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Why inclusive fitness can make it adaptive to produce less fit extra-pair offspring

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Social monogamy predominates in avian breeding systems, but most socially monogamous species engage in promiscuous extra-pair copulations (EPCs). The reasons behind this remain debated, and recent empirical work has uncovered patterns that do not seem to fit existing hypotheses. In particular, some results seem to contradict the inbreeding avoidance hypothesis: females can prefer extra-pair partners that are more closely related to them than their social partners, and extra-pair young can have lower fitness than within-pair young. Motivated by these studies, we show that such results can become explicable when an asymmetry in inbreeding tolerance between monogamy and polygamy is extended to species that combine both strategies within a single reproductive season. Under fairly general conditions, it can be adaptive for a female to choose an unrelated social partner, but inbreed with an extra-pair partner. Inbreeding depression is compensated for by inclusive fitness benefits, which are only fully realized in EPCs. We also show that if a female has already formed a suboptimal social bond, there are scenarios where it is beneficial to engage in EPCs with less related males, and others where EPCs with more related males increase her inclusive fitness. This has implications for detecting general relatedness or fitness trends when averaged over several species.

1. Introduction

Social monogamy is the predominant mating system of birds. Ever since studies in the 1970s and 1980s showed that genetic monogamy is rare, with extra-pair young (EPY) found in the majority of socially monogamous species [1], there has been ongoing debate on whether it is only sires of EPY, or also the female parents, that benefit from having extra-pair offspring [2,3]. Recently, the inbreeding avoidance hypothesis has gained substantial attention in this context (e.g. [4–8]). The idea is that even if there is no selection for extra-pair reproduction via additive genetic value of EPY versus within-pair young (WPY) [9], inbreeding depression is often significant [7,10]. Females that are paired with closely related mates should thus seek extra-pair copulations (EPCs) with more distantly related males, to reduce the number of young that suffer from inbreeding depression.

The inbreeding avoidance hypothesis, like other forms of genetic benefits sought by females, predicts that EPY are fitter than WPY [3,7,11]. Although not explicitly formed as an inbreeding avoidance test, it is noteworthy that an overview of EPC in several avian species did not find support for higher fitness in EPY than in WPY [12] (but see [13,14]), and results from other studies have also been equivocal [3,15]. Moreover, there are recent studies that appear to directly contradict the inbreeding avoidance hypothesis. These include cases where

- (1) extra-pair partners are more closely related than social partners [16–19],
- (2) broods sired by related partners had lower rates of extra-pair paternity (EPP) than outbred broods [20], and
- (3) EPY seem to have lower fitness than WPY [21,22].

Two of these studies [17,18] take note of a recent ‘rediscovery’ of a fact known for more than 70 years [23,24]: inbreeding avoidance is not universally favoured as soon as there is inbreeding depression (reviewed in [7]). Choosing to mate with related partners can be selectively favoured because it allows more alleles identical by descent (to those of the chooser) to be transmitted to future generations [25,26]. Put another way, inbreeding increases a female’s inclusive fitness [27] by allowing a related male to sire more offspring.

However, if it is beneficial to mate with related extra-pair partners, it remains unclear why females would not choose optimally related social partners in the first place [28]. Suggestions include limited choice for related social partners early in the breeding season [18], or that social mates may provide distinct types of fitness benefits, such as parental care, creating different criteria for mate choice for social and extra-pair partners [28].

Motivated by the seemingly anomalous results (cases 1–3), we highlight the possible role of a more fundamental asymmetry in mate choice for social and extra-pair mates: an old result demonstrates that inclusive fitness benefits can differ between monogamous and polygamous mating systems [17,24,29,30]. We show that it is equally relevant to species that combine both reproductive strategies within a single breeding season. This asymmetry exists irrespective of paternal care provided by the social mate and its possible interrelationship with within-brood paternity losses [31,32]. Therefore, the potential inclusive fitness benefits a female can gain from choosing a relative as a socially monogamous mate are generally lower than those that she can gain from engaging in EPCs with a relative. Our results provide a framework where seemingly anomalous results, even ones where EPY are more inbred and less fit than WPY, can nevertheless be adaptive for mothers. They also suggest that, in a broader context, it can be difficult to detect overall signals regarding social partner and EPP relatedness, because it can be adaptive for a female to choose either more or less related males, depending on the scenario.

2. Materials, methods and results

Our analysis of inbreeding in socially monogamous populations proceeds in three stages. Our aim is to examine potential benefits to females, and throughout, we assume that females have control over social mate choice as well as whether an extra-pair mating happens. To keep the focus on the fitness consequences of inbreeding *per se*, we also assume that males are not able to detect compromised paternity, that a male does not pay fitness costs for EPCs and that the sex ratio is unity; see Discussion for consequences of relaxing the last two assumptions.

