Extra-pair parentage: a new theory based on transactions in a cooperative game

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ABSTRACT

Question: What is the adaptive significance of extra-pair parentage?

Theoretical approach: We view parentage as a 'transaction currency' for exchanges of ecological benefits. We develop a multi-player cooperative game, using the core and the Nash bargaining solution as solution concepts.

Model assumptions: Birds can negotiate about who pairs with whom. Parentage can be exchanged between individuals as a result of negotiations. Number of offspring fledged from a nest depends on the experience and situation of the social parents and not on their genes (i.e. only direct benefits, no genetic benefits).

Predictions: We predict extra-pair parentage to occur when individuals with higher breeding capability are paired to individuals with lower breeding capability. Social interactions between males are predicted to precede the occurrence of extra-pair paternity. We give an example experiment to test our model.

Keywords: cooperative games, direct benefits, extra-pair paternity, genetic benefits, negotiation, social selection.

BACKGROUND

Most bird species are socially monogamous and cooperate in raising offspring (Cockburn, 2006). However, with the advent of molecular methods to assign parentage in the wild, the picture changed remarkably: in most species, some nests contain young that are sired by males other than their social parent [called extra-pair paternity (Griffith *et al.*, 2002)]. Less frequently encountered, but still fairly common, are nests that contain young whose genetic mother is not the female tending the nest [extra-pair maternity (Yom-Tov, 2001)].[1] These two phenomena together represent an interesting problem in evolutionary biology: breeders in such nests

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[1] We use the term 'extra-pair maternity' for all cases where the social mother is excluded as a genetic parent. The terms widely used in the literature are intraspecific brood parasitism and quasi-parasitism. In intraspecific brood parasitism, both the social mother and father are excluded as the genetic parent, corresponding to simultaneous extra-pair paternity and extra-pair maternity. On the other hand, quasi-parasitism is extra-pair maternity only. See 'Discussion' for more on the issue.

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invest in offspring that are not their own genetically. Intuition suggests that such an evolutionary 'mistake' should be selected against, yet the fact that extra-pair parentage occurs commonly throughout bird species strongly suggests that there are also selective pressures that favour the occurrence of this phenomenon. Consequently, many researchers are trying to uncover the function of extra-pair parentage.

Extra-pair paternity is the more common of the two extra-pair parentage phenomena, and is studied much more widely. Even before extra-pair paternity began to be documented in birds, Trivers (1972) argued that males in monogamous species should be selected both to seek extra-pair copulations and to guard their mates from copulation attempts by other males. Later, Møller and Birkhead (1993) observed that the frequencies of extra-pair copulations are higher in colonially breeding species than in dispersed nesters, and stipulated that extra-pair paternity should be positively correlated with breeding density. However, comparative evidence failed to provide consistent support for this prediction (Westneat and Sherman, 1997; Griffith et al., 2002). Similarly, Stutchbury and Morton (1995) suggested that breeding synchrony is positively related to levels of extra-pair paternity, but later research again failed to provide conclusive support to this claim (reviewed in Griffith et al., 2002).

Meanwhile, an increasing focus on the role of females in reproductive decisions (Gowaty, 1996) shifted attention to the benefits of extra-pair paternity to females (Petrie and Kempenaers, 1998). This shift came with an emphasis on indirect, genetic benefits (Birkhead and Møller, 1992; Petrie and Kempenaers, 1998). This was based on the argument that material exchanges and other direct benefits are unlikely to be involved in extra-pair copulations compared with within-pair copulations because of the limited social and physical association between individuals who are presumed to come in contact to copulate only. Two different genetic benefits hypotheses, namely the good genes and the compatible genes hypotheses [corresponding to additive and non-additive genetic effects, respectively (Neff and Pitcher, 2005)], became the focus of extensive research effort. In a companion paper (Akçay and Roughgarden, 2007a), we summarize the results of this effort to identify indirect benefits to extra-pair copulations in nature. We found that empirical tests of both of the genetic benefits hypotheses have yielded equivocal results at best that can be interpreted as refuting genetic benefits in general.

Recently, Westneat and Stewart (2003) argued for a new multi-player approach to extra-pair paternity. They suggested focusing on behavioural interactions between the individual birds themselves rather than on their genes, and claimed that the patterns of extra-pair paternity result from conflicts between individuals. In line with their argument, Arnqvist and Kirkpatrick (2005) proposed that extra-pair copulations are the result of male strategies that are simply imposed on the females. According to this view, females are not indifferent to extra-pair copulation attempts, but they are caught between harassment from extra-pair males and the danger of losing parental contribution from their social mate. Thus, they engage in extra-pair copulations while trying to minimize the total cost imposed on them. Although this 'sexual conflict' hypothesis has yet to be directly tested, it already faces difficulties in light of what we know about extra-pair paternity. First, bird reproductive anatomy lends females substantial control over copulation access and fertilization (Gowaty and Buschhaus, 1998), suggesting that females are not greatly susceptible to coercion. Furthermore, behavioural evidence indicates that females are frequently active participants in extra-pair copulations (e.g. Wagner, 1992; Double and Cockburn, 2000) rather than victims of male copulation attempts. Indeed, females sometimes travel outside their territories seeking extra-pair copulations (Westneat and Stewart, 2003). Females can also solicit extra-pair copulations

from males that intrude into their territories in addition to accepting or rejecting extra-pair copulation attempts initiated by intruding males (e.g. Currie *et al.*, 1999). These undermine the empirical foundation of the sexual conflict hypothesis.

A new approach to extra-pair parentage

This paper presents a new approach to possible benefits of extra-pair parentage. We propose that extra-pair parentage should be viewed as a 'transaction currency' in a social breeding system, functioning in the exchange of commodities and services required for offspring production. We use the term 'commodity' to include necessities for breeding such as nest sites and mates (see Wagner *et al.*, 2000, for another instance of such usage). The term 'services', on the other hand, comprises activities such as nest defence and provisioning. We suggest that individuals or pairs can negotiate and agree on gaining access to such services or commodities and 'pay' for them using parentage. This approach is related to reproductive transactions theory (Vehrencamp, 1983; Shellman-Reeve and Reeve, 2000) (see 'Discussion'). We present a model for the exchange of the most basic necessities of breeding: a mate and a breeding territory. The model employs cooperative game theory, which allows agreements and side-payments to take place between individuals (Roughgarden *et al.*, 2006).

In the next section, we introduce and analyse the cooperative game model for the formation of stable pairing arrangements of socially monogamous pairs. Next, we show that this model can predict some of the well-documented patterns of extra-pair parentage. We then outline some predictions unique to our model and discuss how it can be tested and compared with existing models. In the last section, we discuss the major assumptions and limitations of our model in some detail. We conclude with some general comments on the relation of our approach to reproductive transactions theory and the use of cooperative game theory.

