Social mating systems and extrapair fertilizations in passerine birds

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Two alternative hypotheses have been proposed to explain how social and genetic mating systems are interrelated in birds. According to the first (male trade-off) hypothesis, social polygyny should increase extrapair fertilizations because when males concentrate on attracting additional social mates, they cannot effectively protect females with whom they have already paired from being sexually assaulted. According to the second (female choice) hypothesis, social polygyny should decrease extrapair fertilizations because a substantial proportion of females can pair with the male of their choice, and males can effectively guard each mate during her fertile period. To discriminate these alternatives, we comprehensively reviewed information on social mating systems and extrapair fertilizations in temperate zone passerine birds. We found significant inverse relationships between proportions of socially polygynous species and frequencies of extrapair young, whether each species was considered as an independent data point (using parametric statistics) or phylogenetically related species were treated as nonindependent (using contrasts analyses). When social mating systems were dichotomized, extrapair chicks were twice as frequent in monogamous as in polygynous species (0.23 vs. 0.11). We hypothesize that in socially polygynous species, (1) there is less incentive for females and males to pursue extrapair matings and (2) females incur higher costs for sexual infidelity (e.g., due to physical retaliation or reduction of paternal efforts) than in socially monogamous species. Key words: extrapair paternity, monogamy, passerine birds, phylogenetic contrasts, polygyny, social mating system. [Behav Ecol 12:457–466 (2001)]

Recently it has become evident that the social and genetic mating systems of many species are different. Social associations do not necessarily indicate exclusive mating relationships, particularly in birds. Extrapair copulations (EPCs) have been observed in more than 150 species, and extrapair fertilizations (EPFs) have been documented in about 75% of the more than 100 species in which molecular genetic techniques have been used to infer paternity (reviewed by Birkhead and Möller, 1992, 1995; Möller and Ninni, 1997; Möller and Cuervo, 2000; Westneat and Sherman, 1997; Westneat and Webster, 1994; Westneat et al., 1990).

There is considerable variability among populations and species in frequencies of EPCs and EPFs. To understand why, we must consider the fitness costs and benefits of engaging in extrapair sexual activities. For males, the obvious benefit of EPCs is that they can enhance reproductive success (i.e., EPCs result in EPFs). However, seeking EPCs may be costly if such behavior reduces a male’s effectiveness in self-advertisement, territorial defense, mate guarding, or parental care (e.g., Poston et al., 1998; Sherman and Morton, 1988; Westneat, 1988, 1993, 1994) or increases the male’s chances of contracting parasites and diseases (Sheldon, 1993). For females, EPCs may yield indirect benefits, such as “good genes” (Gowaty, 1996; Hasselquist, 1994; Hasselquist et al., 1996; Kempenaers et al., 1992), or direct benefits such as access to territories or other resources (Gray, 1997; Hunter and Davies, 1998; Wolf, 1975), assistance with parental care (Wagner, 1992), or insurance of a fertile mating (Wetton and Parkin, 1991). Potential costs of EPCs for females include contracting ectoparasites and sexually transmitted diseases and retaliation by their social mate. For example, a male might respond to being cuckolded by reducing nest defense (e.g., Weatherhead et al., 1994) or nestling provisioning (Dixon et al., 1994; Kokko, 1999; Möller and Birkhead, 1993a; Möller and Cuervo, 2000; Westneat and Sargent, 1996; Wright, 1998), or by deserting the female (Cézilly and Nager, 1995). Finally, females may sometimes be forced to accept unsolicited EPCs when resistance to sexual harassment could result in physical injuries (e.g., Frederick, 1987; Røskaft, 1983).

