

S13-1 To see or not to see: the role of habitat density on the occurrence of extra-pair paternity and paternity assurance behaviors

Donald BLOMQVIST^{1,2}, Herbert HOI², Ingrid WEINBERGER²

1. Department of Zoology, Animal Ecology, Göteborg University, Box 463, SE-405 30 Göteborg, Sweden; donald.blomqvist@zool.gu.se

2. Konrad Lorenz Institute for Comparative Ethology, Austrian Academy of Sciences, Savoyenstrasse 1a, A-1160, Vienna, Austria; d.blomqvist@klivv.oeaw.ac.at, h.hoi@klivv.oeaw.ac.at, i.weinberger@klivv.oeaw.ac.at

Abstract Several ecological factors have been thought to influence opportunities for extra-pair copulations. Based on an extensive literature survey, we tested the hypothesis that female birds can escape more easily from paternity guards in closed, i.e. visually occluded habitats. Assuming that occurrence of paternity assurance behaviors reflects an increased risk of cuckoldry, we predicted that both extra-pair paternity (EPP) and paternity guarding (mate guarding or frequent within-pair copulations) should be more frequent among species breeding in habitats with reduced visibility. As predicted, we found that species breeding in closed habitats had higher EPP rates than those breeding in more open habitats. Mate guarding was also more frequent in closed habitats, but not high copulation rates. These relationships, however, were influenced strongly by taxonomic position, particularly by differences between passerines and non-passerines, implying that phylogeny and traits associated with it play an important role in explaining the occurrence of EPP and paternity guards.

Key words Habitat density, Extra-pair paternity, Paternity guards, Comparative analyses

1 Introduction

Molecular genetic methods have demonstrated that extra-pair copulations (EPCs) and fertilizations are frequent among birds. Thus, even if most birds are socially monogamous (e.g., Mock and Fujioka, 1990), genetic monogamy is a relatively rare phenomenon. Indeed, less than 25% of the socially monogamous species studied to date are truly genetically monogamous (Griffith et al., 2002). It is still unclear, however, what benefits female birds obtain from EPCs, and why there is such marked variation in extra-pair paternity (EPP), both within and between species (reviewed by Petrie and Kempenaers, 1998; Griffith et al., 2002).

Several ecological or socio-ecological factors, such as food supply, breeding synchrony and density, have been thought to influence opportunities for seeking EPCs (e.g., Westneat et al., 1990). If males are widely dispersed, for example, the time and energy costs to females for finding an extra-pair partner may outweigh any potential benefits (Petrie and Kempenaers, 1998). Westneat and Sherman (1997) found that, within species, EPP increased consistently with increasing breeding density. Across species, however, they found no such correlation, leading them to suggest that confounding factors might have caused the disparity. In particular, they proposed that “other ecological factors, such as the openness of the habitat....could have major effects on extra-pair behaviors”, and that “habitat complexity allows females more opportunity to escape from male surveillance....” (Westneat and Sherman, 1997:

211). Similarly, an earlier study by Westneat et al. (1990: 360) suggested that “visually occluded habitats also make mate guarding more difficult and less efficient at preventing EPC”.

We examine the relationships between EPP, paternity assurance behaviors and habitat density. Based on an extensive literature survey, we tested the hypothesis that females are more able to escape male paternity guards in closed, i.e. visually occluded, habitats (Westneat et al., 1990; Westneat and Sherman, 1997). We predicted that both EPP and paternity assurance behaviors should be more frequent among species breeding in closed habitats compared to those breeding in more open habitats, assuming that occurrence of paternity guards reflects an increased risk of cuckoldry (e.g., Birkhead, 1987; cf. Westneat et al., 1990).

2 Materials and methods

2.1 Extra-pair paternity

We searched the Science Citation Index for pre-January 2002 data on EPP rates. In the analyses, we only included data from DNA screening, thus excluding those based on plumage polymorphism, polymorphic enzymes or sex-differences in heritability estimates (cf. Griffith et al., 2002). We also excluded lekking or cooperatively breeding species, for which EPP is either impossible or difficult to define, as well as EPP estimates influenced by experimental manipulations (cf. Griffith et al., 2002).

Our data set included 114 species, representing 46

families and 12 orders. For species provided with more than one estimate of EPP rate (proportion of young sired by extra-pair males), we used the mean value. A complete list of references, with data on frequencies of paternity guards and breeding habitat classification (see below) as well, can be provided upon request.

2.2 Paternity guards

We scored presence / absence of paternity assurance behaviors, including *mate guarding by close following* in males and *frequent within-pair copulations*: for definitions, see Birkhead and Møller (1992). Data were obtained mainly from a review by Møller and Birkhead (1991), complemented with recent case studies. This data set comprised 155 species, representing 52 families and 15 orders.