First, we rederive the old result that monogamous inbreeding cannot easily invade an outbred monogamous population [24,29]. Second, we show that a female strategy of inbreeding in extra-pair contexts can invade the same population. Finally, we consider the more general situation where a female has a social partner of arbitrary relatedness (this pair having formed for any reason), and must then decide on whether to engage in EPCs.

(a) Monogamous inbreeding cannot invade an outbred, monogamous population

We begin by considering an idealized population, where all individuals form monogamous bonds and there is no

promiscuity. We assume that the population is initially outbred with a 1 : 1 sex ratio, and then investigate whether monogamous inbreeding could invade the population. Offspring fitness is normalized such that the fitness from an outbred clutch is 1, and inbreeding with a partner of relatedness r (greater than 0) leads to fitness $1 - \delta$ per clutch.

A mutant female who prefers related over unrelated males as her monogamous partner can invade the population if her inclusive fitness is higher than that of the resident, outbred females. The inclusive fitness from an outbred clutch is simply $w_o = 1$. There are no kin benefits because the mating partners are unrelated. The mutant female’s inclusive fitness from an inbred clutch in an otherwise outbred population is

$$w_i = (1 - \delta) + r(1 - \delta) - r. \quad (2.1)$$

Here, the first term corresponds to the direct fitness the female gains via her offspring, whereas the second term is the inclusive fitness component gained through the related male. However, this gain is more than negated by a third, negative term that is the female preventing the same male from forming an outbred pair: by definition, monogamy in a population with a 1 : 1 sex ratio implies that by forming a bond with a related female, he must forego the fitness he could have gained with an unrelated, non-mutant female (see Discussion for relaxing the assumption, used here, that all males find a social mate). Therefore, in this context, no additional matings are available to the male regardless of the female’s actions.

The condition for an inbreeding mutant female to invade an outbred, monogamous population is $w_i > w_o$, which implies

$$(1 - \delta) + r(1 - \delta) - r > 1 \Leftrightarrow -\delta(1 + r) > 0 \Leftrightarrow \delta < 0. \quad (2.2)$$

This indicates that inbreeding can only invade if inbred offspring have higher fitness than outbred offspring. Therefore, under the scenario given here, inbreeding cannot invade an outbred, monogamous population as long as there is any inbreeding depression (see also [24,29]).

(b) Inbreeding in extra-pair contexts can invade an outbred, monogamous population

Consider again the same outbred monogamous population as in the previous example. Now we investigate whether a mutant female that is socially monogamous, but engages in promiscuous EPCs, can invade the outbred, monogamous population. We assume that a proportion $1 - q$ of the mutant female’s clutch is fathered by the social partner (relatedness $r_s = 0$), and the remaining proportion q are EPY sired by a partner of relatedness r_e . For example, if a female replaces one WPY with an EPY in a clutch of size N , we have $q = 1/N$.

Now the total inclusive fitness w_p of the promiscuous mutant female is

$$\begin{aligned} w_p &= (1 - q) + q[(1 - \delta_e) + r_e(1 - \delta_e)] \\ &= 1 + qr_e - \delta_e q(1 + r_e). \end{aligned} \quad (2.3)$$

The first term is the fitness gain obtained through WPY production. There are no other inclusive fitness components from these offspring, as the social partner is unrelated to the mother. Given that the female’s behaviour (q) is assumed to have no effect on the extra-pair mate’s offspring production elsewhere (i.e. neither an increase nor a decrease of the number of offspring he fathers with his own social

mate—we relax this assumption in the Discussion), the negative $-r$ term from equation (2.1) is not needed for the EPY component either.

The mutant strategy can invade the resident (faithful) strategy (w_o) if $w_p > w_o$; that is, if

$$1 + qr_e - \delta_e q(1 + r_e) > 1 \quad \Leftrightarrow \quad \delta_e < \frac{r_e}{1 + r_e}. \quad (2.4)$$

The above equation implies that an outbred, monogamous population can be invaded by a mutant female that forms a socially monogamous bond with a non-relative, and then engages in EPCs with a related male. For example, if mating with a brother ($r_e = 0.5$) decreases offspring fitness by one-quarter ($\delta_e = 0.25$), a strategy of engaging in EPCs with a brother can invade a monogamous, outbred population, because $0.25 < 0.5/(1 + 0.5) \approx 0.33$. Note that the female using the invading strategy has ‘replaced’ some of her WPY with EPY that have 25% lower fitness, a seemingly maladaptive decision. However, calculating the mother’s inclusive fitness based on equation (2.3), we find that $w_p = 1 + 0.5q - 0.25q(1 + 0.5) = 1 + 0.125q$, which is greater than $w_o = 1$ for any $q > 0$. Her inclusive fitness therefore increases with each EPY, despite each of them being less fit than the WPY they are replacing.