Increasingly, investigators are taking advantage of the substantial comparative database that now exists to disentangle the ecological and social factors underlying variations in EPCs and EPFs. Two key variables, breeding density and synchrony, have been the focus of considerable interest and debate. Sometimes extrapair activities increased with increasing density (e.g., Hoi and Hoi-Leitner, 1997; Möller, 1987, 1991; Möller and Birkhead, 1991, 1993b) and synchrony (Chuang et al., 1999; Stutchbury 1998a,b; Stutchbury and Morton, 1995), but in other studies EPFs were not correlated with either density (Westneat and Sherman, 1997) or synchrony (Saino et al., 1999; Westneat and Gray, 1998; Yezerinac and Weatherhead, 1997). Some of this variability may be due to lumping of inter- and intrapopulational studies if differences in density and synchrony are more important within than among populations. Regardless, effects of another key variable, the social mating system, have yet to be adequately explored. This is the issue addressed in this paper.

Two social mating systems characterize the majority of birds. The most common is monogamy: in >92% of species a male and female form a pair bond and raise the young together (Ford, 1983; Lack, 1968; Möller, 1986). Social polygyny is a distant second: in about 5% of species >5% of males form pair bonds with multiple females. Two alternative hypotheses have been proposed to explain how social mating systems should affect extrapair sexual activities, and they make opposite critical predictions.

The male trade-off hypothesis
Social polygyny increases EPCs and EPFs, whereas social monogamy decreases both (Arak, 1984; Birkhead and Möller,
1992; Dunn and Robertson, 1993). This hypothesis assumes that in polygynous species there are trade-offs between attracting additional social mates and other breeding behaviors, especially mate guarding. When males concentrate on mate attraction, females with whom they have already paired receive less attention, even though they may still be fertile (Arak, 1984; Hasselquist and Bensch, 1991; Westneat, 1993). On the one hand, this frees females to seek matings with extrapair males. On the other hand, unguarded females are more vulnerable to forced copulations by interloping extrapair suitors. Both effects should increase the frequency of EPCs and EPFs over their occurrence in socially monogamous species, among which males do not have to trade off mate guarding for mate attraction because there is no possibility of having another social mate.

The female choice hypothesis

Social polygyny decreases EPCs and EPFs, whereas social monogamy increases both (Hasselquist, 1994; Hasselquist et al., 1995a; Möller, 1992; Westneat et al., 1990). The enhanced expression of male secondary sexual characters which occurs in socially polygynous species facilitates female identification of extremely attractive males (Gontard-Danek and Möller, 1999). Under the female choice hypothesis, EPCs are reduced both because several females can form pair bonds with the most attractive males and because females that are paired to such males are unlikely to seek or accept EPC attempts by less attractive individuals. In addition, EPCs may be reduced in socially polygynous species if (1) males can simultaneously advertise themselves and guard against territorial intrusions by extrapair suitors, (2) dominant, territory-holding males are especially attractive to females and capable of physically guarding them, or (3) dominant males are so occupied with display and defense of their own territory that they do not have the time or energy to pursue EPCs elsewhere. In contrast, in socially monogamous species a smaller proportion of females in any population can associate socially and sexually with the most attractive males, so a greater proportion of females may benefit from seeking or accepting EPCs with high-quality suitors (Gowaty, 1996).

Birkhead and Möller (1992, 1996; Möller and Birkhead, 1993b) have already explored these ideas. They found no consistent relationship between the social mating system and frequencies of EPCs or EPFs. However, the issue bears reexamination because many new, high-quality genetic data have recently become available. Also, Birkhead and Möller included all birds in their analyses, so their attempts to tease out effects of the social mating system may have been diluted by ecological and evolutionary factors that influence life histories and breeding behaviors in widely divergent taxonomic groups. For example, Westneat and Sherman (1997) reported that EPFs occur in a significantly greater proportion of passerine than nonpasserine species and, among species exhibiting EPFs, at significantly higher frequencies in passerines than nonpasserines.

To focus more directly on how differences in social mating systems affect EPFs, we restricted our analyses to species of passerine birds from temperate regions (predominantly North America and Europe). These are related taxa that live under comparable climatic and habitat conditions, yet there is considerable interspecific variation in frequencies of EPFs among all families and genera. Moreover, temperate-region passerines typically pair with different social mates each breeding season. This is important because lengths of social pair bonds can influence frequencies of EPFs regardless of the social mating system (e.g., Birkhead and Möller, 1996). Here we explore whether EPFs are randomly distributed among social mating systems. We then consider, in light of the results, whether comparative analyses of extrapair sexual activities should henceforth include or can safely ignore species’ social mating systems.

