

The Evolution of Infidelity in Socially Monogamous Passerines: The Strength of Direct and Indirect Selection on Extrapair Copulation Behavior in Females

Göran Arnqvist^{1,*} and Mark Kirkpatrick^{2,†}

1. Department of Ecology and Evolution, Animal Ecology,
Evolutionary Biology Centre, University of Uppsala, Norbyvägen
18D, SE-752 36 Uppsala, Sweden;

2. Section of Integrative Biology C-0930, University of Texas,
Austin, Texas 78712

ABSTRACT: Many studies have been aimed at understanding the maintenance of female infidelity in socially monogamous birds. Because engaging in extrapair copulations (EPCs) is believed to be costly for females, it has been argued that EPC behavior must bring indirect benefits to females by elevating offspring fitness. We use empirical data from the literature to assess the relative strength of indirect and direct selection on female EPC behavior, using quantitative genetic approximations of selection. This analysis confirmed that there is generally negative direct selection on EPC behavior caused by depressed paternal investment by social males. In contrast, there was no significant positive indirect selection on EPC behavior in females. A comparison between the two types of selection suggests that the force of direct negative selection is generally much stronger than that of indirect positive selection. Indirect selection is thus unlikely to maintain EPC behavior in the face of direct selection against it. We suggest that EPCs may instead be the result of antagonistic selection on loci influencing the outcome of male-female encounters and that EPC behavior per se may not be adaptive for females but may reflect sexual conflict due to strong selection in males to achieve extrapair copulations.

Keywords: genetic compatibility, good genes, mate choice, paternal investment, polyandry, sexual selection.

During the past 2 decades, the development of novel genetic techniques has led to the discovery that infidelity is much more common in birds than previously believed (cf. Lack 1968). Among socially monogamous species, on av-

erage, more than 10% of all offspring are sired by a male other than the social father (Griffith et al. 2002). This observation has spurred a large literature on the evolution of extrapair copulations (henceforth, EPCs) in females of such species (reviewed in Petrie and Kempenaers 1998; Griffith et al. 2002; Westneat and Stewart 2003). Because there are reasons to believe that females may suffer direct costs of infidelity, primarily in terms of reduced paternal care of offspring by their social mate, much of this body of research has been a quest for balancing benefits to females. Foremost of these has been the suggestion that females may enjoy balancing indirect genetic benefits through elevated offspring fitness by engaging in EPCs (e.g., Gowaty 1985; Kempenaers et al. 1992; Petrie and Kempenaers 1998; Jennions and Petrie 2000), but this literature remains highly controversial, and there is no general consensus (e.g., Møller and Alatalo 1999; Griffith and Montgomerie 2003; Westneat and Stewart 2003).

Most of the data in this field are purely correlational and do not allow firm conclusions about whether females suffer direct costs or gain appreciable indirect benefits from EPCs. For example, a positive association between success in extrapair paternity among males and some measure of male "quality" may simply be an indirect result of a generally higher activity of males in high phenotypic conditions (Sheldon 1994). Similarly, observations of higher offspring fitness among broods containing extrapair young (EPY) compared with those with only within-pair young (WPY) do not provide evidence for indirect benefits of EPC behavior in females because both high offspring fitness and a high rate of EPY could be the result of a third causal variable (e.g., maternal or other environmental effects). Perhaps the most problematic point is that even if females would enjoy indirect genetic benefits from EPCs, these could be incidental side effects of behaviors that have evolved and are maintained primarily for reasons other than securing indirect genetic benefits (e.g., Cameron et al. 2003; Chapman et al. 2003; Kokko et al. 2003). Thus, strictly speaking, evidence that indirect benefits of EPC

* Corresponding author; e-mail: goran.arnqvist@ebc.uu.se. G. Arnqvist is the main author of this article. M. Kirkpatrick is the sole author of the appendix.

† E-mail: kirkp@mail.utexas.edu.

behavior exist does not demonstrate that this behavior is maintained by indirect selection. Ultimately, a complete understanding must be based on the relative strengths of different forms of selection (Kirkpatrick 1987; Møller and Jennions 2001). As such, the problem is an empirical one and reverberates the long-standing and more general controversy over the evolution of female mate choice (see Mead and Arnold 2004): What is the general potency of indirect selection on female mating behavior, and can it counterbalance direct selection in extant populations?

Here, we adopt a nontraditional approach to the problem of the maintenance of EPCs in socially monogamous passerines. Rather than debating the existence of indirect selection for or direct selection against EPC behavior in females, we show that we can derive meaningful empirical estimates of the force of indirect selection and compare these with corresponding estimates of direct selection. We do so by means of a quantitative genetic model of phenotypic response to selection. To our knowledge, it represents the first comprehensive attempt to quantify the forces acting on a specific female mating behavior in natural populations. We note that an explicit call for such studies that was made almost 20 years ago (Kirkpatrick 1987) has been reiterated more recently (Kirkpatrick and Barton 1997; Møller and Jennions 2001; Mead and Arnold 2004).