The crucial difference between social partner mate choice and extra-pair mate choice is that monogamy (including social monogamy) prevents, by definition, the father from forming any other monogamous bonds [29], whereas EPCs do not diminish the father’s alternative reproductive opportunities in the same way. This means that inclusive fitness benefits that are not accessible via monogamy become available via promiscuous matings.

It should be noted that even if the population is invaded by an inbreeding promiscuous strategy as described above, this does not change the restrictions that monogamy imposes on the social partnerships. Inclusive fitness benefits remain absent in these pairings, and females are therefore still expected to avoid inbreeding in social mate choice. The social mate may now of course engage in EPCs with other females, but as the focal female’s behaviour does not have a direct effect on this part of her mate’s fitness, this does not factor into the inclusive fitness calculations that determine the evolution of female breeding behaviour.

Our model thus far captures a fundamental asymmetry between female choice of social and extra-pair males. From equation (2.2), we conclude that in the presence of inbreeding depression, females should choose unrelated males as their social partner. Equation (2.4) demonstrates that unless inbreeding depression is very strong, females should choose related extra-pair partners, despite the resulting lower fitness of the EPY; this possibility should be taken into account when interpreting empirical data such as in cases 1 [16–19] and 3 [21,22] mentioned in the Introduction.

(c) Extra-pair young production when a potential extra-pair mate is either more or less related than the social mate

Above, we derived the expectation of inbreeding tolerance in extra-pair contexts (up to moderate values of δ) combining with inbreeding avoidance in social pairings. If this outcome was always achieved, a female would never produce EPY

with a less related mate than her social mate. In a real population, however, such situations are clearly not impossible. The social mating can be inbred for reasons of limited mate availability, or if choice is influenced by territory or nest site quality overriding ideal outbreeding. Selection for outbreeding can also become weakened if the population is male-biased (see Discussion). The female’s best option regarding EPY production then depends on her relatedness to the social mate, as well as that of the potentially available extra-pair mate. The equations we have derived so far cannot answer this question, yet case 2 in the Introduction demonstrates that this is an important point to cover: Szulkin *et al.* [20] found that there were significantly fewer EPY in inbred broods relative to outbred broods.

We now therefore examine a more general situation where a female has already (and potentially suboptimally, e.g. due to social constraints) paired with a socially monogamous partner of relatedness r_s , resulting in inbreeding depression δ_s . She then has the option of engaging in EPCs with a male of relatedness r_e , with inbreeding depression δ_e . The question is whether her inclusive fitness increases by doing so.

As we no longer assume that all social partnerships are outbred, the social male’s alternative fitness outcome (that which he would have gained if he had formed a social bond with a different female) is not necessarily equal to 1 (which, in equation (2.1), gave rise to the term $-r$). The resulting genealogical links also make it possible that by choosing a male of relatedness r_s , the focal female has had an effect on another, potentially related female’s fitness by restricting her social pairing opportunities (and this can in turn lead to other knock-on effects on other individuals’ social pairing patterns). We denote these inclusive fitness components combined together as w_x . The value of w_x is unknown, but as we shall see, for the following analysis this is not a problem. It is only relevant that w_x is not dependent on q . This independence follows from our assumption that the social bond has been irreversibly formed before decisions regarding promiscuity are made.

The female’s inclusive fitness is

$$w_p = (1 - q)[(1 - \delta_s) + r_s(1 - \delta_s)] - w_x + q[(1 - \delta_e) + r_e(1 - \delta_e)]. \quad (2.5)$$

We can now determine the conditions under which it pays off to engage in EPCs simply by differentiating the above equation with respect to q . If the derivative is positive, it is adaptive to replace more WPY with EPY, and vice versa

$$\frac{\partial}{\partial q} w_p = -(1 - \delta_s) - r_s(1 - \delta_s) + (1 - \delta_e) + r_e(1 - \delta_e) > 0. \quad (2.6)$$

