Behav Ecol Sociobiol (1998) 43: 217–219

Forum

P.J. Weatherhead · S.M. Yezerinac

Breeding synchrony and extra-pair mating in birds

Received: 29 January 1998 / Accepted after revision: 23 March 1998

Recognition that extra-pair fertilizations (EPFs) are commonplace in birds demands hypotheses that can explain the variation in EPFs within and among species. Stutchbury and Morton (1995) offered such a hypothesis by proposing that synchronous breeding promotes extra-pair mating because it allows females to assess male quality more accurately and enhances opportunities for extra-pair mating for males. In response to criticism of this hypothesis, Stutchbury (1998) expressed concern that the hypothesis was being arbitrarily "brushed aside", even though rejection of the synchrony hypothesis was based on detailed empirical research (Weatherhead 1997; Yezerinac and Weatherhead 1997). Stutchbury (1998) has offered new arguments and evidence in support of the synchrony hypothesis. Here we point out why neither the arguments nor the evidence are compelling, and we propose new proximate causes of EPFs that might account for correlations between synchrony and EPFs between species, without invoking the mechanism proposed by Stutchbury (1998).

Weatherhead's (1997) suggestion that the logic of the original synchrony hypothesis might be faulty prompted Stutchbury (1998) to clarify the proposed mechanism by which breeding synchrony promotes extra-pair mating. Females are assumed to compare displaying males and to choose extra-pair mates whose display behavior signals greater relative quality. Because the intensity of male displays varies across the breeding cycle, Stutchbury argues that greater breeding synchrony allows females to assess and select extra-pair mates more reliably because synchrony tends to standardize the context of male displays.

Patrick J. Weatherhead (✉) · Stephen M. Yezerinac
Department of Biology, Carleton University,
1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada
e-mail: pweather@biology.queensu.ca, Fax: +1-613-5204497

S.M. Yezerinac
Department of Biology, Queen's University, Kingston,
Ontario K7L 3N6, Canada

The only aspect of this scenario that Weatherhead (1997) challenged, and that we challenge here, is the role attributed to synchronous breeding in facilitating female choice. We argue that females that rely on breeding synchrony to standardize the context in which neighboring males are displaying, and then copulate with the male that displays the most, are likely to select males of relatively low quality, not high quality. Low-quality males that either failed to get a mate or whose nesting attempt failed will be able to devote themselves to display, whereas relatively high quality individuals will be occupied with their own breeding commitments. To solve this problem of unequal display effort, females also need to consider the particular nesting stage of individual males when evaluating their displays. A much easier solution is for females to choose males in ways that are not dependent upon breeding synchrony. In fact, Stutchbury (1998) cites evidence from three species indicating that females use specialized tactics to promote competition among potential extra-pair males to facilitate comparisons between them. We view these tactics as inconsistent with the synchrony hypothesis because such tactics allow females to compare males in a way that is independent of whether or not the individual males are breeding synchronously with the rest of the population. For example, when female bearded tits (*Panurus biarmicus*) copulate with the fastest chasing male (Hoi 1997), they are selecting a mate independent of breeding synchrony. Indeed, we propose that a key feature of female assessment tactics should be that they require male performances that are standardized independently of stage of breeding.

Ultimately, the effect of breeding synchrony on extra-pair mating can only be determined empirically. To that end, Stutchbury (1998) added some new species to the comparative analysis presented by Stutchbury and Morton (1995). Across 34 species, Stutchbury (1998) found that the proportion of EPFs increased significantly with breeding synchrony. Although suggestive of a link between synchrony and EPFs, this analysis did not control for phylogenetic relationships among species

(Harvey and Pagel 1991). In an analysis of 13 of those species that did control for phylogeny, Westneat and Sherman (1997) failed to find a significant association between breeding synchrony and the frequency of EPFs ($P = 0.27$).

Stutchbury (1998) did provide some additional comparative evidence that is consistent with the synchrony hypothesis and that does not suffer from the methodological shortcoming of lack of phylogenetic independence in the more general analysis. She compared frequencies of EPFs in nine pairs of related species that differed in breeding synchrony and found that in all pairs, EPFs were more frequent in the more synchronously breeding species. Stutchbury concluded from these data that breeding synchrony increases the frequency of EPFs. We think she has confused correlation with causation. If differences in breeding synchrony cause differences in EPFs between species by the mechanism that Stutchbury has proposed, then synchrony differences should also explain variation in EPFs within these species. Assessing intraspecific patterns provides a more direct test of the proposed mechanism than do comparative analyses. Data are available for three of the species that Stutchbury used in the paired analysis. Breeding synchrony has no effect on EPFs in either tree swallows (*Tachycineta bicolor*, Dunn et al. 1994) or yellow warblers (*Dendroica petechia*, Yezerinac and Weatherhead 1997), both of which are species with among the highest rates of EPFs. Hooded warblers (*Wilsonia citrina*) are the only species of the three in this sample for which intraspecific evidence supports the proposed mechanism linking synchrony and EPFs (Stutchbury et al. 1994). Furthermore, three independent studies of red-winged blackbirds (*Agelaius phoeniceus*) have failed to support the synchrony hypothesis (Weatherhead 1997; D.F. Westneat and E.M. Gray, personal communication), and in the blue tit (*Parus caeruleus*) and American redstart (*Setophaga ruticilla*), synchrony also has no apparent effect on extra-pair paternity (Kempenaers 1997; Perreault et al. 1997). Thus, for five of six species (or seven of eight studies) for which intraspecific evidence is available, the association between breeding synchrony and extra-pair paternity that Stutchbury's hypothesis predicts has not been found.