Methods and Results

Indirect Selection

Measuring indirect selection on female mating behavior/preferences is notoriously difficult (Kirkpatrick 1987, 1996; Kirkpatrick and Barton 1997). This is true also when estimating indirect benefits of EPCs to females. Estimates that are based on comparisons of offspring fitness across broods are particularly problematic because results may be strongly confounded by phenotypic parental effects (Griffith et al. 2002; Westneat and Stewart 2003). In contrast, comparisons between EPY and WPY fitness within broods with mixed paternity offer an uncontaminated source of information regarding the genetic benefits for females simply because it controls for all other sources of variance in offspring fitness across broods, including the female's own genetic contribution (Kempnaers et al. 1997; Sheldon et al. 1997; Griffith et al. 2002). Any difference between EPY and WPY fitness within a brood must reflect paternal genetic effects (but see "Discussion").

We collected data from studies comparing EPY and WPY fitness within broods, considering direct measures of offspring growth, survival, recruitment (recaptured/resighted as a breeding adult during subsequent season or seasons), and/or reproductive success as reasonable fitness

components. We used data from all published studies found, except for that of Strohbach et al. (1998) because the data from this study could not be recovered (E. Curio and T. Lubjuhn, personal communication). A few studies reporting other forms of potential but less direct fitness correlates were also not included (such as immune response; see Granbom et al. 2004).

We combined these data with a mathematical model to predict the force of indirect selection on female EPC behavior. Our measure of the force of indirect selection, which we denote Δ_I , is the number of phenotypic standard deviations that the average rate of EPC in the population would evolve by indirect selection per generation if no other force acted on that behavior.

Indirect selection will favor the evolution of EPC behavior in females if EPY on average have higher lifetime fitness than WPY. From a genetic perspective, this effect arises because genes increasing the tendency to engage in EPCs become correlated (in linkage disequilibrium) with high-fitness genes. This genetic correlation and the force of indirect selection on female EPC behavior can be calculated using the published data on the fitnesses of EPY and WPY and by building on the earlier theoretical results of Kirkpatrick and Barton (1997) and Kirkpatrick et al. (2002). A calculation presented in the appendix shows that a good approximation for the force of indirect selection is simply

$$\Delta_I = h_F^2 \sigma_F d_{EW}. \quad (1)$$

Here, h_F^2 is the heritability of female EPC behavior, σ_F is the phenotypic standard deviation of the rate of EPC behavior, and d_{EW} is the difference in fitness between EPY and WPY. This result assumes that the effects of individual genes on lifetime fitness are not very large (smaller than, say, $s = 0.1$). In the following, we estimate d_{EW} from the literature as the difference in mean fitness between a female's offspring sired by extrapair males and those sired by within-pair males in broods with mixed paternity, averaged over all females as

$$d_{EW} = \frac{1}{n} \sum_{i=1}^n \left(\frac{W_{E_i} - W_{W_i}}{W_i} \right), \quad (2)$$

where W_{E_i} is the mean fitness of female i 's offspring from EPCs, W_{W_i} is the mean fitness of her offspring from WPCs, W_i is the mean fitness for all her offspring, and n is the number of females in the study. This forms our measure of the strength of indirect selection on EPC behavior and is equal to the expected difference in mean offspring fitness that would result from having all or none of the offspring sired by extrapair males. We note that this assumes that

the proportion of EPY within a brood is a phenotypic reflection of the EPC behavior of a given female. Although estimates for h_F^2 and σ_F are not available, we can put upper limits on their values. The heritability h_F^2 cannot be larger than 1, while σ_F cannot be larger than $[\bar{F}(1 - \bar{F})]^{1/2}$, where \bar{F} is the mean rate of EPC in the population. Thus, an absolute upper limit to Δ_I , the force of indirect selection favoring EPC behavior in females, is about half of the difference in relative fitness between extrapair and within-pair offspring. The actual values of h_F^2 and σ_F may, of course, reduce Δ_I substantially below this number.

A meta-analysis (see Shadish and Haddock 1994 for details) of the estimates of d_{EW} presented in table 1, where estimates were weighted by $n - 3$ (n = number of broods with mixed paternity), yielded a weighted average of $d_{EW} = 0.015$. This was not significantly different from 0 (95% confidence interval [CI]: -0.064 – 0.094). Further, the null hypothesis that these estimates share a common effect size could not be rejected ($Q = 11.22$, $df = 15$, $P = .737$). A meta-analysis of the resulting estimates of the force of indirect selection on EPC behavior, assuming a heritability of EPC behavior of 0.4 (a typical heritability of female mating behaviors; see Bakker and Pomiankowski 1995) and a standard deviation of $[\bar{F}(1 - \bar{F})]^{1/2}$, yielded an

average of $\Delta_I = 0.004$. Again, the estimates of Δ_I were not significantly heterogeneous ($Q = 0.30$, $df = 15$, $P > .95$).