The unknown fitness component $-w_x$ vanishes in the differentiation, as it is not a function of q . Therefore, EPY production is adaptive under the condition

$$(1 - \delta_e)(1 + r_e) > (1 - \delta_s)(1 + r_s). \quad (2.7)$$

This is equivalent to a direct comparison of the inclusive fitnesses of social and promiscuous matings. Note that the two sides of the equation differ in their subscripts only. Given that our previous equations demonstrated a fundamental asymmetry between social and extra-pair mate choice (equations (2.2) and (2.4)), the symmetrical form taken by equation (2.7) may appear surprising. The reason is that the social mate choice

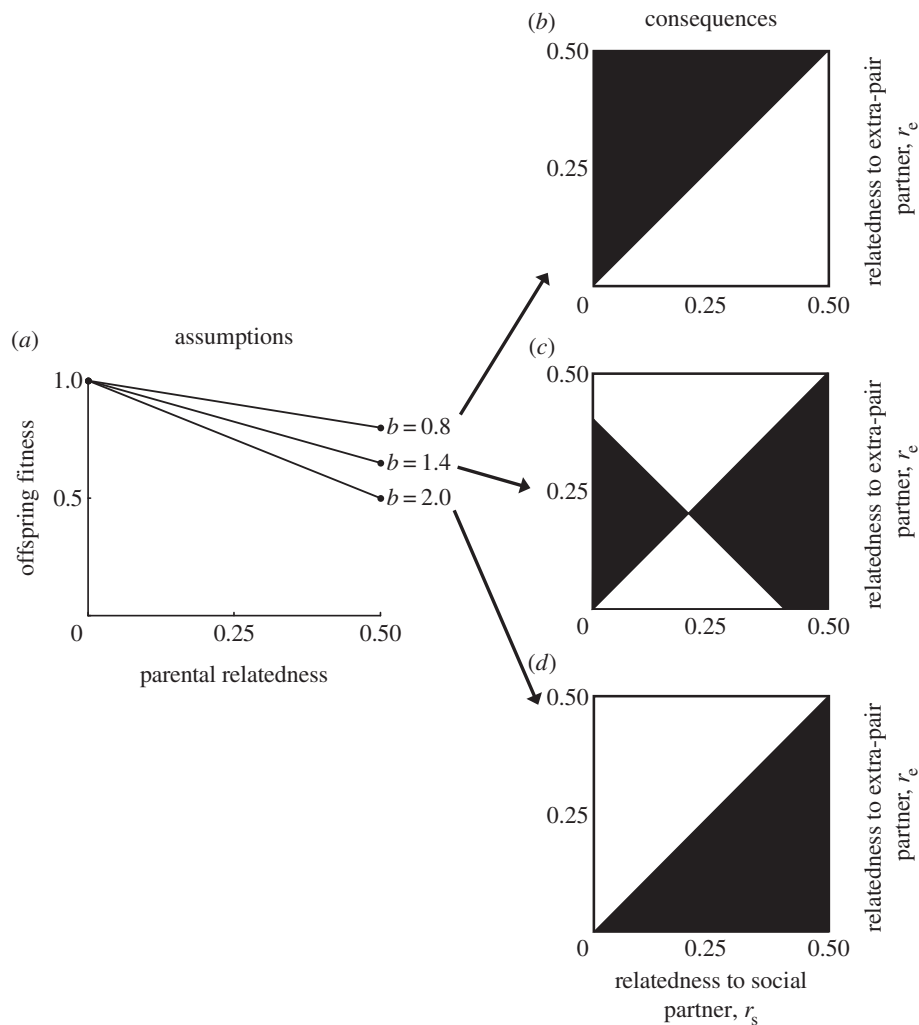


Figure 1. Given that a female has paired up with a social partner of relatedness r_s , she should accept EPCs with males of relatedness r_e in the sections shaded in black, but not in the white regions. These arise from equation (2.7) when combined with the further assumption that inbreeding depression is a linear function of relatedness ($\delta = br/2$), resulting in the condition $(1 - br_e/2)(1 + r_e) > (1 - br_s/2)(1 + r_s)$. The result is strongly dependent on the strength of inbreeding depression as depicted in (a). In (b), inbreeding depression is relatively low, and females are selected to choose extra-pair partners that are more closely related to them than their social partners. Therefore, EPY have lower fitness than WPY. In (d), high inbreeding depression reverses this choice, and EPY are fitter than WPY. In the intermediate case of (c), EPY can have either lower or higher fitness than WPY, and the crossover point indicates an intermediate, optimal level of inbreeding where inclusive fitness cannot be increased by mating with either a more or less related partner. This point corresponds to the optimum relatedness for female mate choice in an outbred population derived previously [33].

has already been locked. The restriction on the social male's potential to form social bonds with other females has already been set and is not affected by the female's further actions. Given that the female's total clutch size is limited, her fitness calculations simply weigh the inclusive fitness gained via an offspring with the social mate (r_s) against that gained via an alternative offspring resulting from an EPC (r_e).