METHODS

Definitions

We define a “pair bond” as an extended social and sexual association between a male and a female, lasting for days to months or more, considerably longer than it takes to copulate (Westneat et al., 1990). An “extrapair copulation” is a mating by a female with a male other than her pair-bonded mate; EPCs may result in extrapair fertilizations. Our definitions exclude birds that do not form pair bonds, especially lekking species (Höglund and Alatalo, 1995) and species in which males defend territories where groups (“harem”) of females nest but the males only associate closely with each female to copulate (e.g., montezuma oropendolas, Psarocolius montezumae Webster, 1994; boat-tailed grackles, Quiscalus major: Poston et al., 1998; aquatic warblers, Acrocephalus agricola: Dyrcz and Zdunek, 1993; Schulze-Hagen et al., 1993, 1995). Our definitions also exclude matings between females and secondary males with whom they have had extensive social associations, such as in polyandrous and polygynandrous species (e.g., dunnocks, Prunella modularis: Burke et al., 1989; alpine accentors, Prunella collaris: Hartley et al., 1995; Smith’s longspurs, Calcarius pictus: Briskie, 1992) and in cooperatively breeding groups (e.g., splendid fairy wrens, Malurus cyaneus: Brooker et al., 1990; white-browed scrubwrens, Sericornis frontalis: Whittingham and Dunn, 1998).

We define “breeding density” as the number of individuals breeding per unit area of suitable nesting habitat (Westneat and Sherman, 1997). “Breeding synchrony” refers to simultaneity of female receptivity, which can be measured as the average proportion of females that are fertile per day during the breeding season (Kempenaers, 1993; Langefors et al., 1991a,b; Sherman and Morton, 1988). We use the fraction of chicks sired by extrapair males (i.e., frequency of extrapair young, EPY) rather than the proportion of broods with EPY as the primary dependent variable in our analyses, because frequencies of EPY yielded the larger sample size, and in our data set these two measures were highly correlated ($r = .95, N = 56, p < .001$). For each population from which EPY data were available, we sought field studies of the social mating system. Data on the proportion of socially polygynous males (i.e., number of polygynous males/number of territorial males) were extracted directly from the original source or were calculated from information provided there or in another study of the same population. In the case of the pied flycatcher Ficedula hypoleuca, we used data reported by Lundberg and Alatalo (1992) to calculate the average proportion of socially polygynous males in the two Scandinavian populations where paternity was investigated. We omitted a few studies because: (1) they were allozyme studies that estimated the proportion of broods with mixed paternity without specifying
whether mismatched chicks resulted from extrapair matings or intraspecific parasitism (McKittrick, 1990; Petter et al., 1990), (2) they inferred rates of extrapair paternity from sexual differences in tarsus heritabilities (Alatalo and Lundberg, 1984, 1986; Alatalo et al., 1989); these were excluded because the reliability of this method is questionable: Dhondt, 1991; Gebhardt-Henrich and Nager, 1991; Hasselquist et al., 1995b; Lifjeld and Slagsvold, 1989), or (3) they were conducted on manipulated populations in which the procedures may have confounded EPF rates (barn swallows, _Hirundo rustica_, with manipulated tail feathers: Smith et al., 1991; dark-eyed juncos, _Junco hyemalis_, with testosterone implants: Ketterson and Nolan, 1992). In total, 40 species met all criteria for inclusion in our analyses (Figure 1).