This exercise yields two insights. First, this analysis strongly suggests that positive indirect selection is not generally present in socially monogamous passerines where females engage in EPCs. If it is, the overall force of indirect selection on female EPC behavior must be very weak indeed because the 95% CI of Δ_I is centered near 0. On the basis of the estimates presented here, indirect selection will at the very most be capable of changing the mean rate of EPCs by only one or possibly a few percent of its standard deviation per generation. Incidentally, this overall conclusion corresponds reasonably well with estimates for the impact of indirect selection on female mating behavior reported earlier by Kirkpatrick and Barton (1997; see also Møller and Alatalo 1999; Møller and Jennions 2001; Kirkpatrick et al. 2002). Second, the available empirical estimates of the magnitude of indirect benefits to females from EPCs are surprisingly consistent; there are no statistical indications of contrasting or contradictory results among these studies. Needless to say, estimates of indirect benefits across studies and/or species should be deemed different only if this conclusion is supported by direct statistical tests. Although there are reasons to believe that the

Table 1: Estimates of the strength of indirect selection on extrapair copulation behavior in females based on comparisons of the fitness of within-pair young and extrapair young within broods with mixed paternity

Species and measure of offspring fitness	Number of broods		Reference
	with mixed paternity (n)	Selection gradient (d_{EW})	
Collared flycatcher (<i>Ficedula albicollis</i>): Fledgling condition	21	-.028	Lindén et al. 1992; Sheldon et al. 1997; Sheldon and Ellegren 1999
Great tit (<i>Parus major</i>): Recruitment	67	-.041	Lubjuhn et al. 1999a
Weight at day 15	10	.006	Krokene et al. 1998
Recruitment	12	-.056	Krokene et al. 1998
Blue tit (<i>Parus caeruleus</i>): Weight at day 15	15	.016	Krokene et al. 1998
Recruitment	16	-.397	Krokene et al. 1998
Survival rate from day 14 to fledging	57	.063	Kempnaers et al. 1997
Coal tit (<i>Parus ater</i>): Recruitment (first broods)	57	-.163	Lubjuhn et al. 1999b; Schmoll et al. 2003
Recruitment (second broods)	44	.364	Lubjuhn et al. 1999b; Schmoll et al. 2003
Number of fledglings produced first year	8	-.019	Lubjuhn et al. 1999b; Schmoll et al. 2003
Tree swallow (<i>Tachycineta bicolor</i>): Weight at day 14	24	.091	Kempnaers et al. 1999
Survival from day 8 to fledging	24	.043	Kempnaers et al. 1999
Egg to fledging survival	43	.098	Whittingham and Dunn 2001
Song sparrow (<i>Melospiza melodia</i>): Survival from day 6 to independence	112	-.052	O'Connor 2003
Survival from independence to age 1	112	.09	O'Connor 2003
Lifetime offspring production	25	-.117	O'Connor 2003

strength of indirect effects may differ between species and/or populations, this has to our knowledge not yet been demonstrated.

The derivation of Δ_I assumes autosomal inheritance, additive genetic variation for all traits, and equal expression of “good genes” effects in offspring of both sexes (see appendix). We note that equation (1) will tend to overestimate the true force of indirect selection in the presence of epistatic variation for fitness (e.g., interacting “compatibility” genes; Kirkpatrick and Barton 1997) or if good genes effects are expressed only in one sex (i.e., half of the offspring; Kirkpatrick and Hall 2004). The conclusions above are therefore, at least in this sense, conservative.

Direct Selection

At least four types of direct selection on EPC behavior have been discussed in the literature. First, females may enjoy a higher fertility as a result of EPCs (Sheldon 1994). Unfortunately, in the absence of any experimental data directly supporting this hypothesis, descriptive data on associations between hatching rate and rate of EPCs across females are particularly likely to be confounded by maternal effects or ecological correlates (see also Griffith et al. 2002). For example, females in better phenotypic condition may exhibit higher rates of EPCs and may also lay clutches with a higher egg hatching rate. Nevertheless, within-population studies show no general relationship between the proportion of EPY and egg hatching rate (Møller and Ninni 1998), and a comparative analysis by Morrow et al. (2002) found no significant correlated evolution between these two variables. Moreover, the generality of this intuitively reasonable hypothesis is somewhat restricted. In order for EPCs to elevate hatching rate, one has to assume efficient pre-mating female choice for compatible extrapair males and/or very strong post-mating bias in fertilization success in favor of such males. There is currently little, if any, unequivocal evidence for this in birds (see Jennions and Petrie 2000). Without such overt and/or cryptic female choice for compatible males, average fertility of females faithful to their social mates will be identical to that of females engaging in EPCs. This can be shown by the following exercise. Consider a case where a proportion p of the males in the population are compatible with any given female and some females engage in EPCs and some do not. Let n be the average clutch size and I be the fertility rate of eggs fertilized by incompatible males (ranging from 0 to <1). For faithful females, the average number of hatched eggs will then be pn [male is compatible] + $(1-p)In$ [male is incompatible]. For a female engaging in EPCs that copulates an equal number of times with a neighboring male and her social male, the average number of hatched eggs will be p^2n [both males

compatible] + $2p(1-p)[(I+1)/2]n$ [one compatible and one incompatible male] + $(1-p)^2In$ [both males incompatible]. Although engaging in EPCs indeed reduces the risk that all eggs are fertilized by an incompatible male, this is exactly offset by an increased risk that at least some eggs are fertilized by an incompatible male such that

$$pn + (1-p)In = p^2n + 2p(1-p) \times \frac{(I+1)}{2}n + (1-p)^2In. \quad (3)$$

Hence, engaging in EPCs will not by itself lead to an increase in the number of hatched eggs a female can expect to attain in the presence of incompatible males in the population (see Kisdi 2003 for a similar argument on multiple mating and hybridization).