EXTRA-PAIR PARENTAGE AND SOCIAL BREEDING ARRANGEMENTS

One of the first breeding decisions by individual birds is to choose a social mate. Individuals of different sexes in a given breeding neighbourhood (such as a patch of woods) can be thought as a pool from which socially monogamous pairs are to be formed. Individuals in such a context can be expected to make adaptive choices that maximize their expected fitness. We model these choices using game theory. Our model is borrowed from the economics literature on human marriages; it is a modified version of Gary Becker's influential 'marriage market' model (Becker, 1973) that initiated the economic study of human marriages.

Let us first consider a numerical example using the simplest pairing problem with two males and two females. We assume that each possible pair can expect to fledge a certain number of young from their nest, and that this number is a function of individual phenotypes (e.g. parental ability or breeding experience) as well as ecological parameters (e.g. territory quality or predation pressure). We assume that all offspring in a given nest are equally likely to survive to fledgling, such that the number of fledglings from a nest does not depend on the actual genetic parents of the offspring. The number of fledglings produced by each pair can then be arranged in what we call a 'pairing matrix'. An example is given in equation (1):

$$
\begin{array}{ccc}
 & \text{Female 1} & \text{Female 2} \\
\text{Male 1} & 4 & 1 \\
\text{Male 2} & 5 & 4
\end{array} \tag{1}
$$

This pairing matrix is to be read as follows: Male 1 can expect to fledge four offspring if he pairs with Female 1, but only one if he pairs with Female 2. Similarly, Male 2 would produce five young with Female 1, but four with Female 2. These numbers denote the fledgling production from the nest; the actual pay-off to each individual is the total number of genetic offspring produced on and off their own nests – that is, total reproductive success. Becker's (1973) original analysis assumes that the production of a pair, and thus the pay-off, is transferable between partners. We cannot allow this in our model, since the unit of production is offspring fledged and each offspring must have exactly one father and one mother. The outcome of the pairing process then depends on whether we allow extra-pair parentage or not. If individuals are the genetic parents of all offspring in their nests and but none other, the pay-offs to each will be:

$$
\begin{array}{ccc}
 & \text{Female 1} & \text{Female 2} \\
\text{Male 1} & (4, 4) & (1, 1) \\
\text{Male 2} & (5, 5) & (4, 4)
\end{array} \tag{2}
$$

where the first entry in each cell is the pay-off to the male and the second to the female. According to these pay-offs, we expect the pairings Male 2–Female 1 and Male 1–Female 2 to form: Male 2 and Female 1 have the highest production with each other, which would also be their actual pay-off. Thus, neither of them would have any incentive to pair with another individual.

Now suppose that we allow individuals to have only partial parentage in their broods and sire eggs in or dump eggs to other nests. Note that Male 1 and Female 2 stand much to lose if they pair with each other, relative to what they could produce with Female 1 and Male 2 respectively. Male 1 can try to avoid this by negotiating with Male 2 to let him pair with Female 1. Initially, Male 2 should not agree, because he would produce a lower number of offspring if he refrains from pairing with Female 1 and pairs with Female 2 instead. But Male 1 can offer him access to Female 1 such that Male 2 fertilizes, say, two of the eggs in the clutch that Male 1 would have with Female 1. Such an arrangement would give Male 2 a total of six offspring, four from his clutch with Female 2, and two from the nest of Male 1 and Female 1. Conversely, Male 1 would sire two offspring in his clutch with Female 1, leading to the following arrangement of pay-offs:

$$
\begin{array}{ccc}
 & \text{Female 1} & \text{Female 2} \\
\text{Male 1} & (2, 4) & (1, 1) \\
\text{Male 2} & (5, 5) & (6, 4)
\end{array} \tag{3}
$$

Such a deal would be acceptable to both males, since both would be siring more offspring relative to the arrangement with no extra-pair paternity. In this way, extra-pair paternity can arise as 'side-payments' that stabilize a certain social pairing arrangement. Note that Male 1 does not need to guarantee Male 2 the paternity of exactly two of the eggs in his nest. Rather, Male 2 simply requires that the expected number of offspring he sires in Male 1's nest to be two, which he can ensure by having adequate copulation access to Female 1 (Burke *et al.*, 1989).

What about the females? In the above arrangement, Female 1 seems to be losing out, since she pairs with Male 1 and produces four offspring instead of five. Two things might happen in this case. First, Female 1 can be compensated for this loss with a similar agreement between the females: to secure Female 1's cooperation, Female 2 can allow her to dump two eggs (fertilized by Male 2) into the nest of Female 2 with Male 2. This would bring the pay-off to Female 1 to six, while keeping the pay-off to Female 2 at two, which is still greater than the one offspring she would mother if she paired with Male 1 instead. This outcome predicts extra-pair maternity in addition to extra-pair paternity. Alternatively, Female 1 might not be compensated and thus would have no incentive to cooperate on this arrangement. She might, for example, refuse to copulate with Male 2, leading to forced extra-pair copulations or other forms of conflict behaviour between Female 1 and the males. The presence and extent of such conflict would be determined by the outside options available to the female as well as other benefits that might be involved.

The pairing market described above is analysed as a cooperative game. In a cooperative game, coalitions can form that act in concert and negotiate the distribution of pay-off they accrue. The solution of a cooperative game describes which coalitions are formed and what pay-off each player accrues from the outcome. Cooperative game theory offers a variety of solution concepts that can be applied to any given game (see Aumann, 1989). Here, we employ the solution concept called 'the core'. The core of a cooperative game is a set of coalitions and pay-off distributions such that for any element of the core, there are no coalitions that can act separately from the rest of the players and still give all coalitions members at least their pay-off in the core distribution. Note that this is analogous to the Nash equilibrium concept in non-cooperative games but much stronger: the Nash equilibrium stipulates that no individual deviation from the equilibrium strategy is profitable. Here, no individual *or* group deviation is profitable. Below, we introduce some notation and give a mathematical definition of the core.