Comparative analyses

Many authors (e.g., Brooks and McLennan, 1991; Harvey and Nee, 1997; Martins and Hansen, 1996) have argued that traits of related species should not be regarded as independent in statistical analyses. Others believe phylogenetic corrections have been overemphasized (e.g., Reeve and Sherman, 2001; Ricklefs and Starck, 1996). In light of these disagreements, we analyzed the data both ways. In analyses that controlled for phylogeny, we used independent contrasts (Felsenstein, 1985; Garland et al., 1992, 1993; Harvey and Pagel, 1991), based primarily on estimates of relationships derived from Sibley and Ahlquist (1990). We followed Westneat and Sherman (1997) in using the more recent phylogenetic studies of Sheldon et al. (1992) and Silkas et al. (1996) for the Paridae and Sheldon and Winkler (1993) for the Hirundinidae; we used the AOU checklist (American Ornithologists’ Union, 1983) to resolve the location of the geospizine finches and the indigo bunting (_Passerina cyanea_) within the Emberizinae.

Statistics

Standard, nonparametric statistical tests were conducted using SYSTAT (SYSTAT Inc., Chicago). Proportions of EPY in populations were transformed (square-root arcsine) before analyses. For the phylogenetic contrasts, social mating systems were characterized either continuously (proportions of males per population with >1 social mate) or dichotomously (monogamous = 0, polygynous = 1), and branch lengths were inferred from genetic distances (Figure 1). We calculated contrasts from the difference between dyad species at each node using the Phenotypic Diversity Analysis Program (PADP-3.0) of Garland et al. (1993). Relationships between contrast values and the standard deviation in branch lengths, calculated with several different methods of transforming branch lengths, were tested for internal biases in the data (e.g., a relationship between the absolute values of contrasts and standard deviations of branch lengths; Garland et al., 1992). We analyzed the association between standardized contrasts of social mating systems and EPFs with linear regression in PADP (Garland et al., 1993).

RESULTS

Species as independent data points

Initially we categorized the social mating system of each of the 40 species in our sample as either socially polygynous or monogamous using the 5% criterion of Lack (1968), Møller (1986), and Verner and Willson (1969). That is, we considered a species to be monogamous or polygynous depending, respectively, on whether <5% or >5% of males paired with multiple females. Although this cutoff is arbitrary, by accepting tradition we made our results comparable to those of previous workers. And, in fact, the traditional cutoff corresponded to a natural break point in our data set, which was decidedly bimodal (Figures 1 and 2): in 29 of 40 species 0–5% of males paired with >1 social mate, and in the other 11 species 12–90% of males paired with >1 social mate.

Rates of extrapair fertilizations differed between social mating systems. Frequencies of EPY were significantly higher in socially monogamous species (mean = 0.233, SE = 0.025) than in socially polygynous species (mean = 0.114, SE = 0.025; ANOVA, _F_ 1,29 = 9.6, _p_ = .004; Figure 2). Moreover, frequencies of broods with EPY were significantly higher in socially monogamous species (mean = 0.392, SE = 0.038) than in socially polygynous species (mean = 0.261, SE = 0.045; _F_ 1,34 = 4.7, _p_ = .036).

When the social mating system was considered as a single, continuous variable (Figure 3), there was a significant negative correlation between proportions of socially polygynous males and frequencies of EPY (_r_ = −.32, _p_ = .044). However, this relationship might be spurious due to confounding effects of breeding synchrony and density. Therefore, we conducted a multiple regression analysis with the social mating system, synchrony (data from Stutchbury, 1998b; Stutchbury and Morton, 1995), and density (data from Westneat and Sherman, 1997) as independent variables and frequencies of EPY as the dependent variable. This halved our sample size because information on all three factors was available for just 20 species. Among the factors, only the social mating system predicted frequencies of EPY (_p_ = .048); neither breeding density (_p_ = .40) nor synchrony (_p_ = .82) was significantly associated with EPY frequencies.