Second, females may enjoy other types of direct benefits from EPCs. This may be true in some specific cases (e.g., Gray 1997), but it is difficult to see what general direct benefits could derive from EPC behavior (see Birkhead and Møller 1992; Ligon 1999). Third, copulations may carry direct costs to females (risk of infection with venereal disease or parasites, elevated risk of predation, time waste, etc.), and EPCs may thus be costly per se. Although such costs may be significant, empirical assessments of their magnitude in socially monogamous birds are currently lacking (Birkhead and Møller 1992; Poiani and Wilks 2000; Westneat and Stewart 2003).

Fourth, the most significant and general cost to females is thought to be a reduction in paternal care by their social mates as a result of EPCs (Trivers 1972; Clutton-Brock 1991; Ligon 1999). However, much recent debate surrounds this issue. Comparative studies across species of biparental birds of the effects of male removal have shown that females suffer reduced reproductive success as a result of decreased paternal care (Clutton-Brock 1991; Ligon 1999) and that the degree of fitness loss depends on how much males contribute to the care of offspring (Møller 2000; Arnold and Owens 2002). Using the comparative data presented by Møller (2000), the predicted reproductive success of a completely deserted female is 0.51 (95% CI: 0.18–0.84) times that of a female with a social partner for a species in which males contribute 50% of the care of offspring. At this level, therefore, male care of offspring is clearly a major female fitness component.

Whether females within species generally suffer reduced paternal care as a result of EPCs is more contentious (see Sheldon 2002; Westneat and Stewart 2003 for reviews). Theory in this field is rich but incongruent, predicting anything from no reduction in paternal care to a gradual reduction to a threshold response with increased EPC behavior in females. Empirical research has also been con-

Table 2: Estimates of direct selection on extrapair copulation behavior in females caused by reduced paternal care

Species	Measure of paternal care	Number of broods (<i>n</i>)	Selection gradient (β_F)	Reference
Alpine accentor (<i>Prunella collaris</i>)	Proportional offspring provisioning rate	16	-.281	Hartley et al. 1995
Dunnock (<i>Prunella modularis</i>)	Feeding/no feeding by male	44	-.261	Burke et al. 1989
Western bluebird (<i>Sialia mexicana</i>)	Proportional offspring provisioning rate	42	-.309	Dickinson 2003
Great tit (<i>Parus major</i>)	Intensity of male's nest defense behavior	17	-.457	Lubjuhn et al. 1993; T. Lubjuhn, personal communication
Great tit (<i>Parus major</i>)	Intensity of male's nest defense behavior	15	-.624	Lubjuhn et al. 1993; T. Lubjuhn, personal communication
Barn swallow (<i>Hirundo rustica</i>)	Proportional part in incubating eggs	9	.427	Smith and Montgomerie 1992
Tree swallow (<i>Tachycineta bicolor</i>)	Proportional offspring provisioning rate	12	.051	Liffield et al. 1993
Purple martin (<i>Progne subis</i>)	Proportional offspring provisioning rate	16	.104	Wagner et al. 1996
Purple martin (<i>Progne subis</i>)	Proportional part in nest building	15	-.335	Wagner et al. 1996
House martin (<i>Delichon urbica</i>)	Proportional offspring provisioning rate	10	-.052	Whittingham and Liffield 1995
Hooded warbler (<i>Wilsonia citrina</i>)	Proportional offspring provisioning rate	12	.102	Stutchbury et al. 1994
Black-throated blue warbler (<i>Dendroica caerulescens</i>)	Absolute offspring provisioning rate	30	-.402	Chuang-Dobbs et al. 2001
Yellow warbler (<i>Dendroica petechia</i>)	Proportional offspring provisioning rate	31	-.07	Yezerinac et al. 1996
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	Proportional offspring provisioning rate	89	.082	Westneat 1995

sidered divergent because males have often but not always been found to significantly reduce the amount of paternal care as a response to a perceived elevation of the rate of EPCs. Experiments studying the effects on paternal care of a temporal removal of the female (or the male himself) have nevertheless provided support for the existence of this form of direct costs to females (reviewed by Sheldon [2002]). Several other types of experiments also lend support to the idea that males often do reduce their share of parental care in response to reduced paternity (reviewed by Ligon [1999]).

Reduced parental care is also the only form of direct effect of female EPC behavior whose impact can currently be quantified. Published data allowed us to estimate the direct selection gradient acting on a female's propensity to engage in EPC, which we denote β_F , that results from reduced paternal care of her social mate. The basis for our estimate is the definition of a selection gradient as the regression of female fitness onto the proportion of EPY in broods after fitness has been standardized to a mean of 1 (Lande and Arnold 1983) and using measures of paternal care as proxies for female fitness (i.e., offspring production). Again, we assume that the proportion of EPY in a brood reflects female EPC behavior.

We used two approaches. First, we compiled all published studies presenting data that allowed us to regress measures of paternal care onto the proportion of EPY across pairs. Ten out of the 14 studies found measured paternal care as the proportion of the total amount of care given over some time period that was provided by the social male (i.e., male care/[male care + female care]). For these studies, we used the slope of the regression as our

estimate of β_F . Four studies reported only the absolute amount of care provided by the social male. For these studies, the slope of the regression was multiplied by 1/2 to yield our estimate β_F . We expect these estimates of β_F to be unbiased when offspring production is proportional to the total amount of parental care given, when the social male contributes with, on average, approximately half of the total amount of care given, and when female compensation for reduced levels of paternal care is negligible. We note that the question of how to correctly estimate β_F when these assumptions are not fulfilled is a nontrivial one that would benefit from attention in the future.