2.3 Habitat density

For each species, we classified the main breeding habitat as (1) closed (dense forests, reeds and thickets, with much reduced visibility), (2) semi-open (open forests, parks and gardens, with intermediate visibility), or (3) open (seacoasts, pastures and meadows, with full visibility). Using an alternative habitat classification for 77 species (35%, $n = 220$) did not change the results presented here. Data were obtained mainly from standard references such as *The Birds of the Western Palearctic* (Oxford University Press) and *Handbook of the Birds of the World* (Lynx Edicions, Barcelona).

2.4 Statistical analyses

We first examined the relationships between EPP, paternity guarding and habitat density using species data. Since, however, species of close ancestry are likely to share many traits, species values may not be statistically inde-

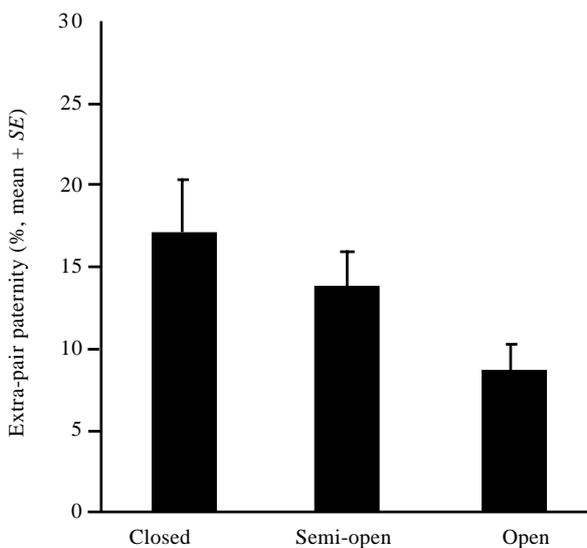


Fig. 1 Frequency of extra-pair paternity (proportion of young) in relation to habitat density (horizontal axis)

Density classifications on the horizontal axis (closed, semi-open, open) reflect presumed visibility in each habitat type. Data from 114 species.

pendent (Harvey and Pagel, 1991). We therefore tried to control for the effects of phylogeny on EPP rate by using the phylogenetic-subtraction method described by Sterns (1983). This procedure removes variation associated with taxonomic similarity from species data, on the assumption that differences among orders, as well as among families within orders, reflect phylogenetic effects.

Since the phylogenetic-subtraction method only corrects for taxonomic-dependent variation in quantitative variables, we examined the presence / absence of paternity guards by first determining the modal habitat type (degree of density) for each order and family. We then tested whether

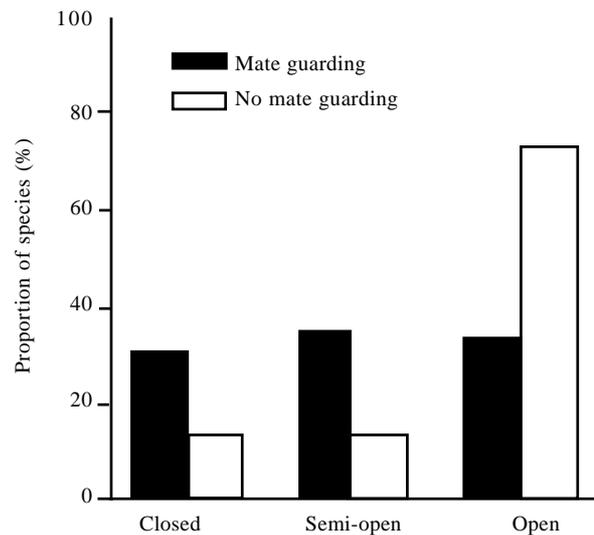


Fig. 2 Frequency of mate guarding by close-following in relation to habitat density (horizontal axis)

Density classifications on the horizontal axis (closed, semi-open, open) reflect presumed visibility in each habitat type. Data from 155 species.

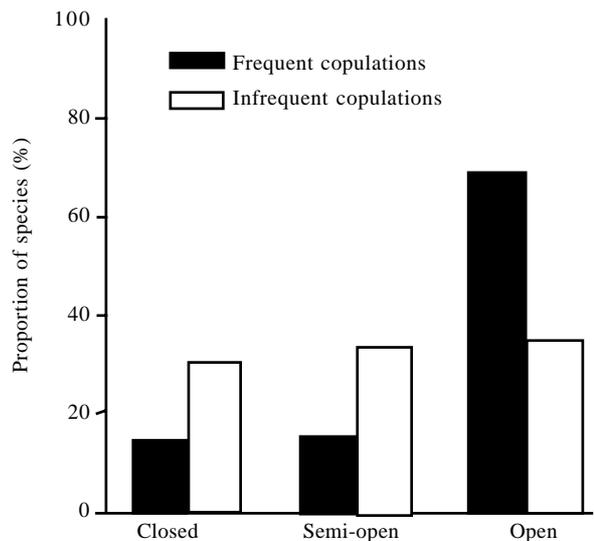


Fig. 3 Frequency of within-pair copulations in relation to habitat density (horizontal axis)

Density classifications (closed, semi-open, open) reflect presumed visibility in each habitat type. Data from 153 species.

the proportion of species showing either mate guarding or frequent copulations differed among habitat types, thus using orders and families as independent sample units.

