

The Evolution of Infidelity in Socially Monogamous Passerines Revisited: A Reply to Griffith

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, University of Texas, Austin, Texas
78712

Submitted September 18, 2006; Accepted September 26, 2006;
Electronically published January 11, 2007

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

We were pleased to see that Simon Griffith (2007, in this issue) welcomes the more stringent and quantitative approach to the study of extrapair copulations (EPC) in birds that we recently introduced (Arnqvist and Kirkpatrick 2005). Griffith argues that our main conclusion may have been premature for, it seems, the following four reasons.

First, Griffith suggests that we did not include all the relevant data. We noted that our estimate of indirect selection was based on all studies reporting direct measures of “growth, survival, recruitment ... and/or reproductive success” (Arnqvist and Kirkpatrick 2005, p. S27) as proxies for offspring fitness. We explicitly stated that “a few studies reporting other forms of potential but less direct fitness correlates were also not included” (p. S27). The study mentioned by Griffith (Johnsen et al. 2000) focused on measures of wing swelling and was not included for this reason. On closer examination, however, we see that Johnsen et al. (2000) also reported measures of offspring growth, and it should thus have been included in our estimate of indirect selection. However, the indirect effects on growth reported by Johnsen et al. (2000) were extremely small (0.0% and 0.2% of total variance in offspring growth) and statistically insignificant, and so its inclusion

would only have added force to our conclusion regarding indirect selection.

Second, Griffith (2007) points out that the relationship between the rate of extrapair paternity (EPP) and EPC behavior is poorly characterized empirically. This is true. However, contrary to what Griffith believes, our analytical approach does not assume that females with no EPP in their broods did not engage in EPCs; it merely assumes that EPP correlates positively with the degree of EPC behavior across females within populations. Although we feel that this is a very reasonable assumption, we agree that more data that allows this assumption to be tested would be useful. That said, it is important to note that because the estimate of indirect selection reported in our article (Arnqvist and Kirkpatrick 2005) is based on 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 (d_{EW}), the estimate will tend to overestimate rather than underestimate the strength of indirect selection on EPC behavior if the correlation between the rate of EPP and EPC behavior is low. In effect, d_{EW} places an upper limit on any indirect effects that could result from EPCs.

Third, Griffith (2007) suggests that selection for increased fertility (i.e., hatching rate of eggs) may be a “neglected component” of selection on EPC behavior. Rather than neglecting fertility benefits, we discussed this at some length (Arnqvist and Kirkpatrick 2005, p. S29) and noted (1) that extant correlational and comparative data lend no general support to this possibility, (2) that this would require female choice for fertile and/or compatible males as EPC mates, and (3) that our main conclusion rested on the assumption that this is not a major source of selection. It is certainly true that this form of selection could be quite strong if it occurred, but, as Griffith correctly notes, there are no data at hand that allow its accurate estimation, unfortunately. We are, however, more puzzled by Griffith’s related and rather convoluted suggestion that cryptic female choice for compatible (or less related) males could generally be another “neglected” form of selection that we did not account for. This is incorrect. Our estimate of indirect selection does not neglect but, rather, fully in-

* Corresponding author; e-mail: goran.arnqvist@ebc.uu.se.

† E-mail: kirkp@mail.utexas.edu.

corporates such effects to the extent that they affect the fitness of hatched offspring. As is clear from our original contribution, existing data generally show no such effect. Further, although “compatibility effects” could in principle be manifested as direct fertility benefits, the lack of general fitness differences between hatched within-pair offspring and their extrapair maternal half-sibs speaks against the possibility that extrapair embryos generally have a sizably higher survival until hatching. This is simply because outbreeding and/or increased mate compatibility tend to affect the survival of embryos and the survival/reproduction of hatched offspring in a similar manner (Abplanalp 1990; Keller 1998; Daniels and Walters 2000).

Fourth, Griffith (2007) argues that decreased paternal investment as a result of EPCs should not occur. This argument is odd since substantial theory and data support such an effect (including our analyses). With regard to models of paternal investment, we referred to the recent review by Sheldon (2002), who concluded that “a wide range of models suggest that certainty of paternity can influence male paternal investment” (p. 348). Further, we certainly did not neglect experimental work in this area but explicitly stated (Arnqvist and Kirkpatrick 2005, p. S30) that “experiments studying the effects on paternal care of a temporal removal of the female (or the male himself) have ... provided support for the existence of this form of direct costs to females,” again referring to Sheldon (2002), who concluded that at least “some experimental evidence supports the existence of facultative responses to variable certainty of paternity” (p. 348). However, contrary to what Griffith claims, we fail to see how these experimental studies could provide quantitative estimates of direct selection on female EPC behavior.

In the face of the large amounts of empirical data at hand in this field, one may take either of two stands. One can, as Griffith seems to do, deem data too incomplete and/or imperfect and conclude that we can gain no general insights from this research. Alternatively, one can, as we did, synthesize the relevant data that are available and see where these data point. Although we fully recognize that these data are not complete, something we repeatedly pointed out in our original contribution, we suggest that within-brood comparisons between sets of maternal half-sibs in birds probably provide the best source of information on the strength of indirect selection in the wild

that we have for any animal taxa. We maintain that our original conclusion is better supported than competing views; extant data strongly suggest that indirect selection on female EPC behavior is generally biologically insignificant. This implies that the chase for yet another elusive and mysterious “true function” of EPCs for females that Griffith is trying to initiate will be unproductive. The view that EPCs are the result of direct selection among males (see also Westneat and Stewart 2003; Albrecht et al. 2006) is better supported by actual data and certainly seems like a less rather than a “more complicated idea” than that advocated by Griffith (2007).

Acknowledgments

Financial support was received from the Swedish Research Council (to G.A.) and National Science Foundation grants DEB-9973221 and EF-0328594 (to M.K.).

Literature Cited

- Abplanalp, H. 1990. Inbreeding. Pages 955–984 in R. D. Crawford, ed. *Poultry breeding and genetics*. Elsevier, New York.
- Albrecht, T., J. Kreisinger, and J. Pialek. 2006. The strength of direct selection against female promiscuity is associated with rates of extrapair fertilizations in socially monogamous songbirds. *American Naturalist* 167:739–744.
- Arnqvist, G., and M. Kirkpatrick. 2005. The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior in females. *American Naturalist* 165(suppl.):S26–S37.
- Daniels, S. J., and J. R. Walters. 2000. Inbreeding depression and its effects on natal dispersal in red-cockaded woodpeckers. *Condor* 102:482–491.
- Griffith, S. C. 2007. The evolution of infidelity in socially monogamous passerines: neglected components of direct and indirect selection. *American Naturalist* 169:274–281.
- Johnsen, A., V. Andersen, C. Sunding, and J. T. Lifjeld. 2000. Female bluethroats enhance offspring immunocompetence through extrapair copulations. *Nature* 406:296–299.
- Keller, L. F. 1998. Inbreeding and its fitness effects in an insular population of song sparrows (*Melospiza melodia*). *Evolution* 52: 240–250.
- Sheldon, B. C. 2002. Relating paternity to paternal care. *Philosophical Transactions of the Royal Society B: Biological Sciences* 357:341–350.
- Westneat, D. F., and I. R. K. Stewart. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. *Annual Reviews of Ecology, Evolution, and Systematics* 34:365–396.

Editor: Allen J. Moore