The weighted average selection gradient among these 14 studies (a meta-analysis of the data presented in table 2) was $\beta_F = -0.14$ and was significantly different from 0 (95% CI: -0.25 to -0.04). The lack of a significant correlation between selection gradient and sample size across studies ($r_s = -0.298$, $P > .25$) strongly suggests that publication bias is not a concern (see Palmer 1999) because a positive correlation would result from such bias (the average effect size is negative). The estimates were somewhat variable, although the null hypothesis of homogeneity among selection gradients could not be rejected ($Q = 16.5$, $df = 13$, $P = .223$). A reanalysis of the data, excluding one disparate study of red-winged blackbirds, which is also potentially biased in this context because males clearly contribute very little to parental care (Westneat 1995), showed highly significant negative selection (weighted average $\beta_F = -0.23$; 95% CI: -0.36 to -0.10; 99% CI: -0.40 to -0.06) and much improved homogeneity among estimates ($Q = 10.5$, $df = 12$, $P = .572$).

The above estimates of selection gradients are, however, somewhat unreliable because they are potentially confounded by causal variables that co-vary in complex ways with both male parental care and the rate of EPCs of his mate (e.g., male condition or local environment; see Kempenaers and Sheldon 1997; Wright 1998; Sheldon 2002). We therefore also used data from the four available studies reporting offspring provisioning rates by the same males in two consecutive breedings within the same season, differing in the rate of EPY in the brood, as a second approach (Dixon et al. 1994; Møller and Tegelström 1997; Buchanan 2001; Peterson et al. 2001). Estimates based on these data are much less problematic because confounding variation across males/pairs is removed, although they are not immune against such variation over time within males/pairs (Sheldon 2002). When paternal care is measured as the proportion of the total amount of care given, the selection gradient is estimated by

$$\beta_F = \frac{1}{N} \sum_{i=1}^N \left(\frac{C_{i_1} - C_{i_2}}{\text{EPY}_{i_1} - \text{EPY}_{i_2}} \right), \quad (4)$$

where C_{i_1} and C_{i_2} are the paternal care (divided by its average) provided by the i th male in his two consecutive breedings, EPY_{i_1} and EPY_{i_2} are proportions of extrapair young in the broods, and N is the number of males. When C instead represents the absolute amount of care provided by the social male, the right-hand side of equation (4) is multiplied by $1/2$ to estimate β_F . We note that these estimates of β_F will be unbiased under the same three assumptions that applied to our first approach. These calculations yielded $\beta_F = -0.85$ for barn swallows (Møller and Tegelström 1997), $\beta_F = -0.36$ for common yellowthroats (Peterson et al. 2001; L. A. Whittingham, personal communication), and $\beta_F = -0.18$ and $\beta_F = -0.64$ for reed buntings (Dixon et al. 1994; Buchanan 2001; G. Buchanan, personal communication). The weighted average selection gradient for these four studies, $\beta_F = -0.43$, was significantly different from 0 (95% CI: -0.83 to -0.02), and there was no evidence for heterogeneity among the four studies ($Q = 1.37$, $df = 3$, $P = .713$). A large effect of mate fidelity on the level of paternal care has also been observed in a few similar but nonquantitative repeated observations of parental behavior of single males (Weatherhead et al. 1994; Hartley et al. 1995). It is worth noting that the absolute value of the estimate of β_F based on variation across broods within males/pairs was about twice as large as the corresponding estimate across pairs. Because the former should be a more reliable estimate, this suggests that the latter type of studies may frequently underestimate rather than overestimate the true covaria-

tion between paternal care and paternity (Kempenaers and Sheldon 1997; Wright 1998; Sheldon 2002).

To compare the impact of direct selection and indirect selection on female EPC behavior, we need to translate our results for these two forces into a common currency. Earlier we measured the force of indirect selection using Δ_p , which is the rate that the mean frequency of EPC evolves per generation, measured in units of phenotypic standard deviations of that frequency. Our estimates for the direct selection gradient can be transformed into the same units. The per-generation change in the mean of a quantitative trait caused by direct selection is the product of the selection gradient and the additive genetic variance (Lande 1981; Lande and Arnold 1983; Falconer and Mackay 1996; Kirkpatrick and Barton 1997). In our case, this rate is reduced by half because the behavior (female EPC rate) is expressed only in one sex. Dividing by the phenotypic standard deviation σ_F and using the definition of heritability gives Δ_D , the per-generation change in the mean rate of EPC caused by direct selection, measured in units of phenotypic standard deviations:

$$\Delta_D = \frac{1}{2} h_F^2 \sigma_F \beta_F, \quad (5)$$

where again h_F^2 is the heritability of female EPC behavior. Assuming a heritability of EPC behavior of 0.4 (see Bakker and Pomiankowski 1995) and a standard deviation of $[\bar{F}(1 - \bar{F})]^{1/2}$, weighted average Δ_D ranges from the potentially biased but more general -0.02 (average from across-males studies) to the more reliable but somewhat restricted -0.04 (average from within-males studies).

