Behav Ecol Sociobiol (2008) 62:1795–1804
DOI 10.1007/s00265-008-0608-2

ORIGINAL PAPER

# Current analyses do not resolve whether extra-pair paternity is male or female driven

**Sigrunn Eliassen · Hanna Kokko**

Received: 24 January 2008 / Revised: 17 April 2008 / Accepted: 22 April 2008 / Published online: 5 June 2008

**Abstract** Recent studies question the importance of indirect genetic effects in explaining female benefits of extra-pair matings in socially monogamous species. Compiling data on 14 wild bird species, Arnqvist and Kirkpatrick (Am Nat 165:S26–S37, 2005) estimated the average direct cost in terms or reduced parental care to be an order of magnitude larger than the potential effect of genetic benefits. This study has sparked a debate regarding potential confounding factors but no consensus appears to have been reached. Here we focus on the implicit assumption that all individuals face the same selective pressures and argue that this assumption is probably too strong in most cases. Using a theoretical model we show that when the amount of resources that a male provides depends on territory quality, his physical condition or prospects for alternative breeding opportunities, a female may respond to such differences by altering her mating behaviour. Such confounding factors may lead to direct fitness effects that result in negative correlations between paternal care and paternity even if females that produce extra-pair young experience a net benefit. Negative correlations can also result when males forcefully seek copulations and females resist them. We discuss the studies included in the analysis in this light, and conclude that current analyses on the net selective pressures remain uninformative. In addition to considering average effects across individuals and species we suggest giving attention to individual differences and the influence of ecological factors such as territory quality and predation pressures on female mating behaviour.

**Keywords** Extra-pair paternity · Parental care · Mate choice · Sexual selection

## Introduction

Extra-pair paternity is common in many bird species (Griffith et al. 2002), but it is currently debated whether extra-pair mating is primarily driven by male or female interests. For males, attaining additional fertilisations is obviously beneficial, but the benefits to females are less clear. The favoured explanation has been that females gain indirect genetic benefits by mating with males that sire offspring of higher reproductive value than offspring sired by their social mate (Jennions and Petrie 2000). Recent studies that quantify the importance of these indirect benefits in birds, however, suggest that female extra-pair behaviours cannot be explained by genetic benefits alone (Arnqvist and Kirkpatrick 2005; Hadfield et al. 2006; Qvarnström et al. 2006; Akçay and Roughgarden 2007). In some systems females may receive material benefits from extra-pair mates (Gray 1997; Blomqvist 2005) but such direct benefits seem to be rare in most bird species (Jennions and Petrie 2000). An alternative explanation is that extra-pair matings are not adaptive for females, and

Communicated by S. Pruett-Jones

S. Eliassen (✉)
Department of Biology, University of Bergen,
P.O. Box 7803, 5020 Bergen, Norway
e-mail: Sigrunn.Eliassen@bio.uib.no

H. Kokko
Laboratory of Ecological and Evolutionary Dynamics,
Department of Biological and Environmental Science,
University of Helsinki,
Helsinki, Finland

H. Kokko
School of Botany and Zoology, Australian National University,
Canberra, Australia

occur as a result of males enforcing copulations or 'seducing' females despite this being harmful for female fitness (Westneat and Stewart 2003; Arnqvist and Kirkpatrick 2005).

Although males generally benefit from attaining extra-pair copulations (EPCs), they have a strong incentive to protect their own brood against cuckoldry. Caring for offspring inflicts opportunity costs, for instance by reducing breeding opportunities or survival. Whenever paternity varies across breeding attempts, males may therefore adjust their parental investment accordingly (reviewed in Houston and McNamara 2002). As a consequence, females that engage in extra-pair matings may experience a direct cost due to reduced parental care from their social mate.

In a comparative analysis of 14 wild bird species Arnqvist and Kirkpatrick (2005) [hereafter A&K] estimated the magnitude of such direct fitness costs to unfaithful females using two approaches. In the majority of studies, A&K correlated relative investment in parental care of the social male, i.e. [male care]/[male + female care], to numbers of extra-pair young (EPY) in his nest. For each study they obtained a regression line with a slope $\beta_F$, which they used as a measure of the selection gradient on female EPC propensity in a given study population. In three other species (four studies) the authors correlated paternal investment in consecutive breeding attempts of the same pair in which the level of EPY varied between the first and second brood. Based on their first approach, they concluded that the direct cost of lost paternal care is approximately ten times higher than the indirect fitness benefit to extra-pair young.

It has been repeatedly argued that facultative relationships cannot be tested by measuring correlations between paternity and paternal care across individuals in a population (as in A&K's first approach) (Kempenaers and Sheldon 1997; Sheldon 2002; Griffith 2007). In his comment to A&K, Griffith (2007) argued that the "correlations in these studies may result from confounding effects such as variation in territory quality or attractiveness among pairs". In their reply, Arnqvist and Kirkpatrick (2007) do not address this issue, although in their original contribution they acknowledge that their across-brood comparisons could be confounded by "causal variables that co-vary in complex ways with both male parental care and the rate of EPCs of his mate" (A&K p. S31). A&K argued that since their estimate of direct cost was so much larger than that of indirect benefits, minor corrections would not affect their general conclusions (A&K p. S33). In a recent study, Albrecht et al. (2006) correlated the selection gradients from A&K with species-specific extra-pair paternity (EPP) levels, concluding that the cost to females from reduced paternal care constrains promiscuity in passerine species. The use of such among-individual correlations in several studies to estimate facultative responses to infidelity motivates a thorough investigation of how correlated factors might confound these relationships and to what extent this would alter the overall conclusions.