Put another way, equations (2.2) and (2.4) combined describe what the female should ideally do, whereas equation (2.7) describes whether EPCs will increase her inclusive fitness regardless of whether her social mate was ideal or not. This result (equation 2.7) is in line with case 2 as described in the Introduction [20]: a female paired to a related social mate has less scope to increase her inclusive fitness via inbred EPCs than one paired to an unrelated social mate. This can lead to lower rates of EPP in broods sired by related males than in outbred broods.

The exact outcome, however, will depend on the strength of inbreeding depression (δ_s and δ_e) as well as relatedness (figure 1 shows examples using linear dependencies between δ and r ;

note that equation (2.7) applies whether or not this is the case). If inbreeding depression is mild, EPY production can pay off to yield kin-selected benefits with related extra-pair males (figure 1b), while if it is strong, EPY production can instead be adaptive as a way to avoid producing (very) inbred young (figure 1d). These two benefits can combine in perhaps surprising ways in intermediate cases (figure 1c), where socially outbreeding females seek to produce EPYs for the former reason, and females in closely inbred pairs seek them for the latter reason.

3. Discussion

Our results show that previous work on adaptive inbreeding, where monogamous and polygamous systems have been considered separately [24,29,30], naturally extends to populations where one individual can combine both strategies within a breeding season (equations (2.2) and (2.4)). It has long been known that the potential for inclusive fitness

effects is much higher in polygamous than monogamous species [24,29,30], but the link to social monogamy combined with extra-pair matings has not been made explicit.

Our basic result is that unless inbreeding depression is very strong, females should choose unrelated social partners, and any EPY should be sired by related extra-pair partners (equations (2.2) and (2.4)). If inbreeding depression is strong, then females should avoid inbreeding in all matings (within or extra-pair). These results are fully analogous to those for strictly monogamous or strictly polygamous populations.

When one additionally considers that female choice is not always ideal in the context of the initial pair formation (social mates), our results suggest that the simple principle of maximizing inclusive fitness can give rise to three different patterns of social partner relatedness and the proportion of EPY in broods (figure 1).

Mild inbreeding depression makes production of inbred extra-pair young adaptive. When inbreeding depression is relatively low, females should engage in EPCs only if they can find a partner who is more closely related to them than their social partner (figure 1*b*). The relatively more inbred EPY will have lower fitness, but this is compensated for by improved inclusive fitness (equation (2.7)). If the social partner is a close relative, there is less scope to do this (right side of figure 1*b*). Therefore, related partners should have less EPY, a pattern found by Szulkin *et al.* [20] (however, the difference was driven largely by immigrant females in this study; inbred females and outbred locally born females did not differ in rates of EPP).

Strong inbreeding depression makes it adaptive to produce outbred extra-pair young. If inbreeding depression is very strong, the opposite pattern is found: females should engage in EPCs only if they can find a partner who is more distantly related to them than their social partner (figure 1*d*); this pattern fits with the findings of Blomqvist *et al.* [4], although their result is complicated by quasi-parasitism (QP), as we explain below. This will help to increase direct fitness, which under strong inbreeding depression can be so severely compromised that inclusive fitness effects are not sufficient to compensate for it.

Intermediately strong inbreeding depression implies mixed outcomes. Finally, with intermediate inbreeding depression, there is an intermediate value of social mate relatedness for which it does not pay off to engage in EPCs, regardless of whether potential EPC partners are of higher or lower relatedness than the social mate (figure 1*c*). However, females experiencing either outbreeding or close inbreeding can increase their inclusive fitness by producing more, or less, outbred EPY, respectively (figure 1*c*).

Note that in figure 1, we consider, for simplicity, situations where inbreeding depression increases linearly with relatedness, but we will return to complications with relatedness in models of inbreeding. Figure 1 should thus be taken as a conceptual illustration of potential outcomes, not as an exact description of natural settings.

Although current evidence is not sufficient to prove or disprove this hypothesis, results seemingly compatible with all three patterns have been found in empirical studies of EPC rates (e.g. [4,20,34] for figure 1*b,c,d*, respectively). Figure 1*b* is also in line with findings of closer relatedness in EPC partners than social partners [16–19]. As a whole,

our modelling supports the idea of Kleven *et al.* [17] that kin selection and avoidance of inbreeding depression have to be considered together to understand the diversity of mating patterns with respect to inbreeding.