We are finally in a position to consider the relative forces of direct and indirect selection. Comparing equations (1) and (5) shows that the evolutionary rate of change in female EPC behavior caused by direct selection is expected to be approximately $\beta_F/2d_{EW}$ times that caused by indirect selection. Our meta-analysis of the empirical data at hand thus suggests that the force of direct selection is approximately one order of magnitude stronger than that of indirect selection. To conclude, the general estimate of positive indirect selection on female EPC behavior presented here suggests that such selection is biologically insignificant, especially when compared with negative direct selection (see fig. 1).

Discussion

The estimates of indirect and direct selection on female EPC behavior derived above imply that the maintenance of EPCs in socially monogamous passerines cannot generally be understood in terms of selection in females alone. Although the literature in this field has, by tradition,

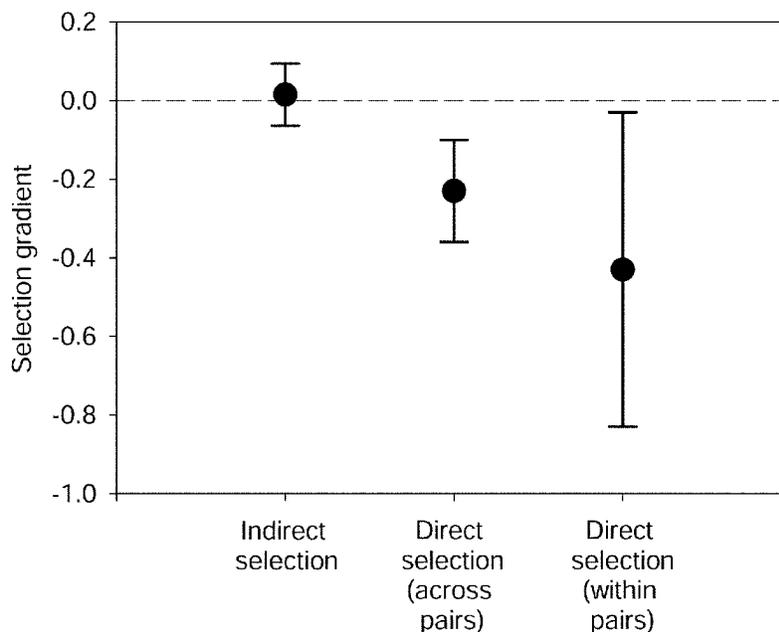


Figure 1: Weighted average selection gradients ($\pm 95\%$ confidence interval) for selection on female extrapair copulation behavior, based on a synthesis of available empirical data. One estimate of direct selection is based on studies comparing different breeding pairs and the other on studies comparing repeated breedings of the same male/pair.

viewed EPC behavior as a female strategy or a female adaptation (but see Westneat and Stewart 2003), the above analysis suggests that this view may be incorrect. While indirect selection on EPC behavior may be a significant evolutionary force in some special cases (such as in hybrid zones; see Veen et al. 2001), the analyses presented here reveal that indirect selection is not generally present and that it should be overwhelmed by the effects of direct negative selection when it is. Below, we first ask how reliable these estimates of selection are and then discuss an alternative scenario for the maintenance of EPCs.

To achieve reliable estimates of the effects of indirect selection on the evolution of female mating behavior under natural circumstances is challenging (Kirkpatrick and Barton 1997; Møller and Jennions 2001). Estimates are made uncertain by, for example, difficulties with quantifying variation in female mate choice behavior (Kirkpatrick 1987, 1996) and by the fact that the magnitude of the heritability of fitness, as well as its genetic covariance with phenotypic traits in males, is poorly understood. The estimates presented here are, however, somewhat different. They are based on directly comparing the fitness of the offspring a given female would have produced had she not engaged in any EPCs with the offspring fitness the same female would have experienced had all her copulations been EPCs. By not directly involving males or male traits, these estimates steer clear of many of the assumptions necessary

for predicting the effect of indirect selection in many other cases (Kirkpatrick and Barton 1997). Note, however, that the estimates of indirect selection presented here will be unbiased only if EPY and their WPY maternal half-sibs within a particular brood experience the same average environment (including maternal effects). This assumption has been tested in several species and has been supported in all cases (see Westneat et al. 1995; Kempenaers and Sheldon 1996). Further, because our estimate of indirect selection is based on broods with mixed paternity, it will underestimate the true effect if the subset of females that do not engage in EPCs generally have more to gain from EPCs in terms of indirect benefits. It is, however, difficult to envision a scenario where this would be true.

A final potential problem might be that the fitness components measured in the empirical research synthesized here are poor representations of net fitness in offspring. At present, it is difficult to firmly assess the gravity of this concern. On the one hand, deriving meaningful empirical proxies of net fitness is generally very problematic (see Hunt et al. 2004). On the other, several long-term studies of birds have shown that both survival between the egg and fledgling stages and survival until the first breeding season are major components of variance in lifetime reproductive success (see Newton 1989). This suggests that most measures of fitness used in the studies analyzed here, such as juvenile survival and recruitment (see table 1),

should relate reasonably well to net fitness. The fact that the existing estimates of indirect selection were not significantly heterogeneous is also at odds with the concern that only some of the measures of offspring fitness relate well to net fitness. This said, we note that studies comparing the reproductive success of WPY and EPY half-sibs of both sexes are very rare. Although this is unsurprising, given the logistic problems involved with gathering such data, it is unfortunate in light of the possibility of sex-specific effects of paternal genes on the reproductive success of offspring (e.g., Chippindale et al. 2001).