Frequencies of EPP varies extensively, both between individuals in the same population and across species (Petrie and Kempenaers 1998; Griffith et al. 2002). Determining whether EPP is randomly distributed across broods presents researchers with considerable statistical challenges. Brommer et al. (2007) showed that for two of seven species this was not the case, while the remaining five could, in principle, be explained by a null model in which the number of EPCs varied in a random fashion among females. On the other hand, many studies (Brommer et al. 2007 included) have not tested whether the inclusion of specific explanatory variables could resolve the data. Performing such an exercise for superb starlings, *Lamprotornis superbus*, revealed that the level of EPP in a brood was negatively correlated with territory quality (Rubenstein 2007).

As long as we have no clear consensus about whether, and how often, females differ consistently in behaviour that causes variation in EPP (see Jennions and Petrie 1997), we must ask if it is appropriate to pool selective pressures comparing mean indirect effects against mean direct effects of a trait. Most studies relating investment in paternal care to extra-pair offspring production focus on male responses to perceived levels of paternity (Houston and McNamara 2002). We will here focus on possible causes of variation in female responses to extra-pair opportunities (or pressures), and examine what kind of comparisons should be performed if females *do* differ.

## The effect of differences in territory quality

Before considering parental care (which was analysed by A&K), it is illustrative to tackle a simpler situation to highlight why non-identical female behaviour can be important. Consider a situation where males differ in the direct and indirect benefits they offer to females. The amount of direct benefits depends on investment in parental care and the quality of the territory that the mate possesses. For simplicity, assume the subscript 'R' denotes territories rich in resources, and the lowercase 'r' denotes resource-poor territories.

To make a conceptual point it is likewise simplest to assume that a fraction of 'high quality' males offer superior genetic benefits compared with the rest ('low quality' males). While this is an obvious simplification, a more realistic model with continuous variation in territory and male qualities would add other uncertain and unmeasured terms (the precise distribution of males of particular quality on specific territories), without adding to the conceptual point.

We do not make any a priori assumptions about the magnitude of direct and indirect benefits (our model also investigates the possibility that they are zero). In our first model, we assume that the indirect benefit gained from a high quality sire ($b_G$) is equal for all females in the population ("good-gene" effects). It is also possible that indirect benefits gained by mating with different males are specific to each female, and recent work suggests that such benefit may potentially be larger than "good genes" effects (Kempenaers 2007). Much of what follows apply to compatibility effects as well, but since this would complicate the analysis somewhat we follow the traditional line of argument with an emphasis on good genes.

We consider the possibility that the amount of genetic and material benefits that a male offers can be positively correlated. For instance in migratory birds arrival time on a breeding ground is typically condition-dependent (Marra et al. 1998; Kokko 1999a; Møller 2001) and similar difficulties in disentangling mate and territory quality arise in non-migratory species (e.g. Gill and Stutchbury 2006). We can investigate covariation between male and territory quality by defining $k$, the proportion of high-quality males that reside in resource-rich territories. If we assume, for simplicity, that 50% of males are of high quality, and likewise 50% of territories are resource-rich, a proportion $1–k$ of low-quality males also resides in resource-rich territories. If $k$=1, ownership of a rich territory is a perfect indicator of a high quality male; lower values imply less clear relationships, $k$=0.5 implies no correlation between male and territory quality, and if $k$<0.5 low quality males reside in rich territories more often than high quality males do (an unlikely scenario, given condition-dependence, but the model allows considering this scenario too).

We assume that a female obtains a baseline fitness $b_0$ if she is paired to a male of low genetic quality that resides in a resource-poor territory and gives no paternal care. The baseline fitness can, without loss of generality, be set to equal zero. Female fitness can be improved if she receives the benefit of care from her social mate ($b_C$) and if she resides in a rich territory ($b_T$). The amount of indirect benefits a female receives reach its maximum value $b_G$ if all offspring are sired by a high-quality male.

This allows us to establish simple rules for female behaviour in response to costs and benefits associated with their mating situation. Our analysis hence examines the implicit assumption made by A&K that all females find themselves in essentially the same situation, but does not challenge some other assumptions: that production of offspring is proportional to the level of parental care, or that females do not significantly compensate for reduced paternal investment (but see the Discussion). Throughout, we ignore complications such as unequal sex ratio and thus assume that all females have a social mate. In our first model, we assume that male care only varies as a response to female EPC behaviour, and we ignore complications of correlations with territory or male quality.

### *Optimal female behaviour if paired to a high quality male*

Under our assumptions a proportion of females are paired to high-quality males (50% in our examples). We assume that a female who seeks EPCs is, in a probabilistic way, punished by her social mate and receives a direct benefit from parenting that equals $(1–p)b_C$, compared with $b_C$ if she does not seek EPCs. For simplicity, we let the parameter $p$ reflect both the probability that extra-pair behaviour is detected and the severity of punishment. In effect, we assume that a 10% detection probability of unfaithful female behaviour, together with a consequence of no paternal care, amounts to the same selective pressure as a 10% reduction in care if social mates recognise all extra-pair seeking females. This assumption could be challenged and modified in future work, but the current form best reflects A&K's assumption that offspring fitness is linearly related to care.

If a female paired to a high-quality male does *not* seek EPCs (and we also assume she is able to resist any attempts from the outside), her fitness equals

$$kb_T + b_C + b_G \tag{1}$$

Here the first term indicates that with probability $k$ she resides on a resource-rich territory, the second term reflects that she is not punished and fully benefits through care by her social mate, and the third term indicates that she enjoys indirect benefits because her social mate is of high genetic quality. The magnitude of each benefit can vary from case to case, and the model also applies if some benefits are absent.

If she does seek EPCs, her fitness will be reduced by $pb_C$ as her mate withdraws some paternal care in response to infidelity:

$$kb_T + (1-p)b_C + b_G \tag{2}$$

It is clear that for any non-zero cost of extra-pair activities ($p$>0), seeking EPC's is never optimal for females paired to high-quality males.

