary females in polygynous species are predicted to have lower paternity than broods of primary females when the value of the mate's parental care for the secondary female is low and equal (high) paternity when this value is high (e.g. Kempenaers *et al.* 1997; Soukup & Thompson 1997). Finally, extra-pair paternity is consistently lower in sex-role-reversed species, which have exclusive male care, than in biparental species, which is strongly in accordance with the model's prediction (Dale *et al.* 1999).

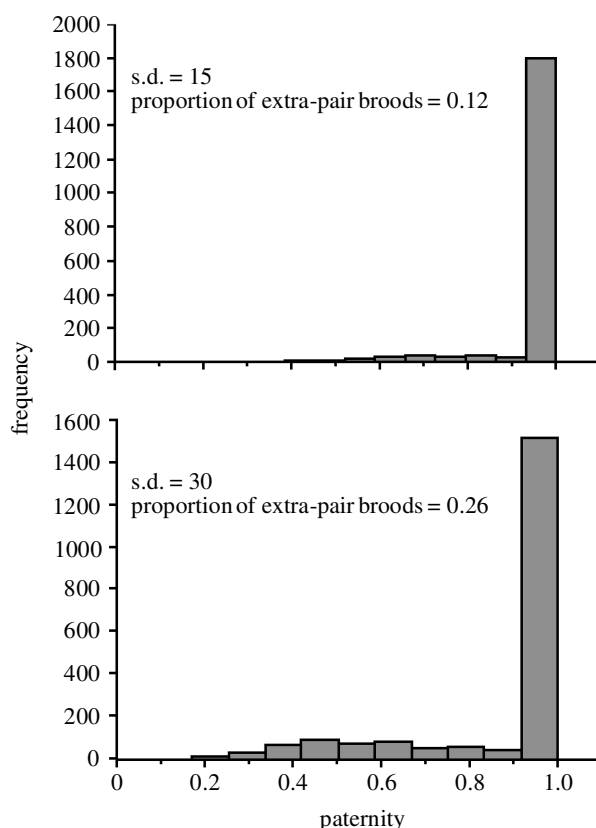


Figure 3. Numerical simulation of the frequency distribution of paternities within broods under the transactional model demonstrating the effect of variance in male genetic quality:  $k = 1.2$  and mean male quality = 100. s.d., standard deviation.

- (iii) The greater genetic variability observed among males in species with higher levels of extra-pair paternity (Petrie & Kempenaers 1998; Petrie *et al.* 1998) is predicted by the transactional model because greater variation in genetic quality among males should increase the expected difference in quality between a male mate and a neighbouring male when the latter has the higher quality. This prediction is illustrated by our numerical simulation (figure 3).
- (iv) The greater levels of extra-pair paternity observed when the breeding density was higher for within-species comparisons (Bjørnstad & Lifjeld 1997; Westneat & Sherman 1997; Møller & Ninni 1998) is predicted by the transactional model because a higher breeding density should increase the probability that a female will have at least one neighbouring male that is of higher quality than her male mate. Some studies have failed to find a breeding density effect within (Tarof *et al.* 1998) or across species (Westneat & Sherman 1997). The former can be explained by the transactional model if the value of male parental care is particularly high within the species studied and the latter can be explained if the value of male parental care is variable across species (thus confounding comparative analyses of breeding density effects).

In summary, we propose that conflicts between paired mates over paternity are amenable to analysis by

evolutionary transaction theory (just as the partitioning of reproduction is among potential same-sexed breeders within an animal society). No other single hypothesis of which we are aware accounts for all of the above patterns. Thus, reproductive transaction is potentially a fundamental feature of many forms of animal cooperation.

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