Independent contrasts analyses

Frequencies of EPY were significantly higher in socially monogamous species, whether mating systems were categorized dichotomously (_r_ 2 = .14, _t_ = −2.4, _p_ < .05, df = 38) or continuously (_r_ 2 = .12, _t_ = −2.3, _p_ < .05, df = 38). However, there was a significant relationship between absolute values of standardized contrasts and standard deviations of observed branch lengths (_r_ 2 = .19, _t_ = −3.0, _p_ < .01, df = 37), violating an assumption of this analytical technique. We therefore converted observed branch lengths of social mating systems (i.e., the dependent variable) to a constant value (i.e., each branch length was set at 1, as recommended by Garland et al., 1992, 1993). There was no significant association between standardized contrasts and standard deviations of constant branch lengths (_r_ 2 = .05, _t_ = −1.4, _p_ > .10, df = 37). Therefore, we conducted the contrast analyses again, this time inferring constant branch lengths for the dependent variable. As before, frequencies of EPY were significantly higher in more monogamous species, whether mating systems were categorized dichotomously (_r_ 2 = .26, _t_ = −3.7, _p_ < .001, df = 38; Figure 4A) or continuously (_r_ 2 = .12, _t_ = −2.5, _p_ = .02, df = 38; Figure 4B).

DISCUSSION

In all our analyses, frequencies of extrapair young were significantly higher in socially monogamous than polygynous passerine species (Figures 2–4). This outcome was evident whether mating systems were considered as two categorical variables or one continuous variable and whether species were treated as independent data points or phylogeny was controlled for using independent contrasts. Of the alternative hypothesized relationships between social and genetic mating systems, our results unequivocally supported the female
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<td>116</td>
<td>Westneat 1990</td>
</tr>
<tr>
<td>Icterus galbula</td>
<td>37 (??)</td>
<td>0 (M)</td>
<td>43</td>
<td>43</td>
<td>D. Richardson unpubl.</td>
</tr>
<tr>
<td>Agelaius phoeniceus</td>
<td>29 (50)</td>
<td>56 (P)</td>
<td>36</td>
<td>36</td>
<td>Gibbs et al. 1990</td>
</tr>
<tr>
<td>Dolichonyx oryzivorus</td>
<td>15 (38)</td>
<td>25 (P)</td>
<td>80</td>
<td>80</td>
<td>Bollinger &amp; Gavin 1991</td>
</tr>
</tbody>
</table>
choice hypothesis (Hasselquist, 1994; Hasselquist et al., 1995a; Møller, 1992; Westneat et al., 1990).

Of course, it is possible that low frequencies of EPY in socially polygynous species were due to confounding effects of some other correlated variable(s). For example, EPFs might be rarer in polygynous species because they breed more or less synchronously or at higher or lower densities. Indeed, Møller and Birkhead (1991, 1993b) reported a positive relationship between density and frequencies of EPFs, and Stutchbury (1998a,b) claimed that breeding synchrony best explains variations in EPFs among species. However, our multiple regression analysis revealed no significant effects of density or synchrony, and many other studies have found either no effects or inconsistent effects of breeding density or synchrony on frequencies of EPY (e.g., Dunn et al., 1994; Kempenaers, 1997; Langefors et al., 1998; Perreault et al., 1997; Saino et al., 1999; Weatherhead, 1997; Westneat and Gray, 1998; Westneat and Sherman, 1997; Yezerinac and Weatherhead, 1997). We infer that confounding variables did not create or cloud the relationship between social mating systems and EPY.

To understand why EPY are more common in socially monogamous species, it is useful to consider separately the reproductive interests of the paired male, the female, and the extrapair male (Lifjeld et al., 1994). Advantages and disadvantages to each of these parties will shape outcomes of conflicts over extrapair activities.

**Females seek EPCs**

Assume first that females seek EPCs, as has been observed in several species (e.g., Ahnesjö et al., 1993; Kempenaers et al., 1992; Otter et al., 1998; Smith, 1988). If so, frequencies of EPY will be determined primarily by benefits and costs for the female.

**Benefits**

In socially monogamous species, not all females can form pair bonds with the highest quality males. Females arriving at the breeding site earliest presumably have first choice. In addition, regardless of when they arrive, large, healthy, experienced females may be able to monopolize access to attractive males by driving rival females away (Breiehagen and Slagsvold, 1988; Sandell and Smith, 1996, 1997; Yasukawa and Searcy, 1982). As a result, in socially monogamous populations the majority of females will not be able to pair with the most attractive males.