### *Optimal female behaviour if paired to a poor quality male*

Female fitness is derived similarly when paired to a poor quality male. With a probability $1–k$ a female will have the benefit of residing in a resource-rich territory and if she does *not* seek extra-pair copulations fitness equals

$$(1-k)b_T + b_C \tag{3}$$

When the female seeks EPCs, we assume that a proportion $a$ of the offspring is sired by high quality males. Female fitness then equals

$$(1-k)b_T + (1-p)b_C + ab_G \tag{4}$$

In other words, females paired to low quality males would be expected to seek EPCs when the indirect benefits gained from extra-pair mates are higher than the direct benefits lost due to reduced parenting by the social male ($ab_{\mathrm{G}} > pb_{\mathrm{C}}$).

*Seeking EPCs can be adaptive even if pooled data suggest that direct costs exceed indirect benefits*

When indirect benefits outweigh the cost of reduced male care, seeking EPCs is adaptive for females paired to low quality males, but not for females paired to high quality males. This is consistent with data showing that females with higher extra-pair paternity have reduced breeding success. To show this, we will make the assumption $ab_{\mathrm{G}} > pb_{\mathrm{C}}$, which predicts that females paired to poor quality males seek EPCs, and ask what is the predicted breeding success of females with and without extra-pair young. Females who do not have EPY in their broods are those paired to high quality males, and according to eq. (1) their fitness is on average

$$kb_T + b_C + b_G$$

Females who do have EPY are those paired to low quality males, and according to eq. (4) their fitness is on average

$$(1-k)b_T + (1-p)b_C + ab_G$$

Having EPY will appear to reduce female fitness, if females paired to high quality males have higher fitness than males paired to low quality males, more precisely if

$$kb_T + b_C + b_G > (1-k)b_T + (1-p)b_C + ab_G \tag{5}$$

From this relationship we obtain the condition for which EPY and fitness will be negatively correlated

$$pb_C > (1-2k)b_T - (1-a)b_G \tag{6}$$

This condition is *always* fulfilled as long as male genetic quality is positively correlated with territory quality ($k$>0.5) and territory quality has at least some positive effect on offspring production ($b_{\mathrm{T}}$>0). This means that even when males do not reduce paternal care in response to infidelity ($p$=0), females with EPY have lower fitness than females without. The more tightly territory quality is linked to male genetic quality (higher $k$), the stronger the correlation between faithfulness and fitness. In socially monogamous, territorial species, $b_{\mathrm{T}}$ is probably large compared with genetic benefits $b_{\mathrm{G}}$. This means that analyses that compare female fitness across all territory qualities can be severely confounded even if the correlation between male and territory quality remains modest.

## The effect of differences in paternal care

Our above example was a simplistic warning against pooling data across broods. The approach taken by A&K is more sophisticated, but at the same time less direct. In their first approach A&K considered the proportion of care provided by males, and concluded that broods with EPY received less male care. They interpret this as a causal link between female behaviour and level of paternal care, but this requires that several factors are considered unimportant: e.g. that the amount of care provided by a male is not influenced by his physical condition or territory quality (Kempenaers and Sheldon 1997).

We now extend our above model to encompass the possibility that care varies with male quality as well as with territory quality. We denote care or punishment given by high (or low) quality males with the subscript H (or L). Territories are indicated with subscripts R and r, resource-rich and resource-poor, respectively.

This flexibility makes the fitness expressions somewhat more complicated, but the general logic is as before. Females mated with high quality males gain fitness

when not seeking EPCs :

$$kb_{\mathrm{T}} + (kb_{\mathrm{CHR}} + (1-k)b_{\mathrm{CHr}}) + b_{\mathrm{G}} \tag{7a}$$

when seeking EPCs :

$$kb_{\mathrm{T}} + (1-p_{\mathrm{H}})(kb_{\mathrm{CHR}} + (1-k)\mathrm{b}_{\mathrm{CHr}}) + b_G \tag{7b}$$

Again, females should be faithful to their high quality mates for any non-zero levels of punishment ($p_{\mathrm{H}}$>0). For females mated with low quality males the expressions are

when not seeking EPCs :

$$(1-k)b_T + [(1-k)b_{\mathrm{CLR}} + kb_{\mathrm{CLr}}] \tag{8a}$$

when seeking EPCs :

$$(1-k)b_{\mathrm{T}} + (1-p_{\mathrm{L}})[(1-k)b_{\mathrm{CLR}} + kb_{\mathrm{CLr}}] + ab_G \tag{8b}$$

These females benefit from seeking EPCs if

$$ab_{\mathrm{G}} > p_L((1-k)b_{\mathrm{CLR}} + kb_{\mathrm{CLr}}) \tag{9}$$

Thus, as expected, females benefit if the punishment by low quality males is rare or of little significance (low $p_{\mathrm{L}}$) or, alternatively, if parental care offered by low quality males is limited to begin with (low $b_{\mathrm{CL}}$).

Again, we can determine whether data with a negative relationship between EPC and male care can arise even if extra-pair behaviour is adaptive for some females. If eq. (9) holds, and we compare care by males whose females are faithful with those whose females are not, then averaged across territories, we obtain values for care provided by males whose mate are

$$\text{faithful :} \qquad kb_{\mathrm{CHR}} + (1-k)b_{\mathrm{CHr}} \tag{10a}$$

$$\text{unfaithful :} \qquad (1-p_{\mathrm{L}})((1-k)b_{\mathrm{CLR}} + kb_{\mathrm{CLr}}) \tag{10b}$$

Consequently, even if there is only an insignificant male response to female infidelity ($p_{\mathrm{L}} \approx 0$) we may still observe that males of unfaithful females provide less care. This happens if there is a positive correlation between territory quality and male provisioning *and* males of high genetic quality more often reside in resource-rich territories ($k > 0.5$). Likewise, under a scenario where ornaments reflect both high parental investment and genetic quality, we expect female EPC behaviour to be negatively correlated with the level of paternal care. If, on the other hand, males of low genetic quality provide more care, the observed correlation will be only weakly negative, or it can become positive.