The fact that the exact same theoretical framework can lead to these alternative outcomes also implies that a simple comparison across species may not yield clear results in support of either inbreeding preference or avoidance (see Conclusion).

Below, we discuss some further implications and limitations of our analysis, as well as limitations imposed on real populations in natural settings.

(a) The effect of skewed sex ratios and male opportunity costs

For clarity, we have derived our main results under the simplifying assumptions of an unbiased adult sex ratio (ASR), and males paying no costs for EPCs. Here, we discuss how relaxing these assumptions affects equations (2.2) and (2.4).

The assumption of an unbiased ASR meant that it is possible for all males to find a social partner. While this is in line with much earlier work and helps bring out the asymmetry between social and extra-pair matings, the assumption's validity can be questioned because socially monogamous bird populations are often known to be male-biased [35]. In that case, the assumption of the term $-r$ in equation (2.1) (and its consequences for equation (2.2)) becomes invalid; the average 'cost' imposed on males by forming a social partnership is smaller, because a fraction of them would never have been able to find a mate otherwise. A male-biased ASR can therefore make it beneficial for a female to choose a related partner even for her social partner. Quantitatively, however, the situation is not changed much. If the ASR (males: females) is denoted by ρ , then a fraction $1/\rho$ of males can acquire a social partner if $\rho > 1$ (assuming all females find a partner). A simple derivation then shows that equation (2.2) generalizes to $\delta_s < (1 - 1/\rho)r_s/(1 + r_s)$, implying increased tolerance of inbreeding depression in social mate choice by females. This is very similar in form to eqn (8) in [24], but with the cost of inbreeding term replaced by the reciprocal of the sex ratio.

Second, we add the assumption that males pay a cost c for each EPC, where c is defined as the number of effective outbred matings lost, analogous to [24]. Opportunity costs are typically assumed to be linked to parental investment [36]; for a male who does not make a significant investment in the offspring and for whom mating does not take a very long time, c is not likely to be very high. This is true even in cases where males can effectively court only a subset of all females in a population (at the extreme, a male who lives on one island of an archipelago will not be 'seen' by females residing on other islands); this type of restriction should not logically be included in c , because c refers to the causal effect that EPC success has on reducing a male's success with other females. The location choices, together with the consequences for which females the male appears visible, have already been made, and the subsequent occurrence or non-occurrence of local EPCs does not change them. In an EPC context (where parental investment by the male is low), the value of c can only be high if another local female (not our focal one for which fitness is computed) would be willing to mate with the focal male, but this mating does not happen because the focal male is permanently too 'busy' with the focal female as a result of their EPC activities.

Although possible (if, for example, forays into neighbouring territories take up so much time that some territories cannot be visited), this form of male mate choice is relatively unlikely for birds who do not spend the majority of their time mating, and who generally have time to develop knowledge of neighbours' identities and mating status.

Still, we can consider any value of c in a model. Consider the possibility that a male risks losing fitness via offspring with his *social* mate based on too high extra-pair effort. Then, if the sex ratio is unity, the term qcr_e must be subtracted from equation (2.3) and the following invasion analysis, because the inclusive fitness of the female potentially engaging in EPCs is also reduced. However, if the sex ratio is biased as above, then the male partner will again only have a social partner with probability $1/\rho$, and qcr_e is replaced by qcr_e/ρ . The invasion criterion of equation (2.4) then becomes $\delta_e < (1 - c/\rho)r_e/(1 + r_e)$, implying decreased tolerance of inbreeding depression in EPCs by females. Again, this criterion is similar to that derived for social polygyny by Waser *et al.* (eqn (8) in [24]), with the exception that the cost term is divided by the (male-biased) sex ratio.

We can now compare the criteria for the invasion of inbreeding in WPY and EPY with these more general equivalents of equations (2.2) and (2.4). Consider, for example, a male-biased sex ratio $\rho = 1.2$ and a cost $c = 0.3$. Inbreeding can invade in the context of social mate choice if $\delta_s < (1 - 1/1.2)r_s/(1 + r_s) \approx 0.17r_s/(1 + r_s)$. Inbred EPCs can invade if $\delta_e < (1 - 0.3/1.2)r_e/(1 + r_e) = 0.75r_e/(1 + r_e)$. In other words, even under this scenario with a male-biased sex ratio, and significant costs to males who engage in EPCs, inbreeding tolerance in EPCs is much higher than in monogamous matings. If male opportunity costs (c) did approach 1, then this difference would disappear, but as explained above, we consider this unlikely in most cases due to low paternal investment in EPY.