Analysing the pairing matrix

We now analyse a general 2×2 pairing matrix. A pairing matrix looks like this:

$$
\begin{array}{ccc}
 & \text{Female 1} & \text{Female 2} \\
\text{Male 1} & x_{1,1} & x_{1,2} \\
\text{Male 2} & x_{2,1} & x_{2,2}
\end{array}
\tag{4}
$$

where $x_{i,j}$ denote the number of offspring fledged from the nest of the pair Male i–Female j. The pay-off to each individual is the number of genetic offspring, which we label with m_i for males and f_j for females. (Specifically, m_i is the expected number offspring sired by male i, which is based on his copulation frequencies with different females; see 'Discussion'.) The numbers m_i and f_j include both the genetic offspring within each individual's own clutch and any extra-pair offspring they might sire or mother, so that m_i and f_j are not necessarily equal to $x_{i,j}$. We denote a pairing arrangement by a vector $\vec{z}$ with two elements, where each element z_i specifies which female Male i is paired with under the pairing arrangement. The total number of offspring fledged from all the n nests is denoted by $X(\vec{z}) = \sum_i x_{i,z_i}$. [Obviously, $\sum_i m_i = \sum_j f_j = X(\vec{z})$.]

The core specifies both a pairing arrangement and how much parentage each individual gains or loses, resulting in the pay-offs m_i and f_j. We can then define the core in terms of

these pay-offs: it is the set of pairing arrangements $\vec{z}$ and pay-off vectors $\vec{m}$ and $\vec{f}$ that satisfy two conditions. First, one or both of the following two inequalities must hold for all $x_{i,j}$:

$$m_i \geq x_{i,j}$$
$$f_j \geq x_{i,j} \qquad . \qquad (5)$$

To see why, suppose that for some $x_{i,j}$ that are not in the core pairing arrangement, neither of the inequalities (5) hold. Then both Male i and Female j would prefer to leave the core arrangement and pair with each other instead. Therefore, the pair of pay-offs m_i and f_j that do not satisfy either (or both) of the inequalities (5) cannot be part of the core.

The second condition for the core is the following:

$$X(\vec{z}) \geq X(\vec{z}\,') \quad \text{for all } \vec{z}\,' , \qquad (6)$$

which says that the core pairing arrangement has to maximize total output from the pairing matrix. To see why again, suppose that the core did not maximize the total output. Then a coalition consisting of all males or all females (or both) could form and adopt the pairing arrangement that does maximize the total output. They could then redistribute parentage between nests, such that every individual receives an equal or better pay-off than what they would be getting at the core, contradicting the definition of the core.

This property of the core provides us with a simple method to determine when and where extra-pair parentage should occur. We first find the pairing arrangement that maximizes the total output to satisfy condition (6), and then we calculate the pay-offs each individual has to get to satisfy condition (5). The discrepancy between the pay-offs calculated in this way and the nest production of each individual under the pairing arrangement determines how much parentage each one loses or gains.

We apply the method to the pairing matrix above (equation 4). There are two distinct patterns of relative productivity of different nests:

1. One individual of each sex, say Male 1 and Female 1, consistently produces more offspring than the other. This can be expressed as $x_{i,1} > x_{i,2}$ and $x_{1,j} > x_{2,j}$ for $i, j = 1, 2$. This corresponds to the case where an individual's traits (or its ecological circumstances) create a consistent effect on its productivity.
2. Each male produces more offspring than the other when paired to a different female (or vice versa). For example, $x_{1,1} > x_{2,1}$ but $x_{2,2} > x_{1,2}$, i.e. Male 1 produces more offspring with Female 1 than Male 2 does, but Male 2 produces more offspring with Female 2 than Male 1 does. In this case, the productivity of the pair is determined by the interaction of individuals' traits such that there is no consistent high productivity individual.

Consider case 2 first: there are two possible pairing arrangements, $\vec{z}_1 = (1, 2)$ and $\vec{z}_2 = (2, 1)$. Condition (6) means that $\vec{z}_1$ is the core arrangement, since $x_{1,1} + x_{2,2} > x_{1,2} + x_{2,1}$. In that situation, no extra-pair parentage is needed to stabilize the arrangement, as each individual already receives the highest pay-off they can get from their own nest. Thus, if there are no consistent differences in offspring production between individuals, our model does not predict extra-pair parentage.

For case 1, there are two sub-cases: either $x_{1,1} + x_{2,2} \geq x_{1,2} + x_{2,1}$, or the reverse. In the former, Male 1 will be paired with Female 1, and Male 2 with Female 2, and there will be no

extra-pair parentage, since each individual's production from its own nest satisfies condition (5). In the second sub-case, however, the core prescribes the arrangement $\vec{z_2}$. But $x_{1,1} > x_{1,2}$ by assumption, and condition (5) requires that $m_1 \geq x_{1,1}$. Thus, Male 1 needs to gain some paternity in Male 2's nest. If we label by p_{min} the minimum amount of extra-pair paternity Male 1 has to gain, we can write:

$$p_{min} = x_{1,1} - x_{1,2} \, . \tag{7}$$

In other words, Male 1 has to gain enough paternity to at least bring him to the number of genetic offspring he would have if he simply paired with Female 1 and sired all young in their nest. Our model thus predicts extra-pair parentage only if some individuals are consistently better at producing offspring than others *and* if these higher productivity individuals are paired with partners of lower productivity. This method for calculating the core arrangement and the extra-pair parentage is directly applicable to general $n \times n$ matrices.

Equation (7) calculates the minimum side-payment that an individual requires to agree to a core pairing arrangement. We can also calculate the maximum side-payment each individual is willing to make to secure the cooperation of other individuals for a core pairing arrangement. This is done by subtracting the production of the non-preferred pairing from the production of the preferred pairing. In the second example for case 1 above, the non-preferred pairing for Male 2 is with Female 2, and the preferred one is with Female 1. Therefore, Male 2 would be willing to concede to Male 1 some paternity of a clutch with Female 1, provided he still retains at least as much paternity as he would get in a pairing with Female 2. Thus, the maximum parentage loss Male 2 will accept is:

$$p_{max} = x_{2,1} - x_{2,2} \, . \tag{8}$$

Any side-payment between p_{min} and p_{max} will stabilize the core arrangement so the core actually specifies a range of parentage. Which value will be selected from this range? The answer to this question depends on the negotiation process between the individuals who are exchanging side-payments. Below, we characterize a plausible outcome of this negotiation process.

Predicting extra-pair parentage

The core arrangement in our pairing matrix results in an increase in total offspring production, creating a surplus pay-off relative to each individual acting alone. Since every individual has to get at least their default pay-offs in any negotiated outcome, we can cast the problem in terms of how to distribute that surplus. We need to consider the males and females separately, because the pay-off (i.e. parentage) cannot be transfered between the sexes. In a 2×2 pairing matrix, this process gives rise to two separate two-player games. The outcome of such two-player bargaining games can be characterized by the Nash Bargaining Solution [NBS (Nash, 1950)], which stipulates that the solution maximizes the product of the two players' pay-offs relative to their default pay-offs.