## Making the best of a bad job

We have thus far pointed out that EPCs may entail a net benefit to some females in the population despite a negative correlation between care and proportion of extra-pair young. More specifically, we have assumed that indirect genetic benefits can outweigh the potential cost of reduced paternal investment in care at the nest. As indicated by A&K's meta-analysis, indirect genetic benefits tend to be small or absent. If males do *not* significantly differ in the genetic benefits they provide to their offspring, we can set $\mathrm{b_G} \approx 0$. As long as extra-pair matings provide no direct benefits, females may strive to resist copulations enforced by males. Assume that females can reject mating attempts at a cost *c*. As before, the level of paternal care depends on a male's physical condition and the quality of his territory. Females paired to males in high condition (H) gain fitness

when resisting EPCs :

$$kb_{\mathrm{T}} + kb_{\mathrm{CHR}} + (1-k)\mathrm{b}_{\mathrm{CHr}} - c \tag{11a}$$

when accepting EPCs :

$$kb_{\mathrm{T}} + (1-p_{\mathrm{H}})(kb_{\mathrm{CHR}} + (1-k)\mathrm{b}_{\mathrm{CHr}}) \tag{11b}$$

Females should consequently accept EPCs when the cost of resisting is higher than the cost associated with reduced paternal care:

$$c > p_{\mathrm{H}}(kb_{\mathrm{CHR}} + (1-k)\mathrm{b}_{\mathrm{CHr}}) \tag{12}$$

We obtain a similar condition for females paired with low condition males (L):

$$c > p_{\mathrm{L}}((1-k)b_{\mathrm{CLR}} + kb_{\mathrm{CLr}}) \tag{13}$$

Whenever EPC reduces paternal care ($p_{\mathrm{L}} = p_{\mathrm{H}} > 0$), females paired to males providing more care are expected to resist EPC attempt more vigorously than females paired to males that contribute less. Males in high condition may provide more care, either because they more often reside in resource-rich territories ($k < 0.5$) or they themselves have more resources to invest in parental care (these two causal routes of course are tightly linked). We consequently expect unequal female behaviours whenever $p_{\mathrm{H}}$ $(kb_{\mathrm{CHR}} + (1\text{–}k)$ $b_{\mathrm{CHs}}) > c > p_{\mathrm{L}}((1\text{–}k)b_{\mathrm{CLR}} + kb_{\mathrm{CLs}})$. The reversed inequality is true if males provide more care when in low condition. Thus, unfaithful females may have mates that provide either more or less paternal care, and this can be largely driven by males' responses to local resources and their own condition. The observed effect, pooling over all broods, is due to condition-dependent paternal care and facultative punishment of EPC females.

Unequal female behaviours are especially likely if facultative responses to infidelity differ between males ($p_{\mathrm{L}} \neq p_{\mathrm{H}}$). We expect such differences if males vary in their mate-guarding efficiency or experience different opportunity costs. If low condition males have less success in attaining EPCs or lower future mating prospects, they may not alter their paternal care much in response to lost paternity ($p_{\mathrm{L}} \approx 0$). Females paired to low condition males may therefore more readily accept EPCs if there are costs of resisting (note that in this section we assume that costs may vary across females while indirect benefits are negligible). If high condition males reduce paternal investment more in response to infidelity ($p_{\mathrm{H}} > 0$), females paired to these males face higher costs. In essence, the larger the potential reduction in paternal care, the more vigorously the female is expected to resist EPC attempts. Under these conditions, pooling data on EPP levels across all females may only reveal differences in care related to male condition and territory quality. Offspring of faithful females may receive more paternal care, even when females having EPY are not punished by their social mate.

## Discussion

Obtaining unbiased estimates of selection acting on male and female extra-pair mating behaviours is not trivial (Kempenaers and Sheldon 1997; Sheldon 2002; Charmantier and Sheldon 2006; Griffith 2007). Our modelling focuses on the plausible assumption that females in a breeding population face different trade-offs: costs as well as benefits offered by the social mate can vary. We show that, when EPCs result from females seeking genetic benefits or, alternatively, are a way to reduce costs of male harassment, the correlation between paternal care and number of EPY can be either positive or negative. The sign depends on facultative responses to cuckoldry and differences in other factors that vary across breeding pairs and correlate with parental care.

Many of these points have been discussed before (Kempenaers and Sheldon 1997; Sheldon 2002; Griffith 2007), but no consensus appears to have emerged regarding how serious these caveats are. Below we give reasons why we believe these factors indeed seriously undermine our current ability to decide whether extra-pair paternity is male or female driven.

## Paternity and parental effort

The basic assumption that males should reduce the level of care in response to a perceived loss of paternity, has been much debated (e.g. Westneat and Sherman 1993; Kokko 1999b; Schwagmeyer 1999; Sheldon 2002; Houston et al. 2005; Griffith 2007). Theoretical models predict that males should only adjust care if paternity varies across breeding attempts and can be readily assessed (reviewed in Houston and McNamara 2002; but see Holen and Johnstone 2007). Our model consequently includes the possibility that males 'punish' unfaithful females, and if the punishment is sufficiently strong this selects against females seeking extra-pair copulations.