The estimates of direct selection on female EPC behavior are perhaps more problematic. Although the estimate based on conventional across-brood comparisons must be interpreted with caution because of confounding selection on correlated characters (Kempnaers and Sheldon 1997; Wright 1998; Sheldon 2002), it is nevertheless interesting to note that the meta-analysis presented above revealed a general negative correlation between paternal care and rate of EPCs within populations. The estimate based on a comparison between repeated breedings of the same male/pair is more reliable (Dixon et al. 1994; Møller and Tegelström 1997; Peterson et al. 2001) and also showed a stronger negative direct selection. It should also be noted that several possible sources of direct selection on EPC behavior in females have been omitted here simply because of a lack of quantitative data. Some of these might reinforce negative direct selection (e.g., risk of infection with venereal disease or parasites, elevated predation risk), while others may reduce the net strength of direct selection (e.g., receipt of direct resources, elevated hatching rate of eggs; see Ligon 1999). Although we suggest that the true general strength of direct selection on EPC behavior is well approximated by the studies reporting data from repeated breedings of the same male/pair, we note that this conclusion rests on the assumption that a reduction of paternal care is a major source of direct selection in natural populations.

In sum, the estimate of indirect selection presented here should represent a fairly accurate quantification of the general force of indirect selection. Even the most reliable estimate of direct selection is probably less precise and may also be an incomplete representation of direct selection. It is, however, difficult to see how relatively minor adjustments of these estimates could alter the main conclusion drawn here, that indirect selection on EPC behavior in females is generally insignificant in comparison with direct selection. We note that empirical studies providing simultaneous and integrative measures of both indirect and direct selection in the same species and population are unfortunately lacking. Such studies would allow tests of the generality of our main conclusion.

If net selection on EPC behavior in females is indeed

negative, a general understanding of the evolutionary maintenance of EPCs must be sought elsewhere. Westneat and Stewart (2003) recently pointed out that the assumption that EPC behavior represents an adaptive female strategy is a dubious one, and they suggested that the conflicting fitness interests of other parties must be given increased attention. The evolutionary interests of males set up two conflicting forms of selection among males (see Parker 1984): to gain extrapair copulations and thus paternity with females other than their social mate (favoring “offensive” adaptations) and to prevent infidelity in their social mate (favoring “defensive” adaptations). In light of the analysis presented above, the only type of selection that generally favors EPCs seems to be selection for offensive adaptations in males. This implies that there should often be sexual conflict over female mating behavior, which in turn points to the possibility that EPCs may be the dynamic result of sexually antagonistic coevolution (e.g., Parker 1979; Rice 1996; Holland and Rice 1998; Gavrilets et al. 2001; Arnqvist and Rowe 2002, 2005; Chapman et al. 2003). Mutations expressed in males may be favored because they increase the relative success in gaining extrapair fertilizations but may at the same time depress the fitness of their mates by reducing the amount of paternal care these receive from their social males. These sexually antagonistic adaptations would then favor the expression of resistance alleles in females, which may in turn fortify selection for offensive adaptations in males. The data on the strength of selection in females presented here is congruent with but does not directly test this alternative hypothesis for the maintenance of EPCs in many species (see also Westneat and Stewart 2003). Available data suggest that there is indeed ample opportunity for selection on offensive adaptations among males; some 10%–60% of the total variance in male reproductive success has been attributed to success in gaining EPCs in different socially monogamous passerines (see Whittingham and Dunn 2005). According to the above scenario, male display traits and ornaments in socially monogamous passerines would then, at least in part, be the result of sexual selection generated by sexual conflict over mating decisions (see Gavrilets et al. 2001). Note that this does not in any way assume that overt coercion is involved in EPCs but rather that EPCs might result from a form of sexually antagonistic “seduction” (sensu Holland and Rice 1998).

The fact that the occurrence of EPY is so high in socially monogamous passerines (Griffith et al. 2002) despite an apparent net cost to females nevertheless begs for an explanation (Griffith and Montgomerie 2003). Observations of cases where females apparently foray for or otherwise seem to initiate EPCs may seem particularly intriguing in the light the analyses presented here. Such observations are, however, rather anecdotal in most cases (Westneat and

Stewart 2003), and it is very difficult to clarify the adaptive value of female visits outside the territory of her social mate (e.g., Neudorf et al. 1997, 2002). One general explanation is that females are in some way constrained from evolving resistance to EPCs such that EPCs might be the “best of a bad job” for females. Strong selection for offensive adaptations in males might then effectively override the relatively weak selection in females (as well as selection for defensive adaptations in males; Clutton-Brock and Parker 1995; Westneat and Stewart 2003). Such constraints may come into play if, for example, rejection of persistent extrapair suitors is costly in a direct sense (i.e., convenience polyandry; sensu Thornhill and Alcock 1983; McKinney and Evarts 1998) or if the evolution of a reduced copulatory response to male courtship signals, in more general terms, carries negative pleiotropic side effects (such as a lower within-pair copulation rate resulting in depressed egg hatching rate). For those who believe that females should be free to reach their optimal reproductive strategy unconstrained by genes expressed in other individuals (males in this case), the evolutionary success of nest parasites such as cowbirds and cuckoos illustrates the fact that very costly reproductive exploitation can indeed be persistent.