(b) Limitations of kin recognition

Even if optimal partners were always available, recognizing kin is not a simple task for an animal [37], and this can have significant consequences for reproductive strategies [38]. It is important to bear in mind the constraints on information available to a female when interpreting our results. In natural settings, the accuracy of information regarding relatedness can vary, and the extent and accuracy of various mechanisms is an active field of study (see, for example, [39] for novel findings on olfactory detection of relatives in zebra finches).

Recognition is simple in some cases: nest-mates can use familiarity as a cue that they are more closely related to each other than to random individuals in the population; however, this gives information on only a small subset of all population members. Conversely, an immigrant female may 'know' that she is on average less closely related to her neighbours than locally born females are, but based on her own status alone she is unlikely to be able to detect differences in her relatedness to various potential mates. However, if a fraction of males migrate, a female with an immigrant male as her social partner might 'know' that she could potentially have EPY with a more closely related local male, and vice versa. There are of course other ways in which females could conceivably gauge their relatedness to males; these will depend on the life history of the study species, and must be taken into account on a case-by-case basis.

Given that kin recognition is not likely to ever be perfect, it is useful to know how crucial the accuracy of recognition is for our results. We explore this in the electronic supplementary material and find that our results are quite robust to the introduction of perception error.

(c) Quasi-parasitism

Our derivations were made under the assumption that the female lays all EPY eggs in her own nest, implying that they take up no space in the social nest of the extra-pair male she mated with. Apart from possible opportunity costs (c), these eggs then directly add to the number of eggs the extra-pair male would otherwise have sired, allowing for kin-selected benefits to arise. A well-known exception to this rule is QP [40], where a female lays the extra-pair egg in the nest of her EPC partner. This can have significant consequences for the potential inclusive fitness benefits that can be gained through EPCs. If the brood size in the nest of the extra-pair male has an upper limit, then the EPC eggs laid in his nest might simply take up space that would have otherwise been used by within-pair eggs, with no overall effect on the total number of offspring sired by him. This removes (or at least reduces) the potential inclusive fitness benefits females can gain from mating with related extra-pair males [18]. Under QP, we should then expect EPCs not to arise through kin selection, and inbreeding avoidance is predicted to prevail in WPY as well as EPY. The argument is qualitatively similar, though quantitatively weaker, if there is no strict upper limit to brood size, but raising larger broods is costly to the male parent and/or diminishes the per capita survival of brood members. In general, when such effects are strong, QP may yield no net demographic benefits to host males [40].

Indeed, genetically similar social pairs had higher rates of QP in a study on three species of shorebirds [4]. Moreover, in a study on ground tits, females preferred more closely related extra-pair partners in normal EPCs, but not in cases of QP [18].

(d) Relatedness structure

We have modelled the decisions of a single female in an initially outbred population, but the evolving inbreeding patterns will have consequences on population structure. It is important to note that as a population becomes more inbred, coefficients of relatedness (in the context of inclusive fitness) no longer directly reflect genealogical relatedness (e.g. [33,41–43]). None of these factors change our main results as such; the binary decisions (replace a WPY with an EPY, or not) remain valid, but the interpretation of r has to be made correctly in each particular case. Any process that makes the population more inbred also changes coefficients of relatedness. As modelled previously, this feeds back on the inclusive fitness benefits, resulting in a lower optimal level of inbreeding than would be predicted if this feedback was not accounted for [33].

This does not invalidate the current analysis, which focuses on an initially outbred population. Nevertheless, it is important to keep Puurtinen's [33] insight in mind: a clear avenue for future work is to investigate by how much the stable optimal level of inbreeding will be lowered by the coevolution between relatedness and inbreeding. The analysis will be more complicated than in [33] because there is now a need to consider a population where both EPY and WPY are being produced: a new generation is now composed of WPY and EPY differing

in their inbreeding coefficients, and the uniform inbreeding assumption of earlier work [33] no longer applies. The calculation of the coefficient of relatedness (which we for simplicity and generality have left as open parameters) will then depend on further features of the population, such as the proportion of EPY produced (q), migration, population size and the exact link between inbreeding coefficients and inbreeding depression. This future avenue is beyond the scope of our current analysis.

(e) Factors affecting the fraction of extra-pair copulations (q)

Our model often gives results where it is in the evolutionary interest of a female to aim for either higher (up to 1, i.e. 100% EPY) or lower (0%) values of q , the proportion of EPY in her brood (equation (2.7), figure 1). Our model does not directly comment on how large we expect the actual proportion to be, if in principle replacing every WPY with an EPY yields fitness benefits. It would clearly be difficult to completely avoid WPY production given her status of being socially paired to a male, and other costs of EPY production can play a role too.