From an empirical point of view, it has been questioned whether males can discriminate between own and extra-pair young (Kempenaers and Sheldon 1996). Alternatively, males may use female behaviour during the fertile period to predict overall paternity levels (Sheldon 2002). Obtaining reliable information on a female's whereabouts may inflict large opportunity costs but, despite the potential importance of such costs, they have yet to be included in models of male responses to cuckoldry.

Only a few studies have experimentally manipulated information on paternity status. The one that was included in the A&K analysis (Dickinson 2003) did not support facultative punishment. In this study young males fed offspring less often than older males, and females paired to young males were more likely to accept EPCs than those paired with older males (Dickinson 2001). The correlation between EPY and low male care, upon which the selection gradient by A&K was based, may therefore reflect differences between male age classes in male care (Dickinson 2003) rather than causal punishment of female infidelity.

## Observations and experiments

While our model shows that one can obtain spuriously negative estimates of direct selection against EPY from observational data, the severity of this effect depends on the potential link between male attractiveness, care and territory quality. The estimates obtained by A&K for the direct selection against EPC behaviour are strongly negative, and are supported by an additional set of analyses on repeated breeding attempts. One might therefore argue that the comparison between direct and indirect selection estimates remains relatively robust even if negative values for direct selection are to some extent expected under adaptive EPC-seeking scenarios. Unfortunately, it is not possible to evaluate this claim in a quantitative manner as long as mate and territory quality correlations remain unknown. However, as a first step in this direction, it is worth evaluating how robust the selection estimates themselves are, both in the first and second set of analyses.

Eight of the 12 studies included in A&K's first analysis reported no relationship between paternity and care. For five of these species, the relatively low selection gradient estimated in the A&K analysis largely agreed with the conclusion of the original studies (Lifjeld et al. 1993; Stutchbury et al. 1994; Westneat 1995; Whittingham and Lifjeld 1995; Yezerinac et al. 1996). In the remaining three (Smith and Montgomerie 1992; Wagner et al. 1996; Dickinson 2003), there is a discrepancy between strong negative selection gradients obtained by A&K and the conclusions of the original studies. There are several potential causes behind this pattern. Firstly, there is a fully legitimate difference between the conclusions drawn from an individual study and a meta-analysis. The former type of study must base its inferences on a single dataset, whereas the latter type can include non-significant effect sizes from several studies to reach a more general conclusion. However, this is not the sole source of discrepancies. There is also variation in decisions to correct for age (applies to Dickinson 2003 and Wagner et al. 1996), and data of some studies clearly violate the assumption made by A&K of 50% average male contribution in care (9% in Smith and Montgomerie 1992; 16–23% in Wagner et al. 1996). If male care is less important to start with, any selection based on reduction of it will be correspondingly weakened.

The relevance of the four observational studies (Burke et al. 1989; Lubjuhn et al. 1993; Hartley et al. 1995; Chuang-Dobbs et al. 2001) that report significant relationships between EPY numbers and paternal care in A&K's first analysis should be evaluated taking the following considerations into account. The title of A&K suggests a focus on socially monogamous birds, yet the dunnock and alpine accentor (Burke et al. 1989; Hartley et al. 1995) do not belong to this category. They commonly breed in groups where males contribute care in proportion to their access to females. Even though per capita contribution of each male resembles punishment (care declines with paternity), multiple mating is easily explained by direct benefits to females (Burke et al. 1989; Davies 1992; Hartley et al. 1995). For the black-throated blue warbler (Chuang-Dobbs et al. 2001), a significant correlation between paternity and parental effort was only reported for old males on one out of 3 days for which offspring feeding rate was measured. The analysis of A&K appears to have included only this subset of data, without explaining why the opposite approach of pooling data across age classes was used for the other studies (see above). In the great tit study (Lubjuhn et al. 1993), male willingness to approach and remain close to an experimentally presented predator (a stuffed owl) was the measure of male paternal effort. Whether differences in this trait represent adjustment of care to paternity levels or a possible link between male boldness and the ability to defend paternity is open for debate. Finally, it is difficult to evaluate whether all relevant studies were included as A&K did not make an explicit statement about the search criteria they applied (see Pullin and Stewart 2006).

The problems of spurious correlations across breeding pairs are considerably diminished in studies that compare parental allocation between breeding attempts of the same individuals (as in the second approach of A&K) (Sheldon 2002). In these studies variation in territory and male quality is of minor importance relative to variation between all mated pairs in the population. However, some of the caveats discussed still apply: parental investment patterns are expected to respond to future opportunities which could change between breeding attempts (for examples see Magrath and Komdeur 2003; Rowe and Weatherhead 2007).

Correlations between paternity and level of paternal care may also have the reversed causality. This has been suggested for Savannah sparrows, *Passerculus sandwichensis*, in which males that provided more care in the first brood achieve greater paternity in their next (Freeman-Gallant 1996). In the American robins *Turdus migratorius*, males providing much care allowed females to re-nest sooner, and the time between successive breeding attempts was positively correlated with the proportion of extra-pair young in the second brood (Rowe and Weatherhead 2007). In other words, parental care may function as mating effort (Kvarnemo 2006), maintained because female respond to poorly providing males by reducing fidelity in subsequent broods (Freeman-Gallant 1996) or by divorcing such males (Dickinson 2003).

When both males and females can adjust their behaviour, investment by one parent often influences the care decision of the other (Houston and McNamara 2002). The analysis of A&K, based on *relative* care provided by males, is therefore sensitive to adjustment both in male and female behaviours. Females (or males) whose social mate is attractive may invest more in their offspring (Burley 1986, 1988) and similar adjustments may be expected from females having EPYs sired by attractive extra-pair mates (Sheldon 2000). For example, in Møller and Tegelstrom (1997), one of four studies included in the second analysis of A&K, fathers of broods with or without EPY fed their offspring at an equal rate (means 4.31±0.72 and 4.29±0.51, $P=0.98$), but females increased, though not significantly feeding rates in the latter case (from 4.71±0.61 to 6.43±0.74, $P=0.08$). Assuming that the effect sizes reflect true differences, higher maternal investment in conditions that lead to high fidelity appears a more parsimonious interpretation of this pattern than male punishment.