To apply the NBS to the negotiation of parentage exchange, consider a 2×2 pairing matrix with a core that prescribes side-payments. Specifically, assume that $x_{i,1} > x_{i,2}$ and $x_{1,j} > x_{2,j}$ for $i, j = 1, 2$, and that $x_{1,2} + x_{2,1} = x_{1,1} + x_{2,2} + d$, with $d > 0$ denoting the surplus that results from the core. Let us consider the negotiation between the males. (The negotiation between the females follows in a similar way.) The default pay-offs are $x_{1,1}$ for

Male 1 and $x_{2,2}$ for Male 2. If the actual pay-offs are m_1 and m_2, the males' gain relative to their default pay-offs are $m_1 - x_{1,1}$ and $m_2 - x_{2,2}$. Furthermore, $m_1 + m_2 = x_{1,1} + x_{2,2} + d$. Thus, the product of the relative gains can be written as:

$$(m_1 - x_{1,1})(m_2 - x_{2,2}) = (x_{2,2} + d - m_2)(m_2 - x_{2,2})$$
$$= 2x_{2,2}m_2 - m_2^2 - x_{2,2}^2 + m_2 d - x_{2,2}d . \tag{9}$$

To find the maximum of this product, we take the derivative of the expression on the right-hand side with respect to m_2, set equal to zero, and solve for m_2:

$$2x_{2,2} - 2m_2 + d = 0$$

$$x_{2,2} + \frac{d}{2} = m_2 \tag{10}$$

Thus, the NBS predicts that Male 2 receives $d/2$ in addition to his default pay-off, which means that Male 1 is also receiving $d/2$ over his default pay-off; the NBS prescribes an equal partitioning of the surplus between the two males. The actual extra-pair paternity gained by Male 1 can be calculated as:

$$p = \frac{d}{2} + x_{1,1} - x_{1,2} . \tag{11}$$

The NBS for the females' game is calculated separately in the same way. Since the surplus d and the default pay-offs are the same for the females as well, the females' NBS prescribes the same division of parentage as that of the males: females will also divide the surplus equally among themselves (if they divide it at all, see above).

We can now apply this result to the pairing matrix in equation (1) above. There, $d = 2$ and thus each individual must receive the parentage of one more offspring in addition to their default pay-offs. The default pay-off for Male 1 and Female 2 is one, so the NBS prescribes a net pay-off of two to them, while for Male 2 and Female 1 the net pay-off has to be six. To achieve this, Male 2 has to receive the paternity of two offspring in the nest of Male 1 and Female 1, while Female 1 has to lay two eggs (fathered by Male 2) into the nest of Female 2 with Male 2.

The NBS can be reached by different behavioural processes (see Roughgarden *et al.*, 2006; Akçay and Roughgarden, 2007b). The behavioural basis of how individuals negotiate an outcome is an empirical question. For example, a candidate might be the dawn chorus of some song birds. A recent study has shown that the dawn chorus has a role in the social dynamics between males in a breeding neighbourhood of banded wrens (Burt and Vehrencamp, 2005). We conjecture that the dawn chorus might also play a role in negotiations between males over paternity exchanges, in which case a correlation between dawn chorus interactions and paternity gain or loss would be expected.

Individual traits and extra-pair parentage

Now, we look in more detail at how the entries $x_{i,j}$ in the pairing matrix are determined and how extra-pair parentage is related to individual traits and/or ecological variables. Note that we assume that the genetic parents of an offspring do not affect their survival to fledgling. The production of each nest depends instead on the phenotypes of the individuals tending

that nest or on ecological factors such as territory quality. As in case 1 in the analysis of the pairing matrix above, some individuals might possess traits (such as age or condition) that enable them to fledge more offspring, regardless of their social partners' traits. Alternatively, the two sexes might have traits (for example, joint breeding experience) with the pair production depending on the combination. Below, we investigate these cases in more detail.

Suppose that individuals vary in some trait that influences offspring production in the nest. We denote the traits in males and females with s and t, respectively, and express the offspring production from a nest as a function of these traits:

$$x_{i,j} = g(s_i, t_j) \ . \tag{12}$$

Suppose also that

$$\frac{\partial g(s, t)}{\partial s} > 0 \text{ and } \frac{\partial g(s, t)}{\partial t} > 0 \ , \tag{13}$$

meaning that offspring production increases with both the male and the female traits (corresponding to case 1 above). We order males and females according to their trait value, such that $s_n > s_{n-1} > \ldots > s_1$ and $t_n > t_{n-1} > \ldots > t_1$. (For simplicity, we assume that no two individuals have the same value for a trait.) Now, if the stable arrangement $\vec{z}$ requires no extra-pair parentage, it must be true that each individual's partner must be of the same rank as themselves. Thus, Male n is paired to Female n, Male $n-1$ to Female $n-1$, and so on. To see why, suppose Male i is paired to Female j with $i > j$. Then, there will be at least one female of rank $k \geq i$ who is paired to a male of rank $l < i$. But because of the inequalities in (13), this means that

$$x_{i,k} > x_{i,j} \quad \text{and} \quad x_{i,k} > x_{l,k} \ .$$

Therefore, if Male i or Female k do not receive any extra-pair parentage, condition (5) is not satisfied for the pairing $x_{i,k}$. Thus, the arrangement $\vec{z}$ cannot be stable without extra-pair parentage. We can also see by a similar argument that whenever there is perfectly assortative pairing, no extra-pair parentage is required. Therefore, our model predicts extra-pair parentage if and only if there are some disassortative pairings – that is, pairings between a low-rank male and a high-rank female.

When is there a perfectly assortative pairing arrangement in the core? Due to condition (6), this is equivalent to asking when the assortative pairing arrangement maximizes the total output. One can show that if

$$\frac{\partial^2 g(s, t)}{\partial s \partial t} > 0 \ , \tag{14}$$

assortative pairing maximizes total offspring production. [A proof can be found in Becker (1973, Appendix, section 1).] Therefore, if inequality (14) holds, assortative pairing will be the core arrangement. Conversely, if the reverse of (14) holds, negative assortment maximizes the total output and is the core arrangement. In this case, disassortative pairing creates a surplus in the total number of offspring produced relative to assortative pairing. This surplus is then redistributed by extra-pair paternity to compensate individuals of higher productivity for not pairing with their preferred mates.