Thus, in real populations, q can be affected by factors not explicitly modelled here. First, different females may find themselves in situations that either favour or disfavour having EPY in broods (e.g. some may be suboptimally socially paired; figure 1), resulting in intermediate population-wide values of q . Second, to provide conceptual clarity, we in our study focused on inbreeding effects and female choice, thus intentionally omitting other factors that can conceivably impact EPP. The list includes correlated selection based on male fitness [44], male behavioural responses to cues of lower paternity [1,12,32,45], insurance against infertility [1–3] and issues of genetic compatibility [3,15]. Which sex has power to decide on whether a copulation occurs is also of relevance; our model gives the baseline expectation in female preferences for social and extra-pair mate choice, if inbreeding is the focal issue.

4. Conclusion

It has proved difficult to find consistently elevated EPY fitness compared with WPY. This has made it difficult to settle the question of what the adaptive basis of EPCs might be [1,3,11,12,15,46]. Here, we have shown that a single underlying process that considers both inbreeding depression and kin-selected benefits of inbreeding has potential to explain a diverse set of patterns found in nature that are in apparent contradiction with each other (equations (2.2), (2.4) and (2.7); figure 1). Therefore, our results have two major implications for studies of EPC adaptiveness.

First, our model highlights the rather counterintuitive possibility that producing EPY can be adaptive for mothers even if they are more inbred and their fitness is lower than WPY fitness. This does not mean that extra-pair sexual behaviour is freed of all sexual conflict, however: females should still be choosier than males over EPC mates, males should still try to prevent females from engaging in EPCs, and females should potentially do the same to males, at least if EPCs elsewhere decrease male participation in care for the current brood. These aspects of conflict remain even if both sexes are selected to engage in EPCs, and if the pairing

process between social mates is relatively conflict-free (at least with respect to relatedness).

Second, while this provides a framework that has potential to explain seemingly contradictory empirical results, figure 1 indicates that drawing conclusions from comparisons of extra-pair partner relatedness or offspring fitness across species may be more complicated than previously assumed. If the same theoretical framework can lead to opposite outcomes (figure 1), it may be difficult to find a clear signal in either direction. For example, a meta-analysis compiling several studies [15] found no difference between EPY and WPY in survival to the next breeding season, nor a significant correlation between pair genetic similarity and rates of EPP, and therefore called for new hypotheses. Similarly, another comparative study [12] found no significant difference between EPY and WPY fitness, while direct negative selection (in the form of decreased paternal investment) of infidelity was stronger. From this, Arnqvist & Kirkpatrick [12] concluded that EPCs are unlikely to be adaptive for females and suggested that EPCs primarily reflect sexually antagonistic coevolution between males and females. Our results suggest that this need not be the case, offering alternative explanations for why EPY need not be more fit or less inbred than WPY.

This does not imply that previous comparative studies that found no clear signal [12,15] can be used as direct evidence in support of our hypothesis. Likewise, the empirical patterns that motivated this study (cases 1–3, Introduction) are diverse enough to retain many open questions, and it would be premature (and probably incorrect) to ignore the possibility that many cases are driven by other processes than the one we highlight (e.g. EPY are fitter than WPY in [19]; [16] and [19] are compatible with random mating with respect to relatedness in EPY contexts, and a very recent study [47] also found this to be the most parsimonious interpretation of the dataset in [21]—raising the possibility that kin recognition might simply be weak or absent). Thus, our goal is not to claim that all cases will fall into the category indicated by our title. Instead our work is intended to serve as a reminder that the magnitude of inbreeding depression, the availability of social mates of suitable relatedness and the magnitude of opportunity costs should all be considered on an equal footing; and that the last factor in particular is likely to differ between within-pair and extra-pair contexts. It also suggests a novel and relatively simple answer to the question of why females should have different preferences regarding their social and extra-pair partners (e.g. [28]).

Our results also have implications for the stability of monogamy. If there is inbreeding depression, females are often predicted to choose an unrelated social mate under both social and genetic monogamy. If costs of inbreeding are not very high, this sets up a situation where females are selected to engage in EPCs with related males (equation (2.4)). This forms a significant category of genetic benefits that can make monogamy vulnerable to invasion by polygynous and polyandrous mating tactics under fairly general conditions, potentially also leading to the loss of biparental care [32,45]. This adds to the list of many reasons why females may be expected to mate multiply [11,48].

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