## Male attractiveness

A key result from our models is that we need more data on how male attractiveness relates to the amount of paternal care provided by each sex. Currently, some studies support the positive correlation predicted by the “good parent hypothesis” (Hoelzer 1989), that ornaments signal provision of parental care (Linville et al. 1998; Buchanan and Catchpole 2000; Hill 1991; Krebs et al. 2004), whereas others find no such relationships (Smiseth et al. 2001; Hadfield et al. 2006; Nakagawa et al. 2007). In yet other species, less attractive males provide more care than attractive ones (Qvarnström 1997; Mitchell et al. 2007). Such across-species variation is predicted by theory (Kokko 1998), and it may indicate a trade-off between success in seeking alternative mating opportunities (EPCs) and caring for young at the nest (“trade-off hypothesis” Magrath and Komdeur 2003) or be a result of differential allocation (Burley 1988).

In our modelling we have assumed that the indirect benefit of mating with an attractive male is equal for all females. There are many reasons why this might not be the case, for instance if indirect effects are related to levels of genetic compatibility between mates (Jennions and Petrie 1997; Kempenaers 2007). The fact that our model also ignores all forms of among-female differences other than responses to the male they are paired to could be seen as an undesirable feature, but it is one that only highlights the possibility of additional confounding factors of uncertain magnitude (e.g. paternal investment might depend on female phenotype, not only her extra-pair behaviour).

Finally, it should be noted that the measures of indirect selection in A&K used components of fitness that were available, typically one proxy for fitness (such as fledgling condition or egg to fledgling survival) but including one welcome case of lifetime offspring production. The magnitude as well as the sign of the indirect benefit is known to depend on the trait being measured and it can be sex-specific (e.g. Fedorka and Mousseau 2004; Oneal et al. 2007). For example, the mating success of male offspring is very rarely reported despite the crucial importance of this trait in models of indirect selection (Head et al. 2005; Kokko et al. 2006; Rundle et al. 2007; Taylor et al. 2007).

### Statistical inference within and across species

The basis of any scientific analysis is a quest to find generalities, instead of seeking idiosyncratic explanations for each data point. However, our analysis also shows that statistical expectations of the behaviour of pooled datasets can change systematically when individual variation is taken into account. Notably, there can be a change from no expected correlation between EPY and female fitness under no genetic benefits (an implicit assumption of many studies) to a negative expected correlation when there *are* genetic benefits.

If treating individual variation as statistical noise can mislead in within-species comparisons, could similar issues arise in analyses that pool data across species (the approach taken by A&K and many others)? Looking for generalities in this context means using the null assumption that all species are under similar selective pressures. However, employing this principle should not prevent further analysis where true differences between species may exist. In the slightly different context of cooperatively breeding birds, Cockburn (2004) identified 23 distinct mating systems. Each of these created different constraints for the individuals, which lead to surprisingly idiosyncratic selective pressures, including variations in extra-pair behaviour.

A recent review on the importance of indirect genetic effects in explaining extra-pair behaviour in birds (Akçay and Roughgarden 2007) reaches a similar conclusion to that of A&K, but discusses the point of pooling studies in more detail. These authors note that when a considerable proportion of studies support a hypothesis and a likewise large proportion of studies fail to do so, a conservative option is to state that no conclusions can be made. Nevertheless, after some statistical considerations these authors cautiously favour the interpretation that data overall do not support the good genes hypothesis. We appreciate their open discussion of statistical inference in this context, yet variations in female circumstances and the associated costs and benefits of EPC could be a biological reality *across* species as well as *within*.

To provide an analogy: some birds migrate and others do not and it is pointless to answer the question “is migration adaptive?” for instance by providing average selection pressures in partial migrants, or by estimating the survival of normally migratory individuals in cases where they fail to depart their breeding grounds. Genetic benefits of extra-pair paternity provide a considerably more subtle question but here, too, there are many theoretical reasons why the adaptive expectation can vary between species. The strength of indirect selection may vary depending on life history and pattern of gene flow from one environment to another. To mention just one example, genotype-by-environment interactions (GEI) can help to maintain genetic variation and select for female choice, while a simple change in a species’ life history (relative timing of dispersal) can make the very same GEI strongly detrimental for any prospects of female choice (Kokko and Heubel 2008 and references therein). The direct benefits offered by different males, and the environmental characteristic determining the importance of male contribution to offspring fitness, are probably even more likely to vary among species. If producing EPY is detrimental for a female in one species (or in one period/environment) and beneficial in another, we need a stronger focus on the ecological conditions and mating constraints causing such differences. Searching for ecological or other correlates that covary with the effect size may hence be a more fruitful approach in these cases (e.g. Jennions et al. 2001; West and Sheldon 2002).

## Conclusions

The A&K approach, despite its limitations, is a healthy reminder that costs of mate choice or multiple mating should never be ignored in the quest to finding potential benefits (see also Kokko et al. 2006). Our modelling indicates that if female EPC behaviour elicits strong male retaliation, a negative correlation between paternal care and paternity is indeed likely. The reverse causality is, however, much harder to establish. Comparisons across broods will be fundamentally confounded by differences in e.g. territory quality, and this effect can be large simply because territory quality can have a substantial direct effect on fitness. Observational data on paternity distribution may, however, point to correlations worth emphasising, such as the link between EPC behaviour and territory quality (Rubenstein 2007). The possibility of very species-specific patterns remains real (Cockburn 2004), and we believe that the many caveats we have discussed make broad generalisations premature at this stage.