The mixed derivative in inequality (14) is an index of whether the male and female traits and their function in offspring rearing are substitutes or complements to each other in the economic sense. For example, the right-hand side will be positive when males and females each perform different tasks that are both necessary for successful breeding, and the traits s and t reflect their effectiveness in their respective tasks. An extreme example is provided by hornbills (Bucerotidae). The female hornbill seals herself off in the nest during egg laying and incubation and depends entirely on male feeding during this period, which can last for 2 months (Stanback *et al.*, 2002). Here, the traits of the female (e.g. health) and the male (e.g. provisioning ability) can be thought as being complementary. Then condition (14) is expected to hold, and the model predicts no extra-pair parentage. Consistent with this prediction, no extra-pair paternity is found in the one hornbill species investigated to date (Stanback *et al.*, 2002), even though sperm storage by the female provided a wide window for extra-pair copulations that could lead to fertilizations.

Such exclusive division of labour is rather rare in birds. In most species, the tasks performed by males and females (such as territory defence or nestling provisioning) widely overlap. If the male and female traits determine how effective each are in these tasks, those traits will be substitutes in the offspring production function. In that case, inequality (14) would be reversed, and extra-pair parentage is predicted. We can calculate from our model the level of extra-pair paternity as a function of different parameters, which we do below to derive predictions about interspecific patterns of extra-pair parentage.

PREDICTING ESTABLISHED PATTERNS

In this section we demonstrate that our model is compatible with currently documented interspecific patterns, and discuss some theoretical advantages of our model over the currently accepted hypotheses.

Extra-pair paternity and male parental contribution

One of the well-established patterns of extra-pair paternity is its relation to male parental contribution across species. We show here that our model correctly predicts the negative relationship between paternal care and levels of extra-pair paternity (Møller, 2000). We use a Monte Carlo simulation approach. First, we specify a production function $g(s, t)$, where s and t are parental abilities of the males and the females, respectively. We take $g(s, t)$ to be an increasing, concave downward function of the sum $hs + t$. The parameter h denotes how much the male's parental ability is important relative to the female's. Thus, $h = 0$ would indicate that offspring production does not depend on paternal care, whereas $h = 1$ means that paternal and maternal contributions affect offspring production equally. We generate 4×4 matrices using random numbers for s_i and t_j, and determine the level of extra-pair parentage at the core arrangement of the resulting matrix. (We use a 4×4 pairing matrix, since it represents a more realistic neighbourhood size than a 2×2 situation, but simulation results are qualitatively unchanged with matrix size. Detailed simulation procedure and code in Mathematica are available in the Supporting Online Material at http://www.evolutionary-ecology.com/data/2204code.nb.) Figure 1 plots the mean levels of extra-pair paternity over 100 iterations for each value of h. Average levels of extra-pair paternity (in terms of the percentage of total offspring) decrease as the relative importance of male parental contribution increases. This is consistent with what has been found in comparisons

across species of extra-pair paternity levels with respect to male contribution (Møller, 2000; Arnold and Owens, 2002). The negative relationship comes about because the importance of female productivity goes up with decreasing male contribution. Consequently, males are willing to pay more to pair with highly productive females. Note that as h becomes greater, the rate of extra-pair paternity goes down, but never quite reaches 0, because we assumed that male and female traits are economic substitutes regardless of the value of h. In reality, for species with essential male parental care (corresponding to $h \gg 1$ in Fig. 1), complementarity effects are likely to be important, and thus the rate of extra-pair paternity should go down faster than depicted here.

The currently accepted explanation for the relationship between extra-pair paternity and paternal care is based on the 'constrained female hypothesis' of Gowaty (1996). The constrained female hypothesis stipulates that female dependence on male help constrains her extra-pair copulation behaviour, with more dependent females not being able to seek extra-pair copulations. However, we note two problems with the constrained female hypothesis. First, the hypothesis assumes a genetic benefit to females from extra-pair paternity to explain why females should seek extra-pair copulations in the first place. This assumption has little empirical support (Arnqvist and Kirkpatrick, 2005; Akçay and Roughgarden, 2007a). Second, the constrained female hypothesis assumes that males respond to paternity loss by withholding care, but experimental studies testing this assumption yielded mixed results (e.g. Lifjeld et al., 1998; Dickinson, 2003). Moreover, theoretical models of parental care do not always predict that males should withhold care in response to loss of paternity (reviewed in Sheldon, 2002).

Male traits and extra-pair paternity

The most studied aspect of extra-pair paternity is its relation to male traits (Møller and Ninni, 1998; Akçay and Roughgarden, 2007a), so we ask what our model can predict about this relationship. The 2×2 example above already provides a hint: Male 1, who has higher
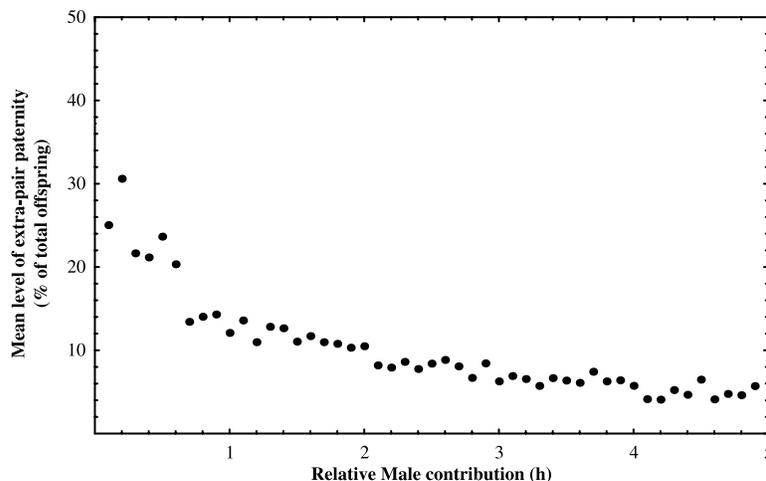

Fig. 1. Plot of mean levels of extra-pair paternity (% of total offspring produced from the pairing matrix) versus the relative contribution of the male to offspring care, as determined by Monte Carlo simulations. The production function used in these simulations is $g(s, t) = \sqrt{hs + t}$.