In conclusion, the analyses presented here strongly suggest that indirect genetic benefits to offspring are unlikely to provide a general explanation for the evolutionary maintenance of EPC behavior in socially monogamous passerines because such effects are very weak at most and are overwhelmed by negative direct selection. If and when indirect genetic benefits to offspring do occur, they may represent incidental side effects rather than provide the adaptive basis for this behavior. We suggest that EPCs primarily reflect antagonistic coevolution between offensive male adaptations to gain extrapair paternity on the one hand and resistance adaptations in females and defensive adaptations in males on the other. At the very least, this scenario offers a viable alternative hypothesis for the evolutionary origin and maintenance of EPCs (see also Westneat and Stewart 2003).

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APPENDIX

The Force of Indirect Selection

Here, we develop a method to estimate the force of indirect selection acting on a female's propensity to engage in extrapair copulations (EPCs). By “indirect selection,” we mean the force favoring change in the behavior caused by selection on genes that do not themselves contribute to variation in the behavior. A set of “fitness genes” that experience direct selection will cause the female behavior to evolve if they are statistically associated (in linkage disequilibrium) with the genes for that behavior. These genetic associations will develop naturally when a female's probability of mating a male is correlated with his genetic quality, that is, his additive genetic value for lifetime fitness (Fisher 1952; Kirkpatrick and Barton 1997). In the present context, this will happen if EPCs involve males whose average genetic quality differs from that of males involved in within-pair copulations (WPCs). Then, the propensity for a female to engage in EPCs will become genetically correlated with genes affecting lifetime fitness, causing that female behavior to experience indirect selection.

We define the force of indirect selection, denoted Δ_b , as the number of phenotypic standard deviations that the average value of the female mating behavior changes per generation. The behavior of interest here is the fraction of a female's offspring that is sired by EPCs, denoted F . Kirkpatrick and Barton (1997) show that when the loci affecting a female mating behavior and fitness are autosomal, the strength of indirect selection on that behavior is approximately

$$\Delta_b \approx \frac{1}{2} h_F^2 \rho_{FW} \sqrt{G_W} \quad (\text{A1})$$

where h_F^2 the heritability for the behavior (here, the frequency of EPCs), ρ_{FW} is the phenotypic correlation between a female's behavioral phenotype and the genetic quality (in terms of lifetime fitness) of her mate, and G_W is the additive genetic variance for lifetime fitness (which has been normalized to have a mean of 1). Although equation (A1) was originally derived from a haploid model, the results of Kirkpatrick et al. (2002, p. 1,743) imply that this equation also applies when the loci involved are diploid and autosomal. The derivation is based on approximations that assume the effects of individual loci on the preference and fitness are small and that the correlation ρ_{FW} is not too large (say, smaller than 0.4). The calculations further assume that the fitness genes have additive effects and that they are expressed the same in males and females. If either of these assumptions is violated, for example, if there is epistatic or dominance variance for fitness, then

the force of indirect selection is less than equation (A1) (Kirkpatrick and Barton 1997).

Our goal is to estimate Δ_I using the data collated, specifically the within-brood difference between the fitnesses of extrapair young (EPY) and within-pair young (WPY), which we denote d_{EW} . As discussed in the text, this difference is an attractive statistic because it controls for many of the confounding variables that contribute to differences between offspring fitness. To reach our goal, we first use the definitions of a correlation and a regression to rewrite equation (A1) as

$$\Delta_I \approx \frac{1}{2} h_F^2 \left(\frac{b_{WF} \sigma_F}{\sqrt{G_W}} \right) \sqrt{G_W} \quad (\text{A2})$$

where b_{WF} is the regression of the male's genetic component for fitness, W , on the female's behavioral phenotype, F , and σ_F is the phenotypic standard deviation of that behavior. Now assume that the genes contributing to additive genetic variance in fitness are autosomally inherited. Then, the covariance between a female's phenotype, F , and her mate's additive genetic value for fitness, W , is twice the covariance between F and W^* , the genetic component of fitness that her offspring inherit from that male. Consequently, the value of the regression coefficient b_{WF} is twice that of the regression coefficient b_{W^*F} . Last, the regression coefficient b_{W^*F} is equal to the difference in fitnesses between EPY and WPY from within the same brood, d_{EW} . Putting these facts together gives

$$\Delta_I \approx h_F^2 \sigma_F d_{EW} \quad (\text{A3})$$

This expression is intuitively reasonable. With no heritability or no phenotypic variation between females in the propensity for EPC ($h_F^2 = 0$ or $\sigma_F = 0$), then behavior cannot evolve by any form of selection. If there is no difference between the fitness of EPY and WPY ($d_{EW} = 0$), then no indirect selection is generated.

We know of no estimates for h_F^2 , but note that in any case a heritability cannot have a value greater than 1. Similarly, we can put an upper limit on σ_F , the between-female standard deviation in the fraction of offspring sired by EPC. This quantity is maximized when either none or all of a female's offspring are from EPC. In that case $\sigma_F = [\bar{F}(1 - \bar{F})]^{1/2}$, where \bar{F} is the average frequency of EPC in the population.

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