**Acknowledgements** We thank Göran Arnqvist, Oren Hasson, Michael Jennions, Bart Kempenaers, Naomi Langmore, Dustin Rubenstein and two anonymous reviewers for their many very helpful comments and suggestions. Funding was provided by the Academy of Finland (HK) and the University of Bergen (SE).

## References

Akçay E, Roughgarden J (2007) Extra-pair paternity in birds: review of the genetic benefits. Evol Ecol Res 9:855–868

Albrecht T, Kreisinger J, Pialek J (2006) The strength of direct selection against female promiscuity is associated with rates of extrapair fertilizations in socially monogamous songbirds. Am Nat 167:739–744

Arnqvist G, Kirkpatrick M (2005) The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behaviour in females. Am Nat 165:S26–S37

Arnqvist G, Kirkpatrick M (2007) The evolution of infidelity in socially monogamous passerines revisited: a reply to Griffith. Am Nat 169:282–283

Blomqvist DD (2005) High frequency of extra-pair fertilisations in the moustached warbler, a songbird with a variable breeding system. Behaviour 142:1133–1148

Brommer JE, Korsten P, Bouwman KM, Berg ML, Komdeur J (2007) Is extrapair mating random? On the probability distribution of extrapair young in avian broods. Behav Ecol 18:895–904

Buchanan KL, Catchpole CK (2000) Song as an indicator of male parental effort in the sedge warbler. Proc R Soc Lond B 267:321–326

Burke T, Davies NB, Bruford MW, Hatchwell BJ (1989) Parental care and mating-behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. Nature 338:249–251

Burley N (1986) Sexual selection for aesthetic traits in species with biparental care. Am Nat 127:415–445

Burley N (1988) The differential-allocation hypothesis—an experimental test. Am Nat 132:611–628

Charmantier A, Sheldon BC (2006) Testing genetic models of mate choice evolution in the wild. Trends Ecol Evol 21:417–419

Chuang-Dobbs HC, Webster MS, Holmes RT (2001) Paternity and parental care in the black-throated blue warbler, *Dendroica caerulescens*. Anim Behav 62:83–92

Cockburn A (2004) Mating systems and sexual conflict. In: Koenig WD, Dickinson J (eds) Ecology and Evolution of cooperative breeding in birds. Cambridge University Press, Cambridge, pp 81–101

Davies NB (1992) Dunnock behaviour and social evolution. Oxford University Press, Oxford

Dickinson JL (2001) Extrapair copulations in western bluebirds (*Sialia mexicana*): female receptivity favors older males. Behav Ecol Sociobiol 50:423–429

Dickinson JL (2003) Male share of provisioning is not influenced by actual or apparent loss of paternity in western bluebirds. Behav Ecol 14:360–366

Fedorka KM, Mousseau TA (2004) Female mating bias results in conflicting sex-specific offspring fitness. Nature 429:65–67

Freeman-Gallant CR (1996) DNA fingerprinting reveals female preference for male parental care in savannah sparrows. Proc R Soc Lond B 263:157–160

Gill SA, Stutchbury BJM (2006) Long-term mate and territory fidelity in neotropical buff-breasted wrens (*Thryothorus leucotis*). Behav Ecol Sociobiol 61:245–253

Gray EM (1997) Female red-winged blackbirds accrue material benefits from copulating with extra-pair males. Anim Behav 53:625–639

Griffith SC (2007) The evolution of infidelity in socially monogamous passerines: neglected components of direct and indirect selection. Am Nat 169:274–281

Griffith SC, Owens IPF, Thuman KA (2002) Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol Ecol 11:2195–2212

Hadfield JD, Burgess MD, Lord A, Phillimore AB, Clegg SM, Owens IPF (2006) Direct versus indirect sexual selection: genetic basis of colour, size and recruitment in a wild bird. Proc R Soc Lond B 273:1347–1353

Hartley IR, Davies NB, Hatchwell BJ, Desrochers A, Nebel D, Burke T (1995) The ploygynandrous mating system of the alpine accentor, *Prunella collaris*. 2. Multiple paternity and parental effort. Anim Behav 49:789–803

Head ML, Hunt J, Jennions MD, Brooks R (2005) The indirect benefits of mating with attractive males outweigh the direct costs. PLOS Biology 3:e33

Hill GE (1991) Plumage coloration is a sexually selected indicator of male quality. Nature 350:337–339

Hoelzer GAD (1989) The good parent process of sexual selection. Anim Behav 38:1067–1078

Holen ØH, Johnstone RA (2007) Parental investment with a superior alien in the brood. J Evol Biol 20:2165–2172

Houston AI, McNamara JM (2002) A self-consistent approach to paternity and parental effort. Philos Trans R Soc Lond B Biol Sci 357:351–362

Houston AI, Szekely T, McNamara JM (2005) Conflict between parents over care. Trends Ecol Evol 20:33–38

Jennions MD, Petrie M (1997) Variation in mate choice and mating preferences: a review of causes and consequences. Biol Rev 72:283–232

Jennions MD, Petrie M (2000) Why do females mate multiply? A review of the genetic benefits. Biol Rev 75:21–64

Jennions MD, Møller AP, Petrie M (2001) Sexually selected traits and adult survival: a meta-analysis. Q Rev Biol 76:3–36

Kempenaers B (2007) Mate choice and genetic quality: a review of the heterozygosity theory. Adv Study Behav 37:189–278

Kempenaers B, Sheldon BC (1996) Why do male birds not discriminate between their own and extra-pair offspring? Anim Behav 51:1165–1173