We suggested above that Stutchbury (1998) has confused correlation with causation in interpreting the comparative evidence. If better comparative analyses confirm the positive association between synchrony and EPFs, but most intraspecific evidence shows no such association, then the pattern across species seems best interpreted as a consequence of both breeding synchrony and extra-pair mating being correlated with some other variable(s), rather than being causally related to each other. We offer two potential explanations for how apparently contradictory interspecific and intraspecific patterns could arise. First, if females use EPFs to increase the genetic quality of their offspring, their need to do so may be greatest when the correlation between male genetic quality and territory quality is weakest, thus divorcing nest site choice (i.e., social mate choice) from choice of a genetic mate. Extensive evidence from red-winged blackbirds indicates that chance (i.e., who establishes a territory first) plays a much greater role in territory ownership and territory quality than the males' intrinsic competitive ability (e.g., Eckert and Weatherhead 1987; Shutler and Weatherhead 1991). The importance of chance in determining territory ownership should increase when less time is available for territory establishment. If territory establishment is more synchronous in species that breed more synchronously, then the link between male quality and territory quality should also be weaker in synchronously breeding species, and thus the occurrence of extra-pair mating should be more frequent.

Second, even where male territoriality is a meritocracy, if territorial settlement by females (i.e., social pairing) occurs rapidly, e.g., due to an ecological need to initiate nesting quickly, choice of genetic mate may be deferred until after social pairing. There is evidence that female songbirds only assess a few potential mates before territory settlement (e.g., Bensch and Hasselquist 1992; Dale and Slagsvold 1996). The need to settle quickly, and thus the value of extra-pair mating, seems likely to increase with breeding synchrony. Both of these proposed mechanisms would result in higher-quality females mated to low-quality males more often when breeding is synchronous, and these females may be more willing or able than low-quality females to obtain extra-pair matings in the same situation. By either of these two mechanisms, interspecific differences in synchrony are predicted to result in interspecific differences in rates of EPFs. Importantly, however, neither mechanism predicts any association between synchrony and EPFs within species, and each is therefore consistent with both the intra- and interspecific patterns in current data.

Testing our "conflicting-choices hypothesis" requires knowing the extent to which male quality is disassociated from territory quality, the extent to which that disassociation is correlated with breeding synchrony, how females choose social and genetic mates when male and territory quality are disassociated, and how female quality affects those choices. It seems likely that synchrony of territory establishment and breeding synchrony will be broadly correlated (e.g., at the level of migratory vs non-migratory species), but it remains to be determined whether that correlation occurs within those groups. Testing the "settlement speed hypothesis" requires determining whether the choice of social mate is limited by constraints on prospecting, and the extent to which synchrony contributes to that constraint. However, as we argued above, we first need more data and better analyses to assess the correlation between synchrony and EPFs. Thus, far from brushing aside synchrony as something one need not consider in research on extra-pair paternity, we think synchrony warrants more study. However, given the evidence currently available, we do not think that synchrony contributes to extra-pair paternity in the manner that Stutchbury (1998) has argued.

Acknowledgements We thank Bob Montgomerie and Bill Searcy for commenting on the manuscript. Our research is supported by the Natural Sciences and Engineering Research Council of Canada.

References

Bensch S, Hasselquist D (1992) Evidence for active female choice in a polygynous warbler. Anim Behav 44:301–311

Dale S, Slagsvold T (1996) Mate choice on multiple cues, decision rules and sampling strategies in female pied flycatchers. Behaviour 133:903–944

Dunn PO, Whittingham LA, Lifjeld JT, Robertson RJ, Boag PT (1994) Effects of breeding density, synchrony, and experience on extrapair paternity in tree swallows. Behav Ecol 5:123–129

Eckert CG, Weatherhead PJ (1987) Competition for territories in red-winged blackbirds: is resource holding potential realized? Behav Ecol Sociobiol 20:369–375

Harvey PH, Pagel MD (1991) The comparative method in evolutionary biology. Oxford University Press, Oxford

Hoi H (1997) Assessment of the quality of copulation partners in the monogamous bearded tit. Anim Behav 53:277–286

Kempenaers B (1997) Does reproductive synchrony limit male opportunities or enhance female choice for extra-pair paternity? Behaviour 134:551–562

Perreault S, Lemon RE, Kuhnlein U (1997) Patterns and correlates of extrapair paternity in American redstarts. Behav Ecol 8:612–621

Shutler D, Weatherhead PJ (1991) Owner and floater red-winged blackbirds: determinants of status. Behav Ecol Sociobiol 28:234–241

Stutchbury BJ (1998) Female mate choice of extra-pair males: breeding synchrony is important. Behav Ecol Sociobiol 43:213–215

Stutchbury BJ, Morton ES (1995) The effect of breeding synchrony on extra-pair mating systems in songbirds. Behaviour 132:675–690

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

Weatherhead PJ (1997) Breeding synchrony and extra-pair mating in red-winged blackbirds. Behav Ecol Sociobiol 40:151–158

Westneat DF, Sherman PW (1997) Density and extra-pair fertilizations in birds: a comparative analysis. Behav Ecol Sociobiol 41:205–215

Yezerinac SM, Weatherhead PJ (1997) Reproductive synchrony and extra-pair mating strategy in a socially monogamous bird, *Dendroica petechia*. Anim Behav 54:1393–1403