productivity, receives paternity in Male 2's nest in the core arrangement. More generally, the condition for extra-pair parentage to occur is that high-productivity individuals should pair with partners of lower productivity. Then, higher productivity individuals need to be compensated for the loss of production they experience in their own nest. At the same time, lower productivity individuals will be willing to concede some proportion of their nests' parentage in exchange for the right to breed with highs. Put together, these indicate that our model predicts positive correlations between individual productivities and the levels of both within-pair paternity and extra-pair paternity. This is confirmed by Monte Carlo simulations with random pairing matrices; Figs. 2 and 3 depict the results of two such
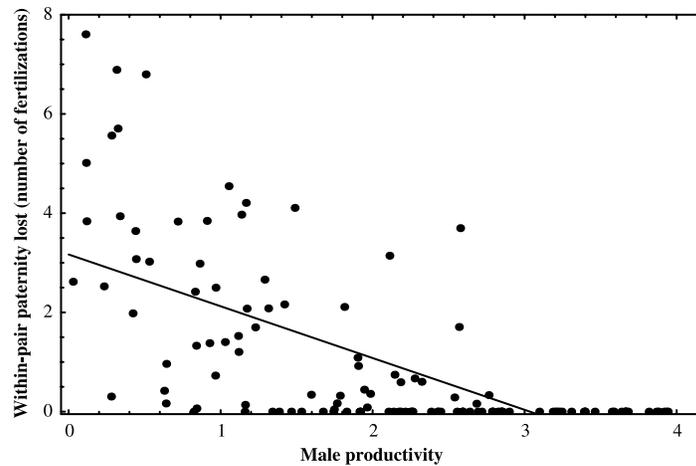

Fig. 2. Plot of within-pair paternity lost (in terms of number of extra-pair young in the nest) versus male productivity in 30 randomly generated 4×4 games, corresponding to 120 males. The production function is $g(s, t) = 5\sqrt{s} + t$. The line denotes the linear regression on all the points.
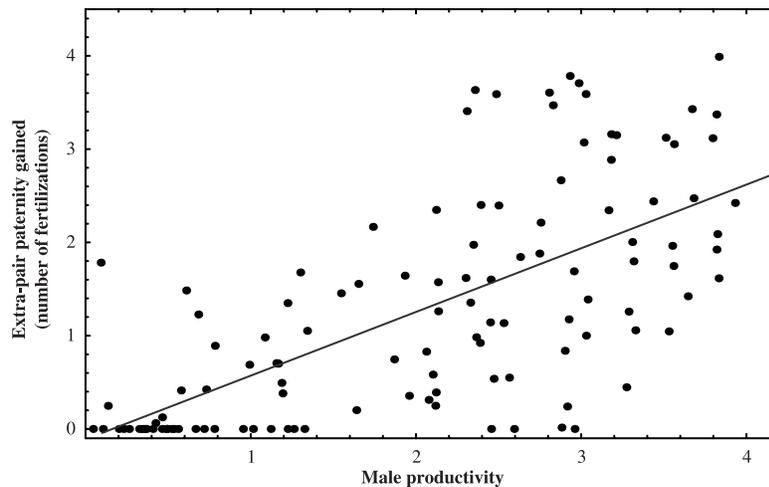

Fig. 3. Plot of extra-pair paternity gains in terms of number of offspring versus individual male productivity in randomly generated games. The line denotes the linear regression; simulation details as in Fig. 2.

simulations. Figure 2 shows that loss of paternity in absolute terms decreases as male productivity increases. The same is true if one plots percent of paternity in the nest, thus controlling for clutch size (not shown). The number of extra-pair young sired in other nests also increases with individual productivity. However, both graphs exhibit substantial variation because the level of extra-pair paternity at the core arrangement depends on the whole pairing matrix. Thus, an individual with a given trait value might end up with different levels of extra-pair paternity and within-pair paternity in different matrices.

Our model thus predicts a positive relationship between male traits that increase offspring production and both within-pair paternity and extra-pair paternity. Evidence from several species suggests that such a correlation exists. For example, male and female black-capped chickadees (*Poecile atricapilla*) spend winter in flocks with linear dominance hierarchies that determine access to food sources (Smith *et al.*, 1991). Males higher in the dominance hierarchy fledge more offspring (Otter *et al.*, 1999), have higher within-pair paternity, and are more likely to gain extra-pair paternity (Otter *et al.*, 1998). Another example comes from blue grosbeaks (*Passerina caerulea*), where males with brighter (bluer) breast plumage are less likely to have extra-pair paternity in their nests. These males also provide more parental care and have territories with higher insect abundance (Keyser and Hill, 2000). Finally, extra-pair paternity and within-pair paternity are frequently correlated with age (Akçay and Roughgarden, 2007a), which is also a robust correlate of breeding success in many species (see Mauck *et al.*, 2004, and references therein). These patterns have been previously interpreted as supporting the genetic benefits hypotheses. Our model provides an alternative interpretation. We discuss in more detail below ('Tests of the model') how to distinguish between genetic benefits and the current model.

Patterns of extra-pair maternity

Our model can also be used to predict interspecific patterns of extra-pair maternity (Arnold and Owens, 2002). The most consistent correlate of extra-pair maternity is annual fecundity in a species (Geffen and Yom-Tov, 2001; Arnold and Owens, 2002), where levels of extra-pair maternity as a percentage of total offspring increase with increasing fecundity. One property that can cause this pattern in our model is that maternity comes in strictly discrete units (i.e. eggs), whereas paternity is probabilistic and thus can vary more or less continuously (in terms of its expected value). Therefore, a maternity exchange prescribed by the core arrangement in a given pairing matrix may simply not be feasible if it requires the transfer of, say, half an egg. In species with high fecundity, however, transactions would be prohibited less often by the discrete nature of maternity, since the proportion of maternity in a clutch approaches a continuous variable. Therefore, all else being equal, high-fecundity species should exhibit more extra-pair maternity. This is shown in Fig. 4, which depicts the results from Monte Carlo simulations, where transactions of maternity occur only if they exceed a certain threshold value. The prevailing hypothesis (Geffen and Yom-Tov, 2001) attributes this pattern to the lower marginal cost of accepting an extra egg in species with large clutches. Although our model differs somewhat from this hypothesis, the two models are compatible.
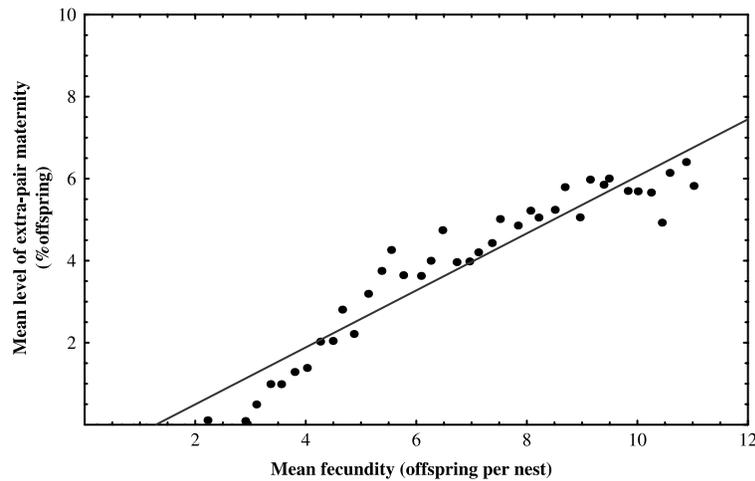
Fig. 4. Plot of mean fecundity versus mean levels of extra-pair maternity in 100 simulations with 4×4 matrices. The production function is $g(s, t) = f\sqrt{s + t}$, where f is the parameter determining fecundity. A maternity exchange only takes place in discrete units.