Kempenaers B, Sheldon BC (1997) Studying paternity and paternal care: pitfalls and problems. Anim Behav 53:423–427

Kokko H (1998) Should advertising parental care be honest? Proc R Soc Lond B 265:1871–1878

Kokko H (1999a) Competition for early arrival in migratory birds. J Anim Ecol 68:940–950

Kokko H (1999b) Cuckoldry and the stability of biparental care. Ecol Lett 2:247–255

Kokko H, Heubel K (2008) Condition-dependence, genotype-by-environment interactions, and the lek paradox. Genetica 132:209–216

Kokko H, Jennions MD, Brooks R (2006) Unifying and testing models of sexual selection. Annu Rev Ecol Evol Syst 37:43–66

Krebs EA, Hunte W, Green DJ (2004) Plume variation, breeding performance and extra-pair copulations in the cattle egret. Behaviour 141:479–499

Kvarnemo C (2006) Evolution and maintenance of male care: is increased paternity a neglected benefit of care? Behav Ecol 17:144–148

Lifjeld JT, Dunn PO, Robertson RJ, Boag PT (1993) Extra-pair paternity in monogamous tree swallows. Anim Behav 45:213–229

Linville SU, Breitwisch R, Schilling AJ (1998) Plumage brightness as an indicator of parental care in northern cardinals. Anim Behav 55:119–127

Lubjuhn T, Curio S, Muth SC, Brün J, Epplen JT (1993) Influence of extra-pair paternity on parental care in great tit (*Parus major*). In: Pena SDJ, Chakraborty R, Epplen JT, Jeffreys AJ (eds) DNA fingerprinting: state of the science. Birkhäusen, Basel, pp 379–385

Magrath MJL, Komdeur J (2003) Is male care compromised by additional mating opportunity? Trends Ecol Evol 18:424–430

Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886

Mitchell DP, Dunn PO, Whittingham LA, Freeman-Gallant CR (2007) Attractive males provide less parental care in two populations of the common yellowthroat. Anim Behav 73:165–170

Møller AP (2001) Heritability of arrival date in a migratory bird. Proc R Soc Lond B 268:203–206

Møller AP, Tegelstrom H (1997) Extra-pair paternity and tail ornamentation in the barn swallow *Hirundo rustica*. Behav Ecol Sociobiol 41:353–360

Nakagawa SD, Gillespie DOS, Hatchwell BJ, Burke T (2007) Does the badge of status influence parental care and investment in house sparrows? An experimental test. Oecologia 153:749–760

Oneal E, Connallon T, Knowles LL (2007) Conflict between direct and indirect benefits of female choice in desert Drosophila. Biol Lett 3:29–32

Petrie M, Kempenaers B (1998) Extra-pair paternity in birds: explaining variation between species and populations. Trends Ecol Evol 13:52–58

Pullin AS, Stewart GB (2006) Guidelines for systematic review in conservation and environmental management. Conserv Biol 20:1647–1656

Qvarnström A (1997) Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. Proc R Soc Lond B 264:1225–1231

Qvarnström A, Brommer JE, Gustafsson L (2006) Testing the genetics underlying the co-evolution of mate choice and ornament in the wild. Nature 441:84–86

Rowe KMC, Weatherhead PJ (2007) Social and ecological factors affecting paternity allocation in American robins with overlapping broods. Behav Ecol Sociobiol 61:1283–1291

Rubenstein DR (2007) Female extrapair mate choice in a cooperative breeder: trading sex for help and increasing offspring heterozygosity. Proc R Soc Lond B 274:1895–1903

Rundle HD, Ödeen A, Mooers AØ (2007) An experimental test for indirect benefits in *Drosophila melanogaster*. BMC Evol Biol 7:36

Schwagmeyer PL (1999) Species differences in male parental care in birds: a reexamination of correlates with paternity. The Auk 116:487–503

Sheldon BC (2000) Differential allocation: tests, mechanisms and implications. Trends Ecol Evol 15:397–402

Sheldon BC (2002) Relating paternity to paternal care. Philos Trans R Soc Lond B Biol Sci 357:341–350

Smiseth PT, Ornborg J, Andersson S, Amundsen T (2001) Is male plumage reflectance correlated with paternal care in bluethroats? Behav Ecol 12:164–170

Smith HG, Montgomerie R (1992) Male incubation in barn swallows—the influence of nest temperature and sexual selection. Condor 94:750–759

Stutchbury BJ, Rhymer JM, Morton ES (1994) Extrapair paternity in hooded warblers. Behav Ecol 5:384–392

Taylor ML, Wedell N, Hosken DJ (2007) The heritability of attractiveness. Curr Biol 17:R959–R960

Wagner RH, Schug MD, Morton ES (1996) Confidence of paternity, actual paternity and parental effort by purple martins. Anim Behav 52:123–132

West SA, Sheldon BC (2002) Constraints in the evolution of sex ratio adjustment. Science 295:1685–1688

Westneat DF (1995) Paternity and paternal behaviour in the red-winged blackbird, *Agelaius phoeniceus*. Anim Behav 49:21–35

Westneat DF, Sherman PW (1993) Parentage and the evolution of parental behaviour. Behav Ecol 4:66–77

Westneat DF, Stewart IRK (2003) Extra-pair paternity in birds: causes, correlates, and conflict. Annu Rev Ecol Evol Syst 34:365–396

Whittingham LA, Lifjeld JT (1995) High paternal investment in unrelated young—extra-pair paternity and male paternal care in house martins. Behav Ecol Sociobiol 37:103–108

Yezerinac SM, Weatherhead PJ, Boag PT (1996) Cuckoldry and lack of parentage-dependent paternal care in yellow warblers: a cost-benefit approach. Anim Behav 52:821–883