3 Results

EPP frequency in species breeding in closed habitats was higher than in those breeding in more open habitats (Fig. 1; $P = 0.01$, $n = 114$ species, Kruskal-Wallis ANOVA). We also found a significant association between the presence of paternity guards and habitat structure. Mate guarding was relatively more frequent among species breeding in closed or semi-open habitats than in those breeding in open habitats (Fig. 2; $P < 0.001$, $n = 155$ species, log-linear analysis), whereas the opposite was true for species in which within-pair copulations were frequent (Fig. 3; $P < 0.001$, $n = 153$ species, log-linear analysis).

The above results seem to support our prediction: both EPP and mate guarding (but not high copulation rates) were more frequent among species breeding in habitats of reduced visibility. There was, however, a strong phylogenetic effect as well. When we controlled for taxonomic position, the significant differences in the frequencies of EPP among habitat types disappeared ($P = 0.74$, $n = 114$ species, Kruskal-Wallis ANOVA). So did those for the proportion of species with paternity guards: mate guarding, $P = 0.19$ (orders) and 0.20 (families); frequent copulations, $P = 0.22$ (orders) and 0.50 (families); $n = 13$ orders and 37 families (Kruskal-Wallis ANOVA).

4 Discussion

Species breeding in closed habitats with reduced visibility have significantly higher EPP rates than those breeding in more open habitats. Male mate guarding was also more frequent among species breeding in dense habitats, supporting the idea that such behavior is a response to the risk of cuckoldry (e.g., Birkhead, 1987). On the other hand, frequent within-pair copulations occurred predominantly among species breeding in open habitats. Since the frequencies of EPP were significantly lower in these habitats, this result suggests that copulation rate does not reflect the risk of losing paternity.

Yet such paternity assurance behavior may be more effective in preventing extra-pair fertilizations than is commonly assumed (Møller and Birkhead, 1991). Frequent copulations typically occur in species in which males cannot guard their mates by close following, for example where one of the mates has to guard the nest (review in Birkhead and Møller, 1992). Therefore, this behavior has been interpreted as an alternative but inferior paternity guard (e.g., Møller and Birkhead, 1991). Yet even if frequent within-pair copulations have functions other than ensuring paternity (Møller and Birkhead, 1991), the relatively low frequency

of EPP in species that have it questions whether it really is inferior in paternity guarding.

Our analyses indicate a strong phylogenetic influence in the above patterns. Thus, when we controlled for the effects of taxonomy position, the significant relationship between EPP rate and habitat density disappeared. We conclude that the underlying reason for this result is the considerably higher rate of EPP in passerine than nonpasserine birds (Westneat and Sherman, 1997). Furthermore, passerines in our data set occurred more in closed habitats, and nonpasserines more in the open (D. Blomqvist et al., in prep.). As passerines were biased towards mate guarding and nonpasserines to frequent copulations (D. Blomqvist et al., in prep.), this could also explain why the relationship between paternity guarding and habitat density disappeared when we controlled for taxonomic position.

To summarize, our results support the hypothesis that habitat density affects the frequency of EPP and paternity guarding. Since the phylogenetic-subtraction method may not be the best way to control for the effects of phylogeny (cf., Harvey and Pagel, 1991), further studies are needed to determine whether these eco-behavioral relationships remain after ancestry has been accounted for. Within-species comparisons should also help to clarify the influence of habitat density on variation in EPP and paternity assurance behaviors.

Acknowledgements The study was supported by the Konrad Lorenz Institute, Vienna. We are also grateful to A. Pauliny for valuable comments on the manuscript.

References

- Birkhead TR, 1987. Sperm competition in birds. *Trends Ecol. Evol.* 2: 268–272.
- Birkhead TR, Møller AP, 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences*. London: Academic Press.
- Griffith SC, Owens IPF, Thuman KA, 2002. Extra-pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol.* 11: 2 195–2 212.
- Harvey PH, Pagel MD, 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Mock DW, Fujioka M, 1990. Monogamy and long-term pair bonding in vertebrates. *Trends Ecol. Evol.* 5: 39–43.
- Møller AP, Birkhead TR, 1991. Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. *Behaviour* 118: 170–186.
- Petrie M, Kempenaers B, 1998. Extra-pair paternity in birds: explaining variation between species and populations. *Trends Ecol. Evol.* 13: 52–58.
- Stearns SC, 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in mammals. *Oikos* 41: 173–187.
- Westneat DF, Sherman PW, 1997. Density and extra-pair fertilizations in birds: a comparative analysis. *Behav. Ecol. Sociobiol.* 41: 205–215.
- Westneat DF, Sherman PW, Morton ML, 1990. The ecology and evolution of extra-pair copulations in birds. In: Power DM ed. *Current Ornithology*, Vol. 7. New York: Plenum Press, 331–369.