TESTS OF THE MODEL

We noted above that our cooperative game model predicts patterns that agree with current evidence. In this section, we concentrate on how future empirical studies can distinguish between the current model and others, specifically the genetic benefits hypotheses.

Our model predicts that individuals with higher offspring production will have higher within-pair paternity and extra-pair paternity, which is similar to the genetic benefits hypotheses at first glance. However, several features of our model can be used to distinguish between these two hypotheses. First, the genetic benefits hypotheses postulate that extra-pair young are consistently better than within-pair young (e.g. in survival to adulthood), whereas our model makes no such prediction. This assumption of the genetic benefits hypotheses is not supported by empirical data (Arnqvist and Kirkpatrick, 2005; Akçay and Roughgarden, 2007a). Although this by itself does not indicate direct support for the current model, it does weaken the genetic benefits hypotheses.

We also predict that individual traits should be related to extra-pair paternity only when they influence current offspring production from the nest, but regardless of whether they are heritable or environmental. In contrast, the genetic benefits hypotheses predict that any trait that influences total fitness (such as attractiveness, which is not necessarily related to current nesting success) should be correlated with paternity, but only if it is heritable. Currently, almost all empirical studies interpret any correlation between male traits and paternity as a good genes effect, mostly without testing for the heritability of the trait or its relation to total fitness. The reason for this seems to be a lack of alternative interpretations. Our model, however, provides one, and many of the cases currently accepted as supporting the good genes hypothesis might turn out to rely on non-heritable traits that are related to current nest production (see Table 1). This can be assessed using a meta-analytic or comparative approach for traits where measurements of heritabilities and fitness effects exist.

Table 1. Comparison between the predictions of the current model and the genetic benefits hypothesis on whether male traits are correlated to within-pair and extra-pair paternity

Trait affects:	Trait is heritable		Trait is not heritable	
	Current nest	Other fitness	Current nest	Other fitness
Current model	Yes	No	Yes	No
Genetic benefits	Yes	Yes	No	No

Another prediction from our model is that extra-pair paternity should be associated with disassortative pairing: extra-pair paternity occurs only when individuals with a lower trait value are paired with individuals with a higher trait value. Such interactions are not predicted by genetic benefits, and rarely measured in existing studies. Nonetheless, at least one study indicates such an effect: Dietrich *et al.* (2004) showed that the level of extra-pair paternity in their brood was repeatable within pairs, but not within individuals when they change partners. Furthermore, they show that younger males paired to older females lose more paternity than other pairings with respect to age. We suggest that future empirical studies focus on the interaction between male and female traits.

Experimental studies can distinguish the current model from existing ones, such as the constrained female hypothesis or the mate-guarding hypothesis. Both of the latter hypotheses predict that levels of extra-pair paternity should be affected by environmental factors such as food availability in the territory. The constrained female hypothesis predicts that supplementing territories with food should decrease female dependence on male help, which should result in increased extra-pair paternity in supplemented territories. Conversely, the mate-guarding hypothesis predicts that extra-pair paternity should decrease in supplemented territories, because both males and females spend more time at the nest and it becomes easier for males to guard their partners. Three studies have measured the effects of food addition. Two of them report decreases in extra-pair paternity (Westneat, 1994; Václav *et al.*, 2003) while one reports an increase (Hoi-Leitner *et al.*, 1999).

Our model makes a more complex prediction. If food availability is an important determinant of breeding success (i.e. influences the entries in the rows of the pairing matrix), then supplementing poorer territories with food would amount to increasing the entries for less productive males while leaving the other rows unchanged. Consequently, the core arrangement would require less extra-pair parentage relative to controls. On the other hand, if territories with richer than average food resources are supplemented, the entries for more productive males will go up, which would increase the amount of extra-pair paternity prescribed by the core allocation up until the point where the core switches to an assortative pairing arrangement. Our model thus predicts that extra-pair paternity should decrease with food addition in poor territories but increase in richer ones.

We have listed several possible tests to distinguish between the model presented here and existing hypotheses. One can devise correlational and experimental tests in other cases by first determining which ecological or phenotypic factors influence breeding success, and then manipulating those factors to bring about changes in the pairing matrix, leading to changes in the occurrence of extra-pair paternity. This experimental approach enables immediate testing of the model without any major change in research methods.

At the same time, we believe that more research effort should be focused on behavioural interactions between individuals. Considering the amount of effort poured into field studies of the phenomenon in the last two decades, remarkably little is known about the actual behavioural processes that lead to extra-pair parentage (a point made by Westneat and Stewart, 2003). Perhaps the inattention to behaviour arose from the focus on genetic benefits. This focus did not attribute great significance to behaviour, except to say when and with whom extra-pair copulations should occur. But both the sexual conflict hypothesis and our model attribute significance to actual behavioural events leading to extra-pair copulations, and both make predictions about them. So these new hypotheses should spur the behavioural investigations needed to test them. Our model explicitly stipulates the existence of a negotiation set-up between individuals. Whether such mechanisms exist, and what their behavioural basis is, need to be determined by observational studies. A possible candidate for the behavioural basis of negotiations is male–male singing interactions [such as the dawn chorus (Burt and Vehrencamp, 2005)], which are known to play important roles in territorial and social relations. In the context of extra-pair paternity, for example, our model predicts that the extra-pair males should be seen interacting with within-pair males before extra-pair copulations take place. The presence of such correlations between behavioural interactions among males and extra-pair copulations is readily testable but it requires a change of focus in field methods on extra-pair paternity.

DISCUSSION

We make several assumptions in our model that are worth discussing more explicitly. The first is that individuals can sense the pairing matrix and are able to calculate side-payments. Theory has shown that honest signalling of phenotypic quality can be evolutionarily stable (Grafen, 1990) and this notion has been confirmed empirically in several bird species (e.g. Hill, 1991; Keyser and Hill, 2000). Thus it is reasonable to assume that birds can assess other individuals' phenotypes, and with them, the entries to the pairing matrix. Furthermore, the core is structurally stable with regard to small errors that individuals might make in their assessment of the pairing matrix. Such small errors would perturb equations (7) and (8), but only linearly. Some part (or the whole) of the real core would still be acceptable to all players. A different class of information that might influence the outcome of negotiations concerns individuals' previous moves (e.g. whether they negotiate with a single individual or with multiple individuals). Negotiations are likely to involve conspicuous signals such as song, and it is reasonable to assume that individuals in a breeding neighbourhood have common knowledge of them [e.g. due to 'eavesdropping' (Peake et al., 2001; Burt and Vehrencamp, 2005)].

The second assumption of the model is that no outside options are available to individuals, such as settling in a different patch of woods, or postponing breeding altogether. If these outside options can be expressed as an expected pay-off, they can easily be incorporated into condition (5), without any major change to the model. A more complicated situation can occur when one considers a patch of habitat occupied by contiguous breeding territories, where individuals can choose both whether or not to join a pairing matrix and which matrix to join. One would have to build a model that considers all possible pairing matrices and predicts which pairing matrices should emerge from that breeding neighbourhood. Our model can then be employed as a sub-model that generates the pay-off consequences of each possible pairing matrix. Indeed, such an extended model can explain the formation of breeding colonies (Wagner et al., 2000).

Another issue concerns the assumption that parentage can be transferred without cost and in a continuous and reliable manner. For paternity, we suggest that these assumptions are reasonable. Even if males do not control the transfer of paternity directly, they might trade copulation access to the female. This is well documented, for example, in dunnocks (Burke et al., 1989). The genetic pay-offs for males in our model then should be interpreted as expected paternities.

On the other hand, constraints that are not incorporated in our model are likely to be important for maternity exchanges. Our model starts by regarding paternity and maternity as symmetrical. However, the nature of maternity transfers is clearly different from paternity transfers, and interspecific patterns indicate that extra-pair paternity is more common than extra-pair maternity (Arnold and Owens, 2002). Taking into account the discrete nature of eggs, as is done above (see 'Patterns of extra-pair maternity'), breaks this symmetry. Another property that would break the symmetry is that eggs are laid after being fertilized, and therefore egg dumping is likely to involve transfer of paternity in addition to maternity. A female laying eggs into another female's nest might copulate with the male at that nest and thereby grant him the paternity of some of her eggs (not necessarily the one that she lays in his nest). However, this presumably would impose higher transaction costs, making extra-pair maternity less likely to happen than our model predicts. The implication is, then, that females frequently might not be compensated, which could lead to disagreements, and possibly overt conflict. Nonetheless, overt conflict might not happen if other types of benefits are also involved.

Another possibility is that females might not actually be players in the same game as the males. This might happen if males arrive early, hold territories and negotiate, for example, about territory boundaries among themselves. In that case, the columns of the pairing matrices would correspond not to different females, but to different territory configurations. Thus, the stable arrangement would only need transfer of parentage between males. Such a situation might arise in many migratory bird species with males-first arrival patterns.

Reproductive transactions theory and cooperative games

We have discussed a new theoretical framework to study extra-pair parentage. We suggest that extra-pair parentage (encompassing both extra-pair maternity and extra-pair paternity) arises as reproductive transactions that stabilize the social pairing arrangement. A similar role for extra-pair paternity has previously been proposed by Shellman-Reeve and Reeve (2000), who stipulated that the social mates receive paternity in exchange for the parental care they supply. Their model assumes that females prefer to mate with an extra-pair male because of some genetic benefit, but at the same time need full-time parental provisioning from their social mate. Our proposal agrees with their approach in principle, but we demonstrate here that genetic benefits (which are not well supported by data) do not need to be assumed for a transaction set-up to function.

More broadly, the current model can be seen as extending reproductive transactions theory of cooperative breeding groups (Vehrencamp, 1983) to exchanges between monogamous pairs. The basic idea in our model, namely that parentage can be exchanged for some ecological benefit, is analogous to the logic of reproductive skew models. In this context, cooperative games can be viewed as a new modelling tool for reproductive transactions theory. A major advantage of cooperative game theory over existing reproductive skew models is that it lets the coalition structure (group composition) as well as the pay-off

distribution (skew) emerge from the model. Here, we have constrained the groups to be monogamous pairs. However, the model can easily be extended to polygynous and polyandrous groups as well. In that way, cooperative game theory can enable a generalization of reproductive skew theory to all mating systems.

The model presented here would apply to a broad variety of bird species, but other types of exchanges might also cause extra-pair parentage. Therefore, we suggest that parentage should be viewed as the common currency across bird species that can buy different commodities and services. These include provisioning, nest defence, viable sperm, as well as risk sharing through dispersing parentage over different nests. Specifically for extra-pair paternity, the relation of such ecological benefits to extra-pair parentage, with the possible exception of viable sperm (Griffith, 2007), remains understudied compared with putative genetic benefits. A reproductive transactions approach will focus attention on these understudied possibilities. Such an approach might potentially lead to a unified explanation of extra-pair parentage by mapping the variation in the patterns of such parentage to the variation in the ecologically relevant commodities and services.

Our approach here forms part of the social selection research program outlined in Roughgarden *et al.* (2006). In a recent article, McNamara *et al.* (2006) criticized this program for its use of cooperative game theory. McNamara *et al.* claim cooperative games cannot describe animal interactions, because animals 'do not have a legal system', and so cannot engage in binding 'contracts'. However, the only requirements for binding contracts are the abilities to monitor the bargain and to revert to the default pay-offs if the agreement is not honoured. Such abilities appear well within the range of animal capabilities. Given these abilities, neither party would have an incentive to deviate from an agreement, as this would result in a lower individual pay-off.

The basic theoretical structure of the social selection program relies on a two-tier approach. One tier is behavioural: interactions between animals result in the formation of social systems and generate pay-offs. The other tier is evolutionary: traits that function in social interactions evolve according to their fitness consequences. In this formulation, natural selection may well select for behavioural mechanisms that enable negotiations and agreements, and allow the behavioural tier to be modelled using cooperative games. The evolutionary tier, on the other hand, will still employ conventional evolutionary game theory and population genetics as explicit models of the natural selection process.

To summarize, we propose to reconsider the traditional view of extra-pair parentage that relies on empirically unsupported genetic benefits hypotheses. We also suggest that newer approaches based on sexual conflict do not provide a satisfactory answer. Instead, we suggest that extra-pair parentage can be the result of commodity or service exchanges that are negotiated and agreed upon. Individuals belong to a social and economic breeding system that co-exists alongside the genetic. In this non-genetic system, individuals trade in the currency of parentage. We propose to model such transactions using cooperative game theory, and present a model for one type of commodity, breeding mates. We believe that an approach based on reproductive transactions to gain ecological benefits will bring new insights to the study of extra-pair parentage.

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