A female can make the best of this situation by forming a social pair bond with the most attractive male that is available and also seeking extrapair matings with higher quality males than her social mate when the opportunity arises (Gowaty, 1996). Females benefit by adopting this mixed reproductive strategy if offspring sired by the most attractive males are predictably larger, healthier, more likely to survive, or more likely to be chosen by other females (Hasselquist et al., 1996; Kempenaers et al., 1992; Møller, 1992; Otter et al., 1998; Sundberg and Dixon, 1996; Yezerinac and Weatherhead, 1997). In socially polygynous species, in contrast, even late-arriving and less competitive females potentially can pair with high-quality males, at least until breeding territories of the most attractive males are saturated (e.g., Bensch, 1996; Davies, 1989; Hasselquist et al., 1995a). Because a greater fraction of females can pair with the male of their choice, fewer females should be inclined to seek EPCs. The result is that EPFs and EPY should be less common in socially polygynous than monogamous species.

**Costs**

If EPCs are more costly for females in socially polygynous species, their occurrence and thus the frequency of EPY may be reduced relative to that in socially monogamous species. There are two reasons that costs of EPCs might be greater in socially polygynous species. First, risks of exposure to sexually transmitted diseases (Sheldon, 1993) should be higher because many individuals have multiple sex partners. Moreover, such sexually transmitted diseases may be more numerous and virulent due to frequent horizontal transmission (Ewald, 1994). Second, in socially polygynous species, cuckolded

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**Figure 1**

Phylogeny of 40 passerine species in which patterns of paternity have been investigated using genetic markers, and information on (1) proportions of young sired by extrapair males (EPY), (2) proportions of broods containing EPY, (3) proportions of males with >1 social mate, (4) social mating system category of the studied population (M = monogamy, P = polygyny) of 40 species of passerine birds (see Figure 1; p = .004). Numbers in the phylogeny refer to branch lengths between species and groups of species.
males may be able to retaliate against mates that engage in EPCs more effectively than in socially monogamous species. Due to strong sexual selection, males in socially polygynous species often are larger than females (Jehl and Murray, 1986; Webster, 1992). Physical attacks by larger males are more damaging (Clutton-Brock and Parker, 1995a,b) in these species than in species in which the sexes are similar in size. Moreover, if a socially polygynous male observes one of his females mating with another male, or infers that she did so, he may either reduce his parental care to that brood in favor of broods where his likelihood of paternity is greater or else “divorce” the unfaithful female (e.g., Cézilly and Nager, 1995). Among many socially polygynous species males divide their nestling provisioning efforts unequally among nests (e.g., Bensch and Hasselquist, 1994; Dyracz, 1986; Johnson et al., 1993; Patterson et al., 1980; Sejberg et al., 2000; Wittenberger, 1982). We believe that female extrapair mating activities underlie some of these asymmetries in paternal efforts (Westneat and Sherman, 1993; Möller and Cuervo, 2000).

Retaliation may not be as effective a deterrent in socially monogamous species. Although males sometimes attack unfaithful females (e.g., Barash, 1976), because the sexes are about the same size such attacks are less likely to be physically damaging. Moreover, retaliation by withholding parental care from a brood may not yield much benefit for males. First, males usually have no other reproductive options, such as finding a new mate, by the time nestlings are being fed (Kokko, 1999). Second, some of the chicks in a mate’s nest usually are the male’s own offspring (Westneat and Sherman, 1993; Whittingham et al., 1992); a male that neglects the whole brood thus risks starvation of his own progeny (there is no evidence that males can discriminate their own offspring from unrelated chicks in their nest; Kempenaers and Sheldon, 1996; Westneat et al., 1995). Third, females may use male feeding effort as a cue for subsequent matings with that male, and withholding care may result in divorce (Freeman-Gallant, 1996; Wagen et al., 1996). Fourth, benefits from reducing parental efforts usually cannot be gained until the subsequent breeding season, but there is no guarantee that withholding care will enable males to survive that long, or that, even if males do survive, they will then be paired to a more faithful female than their current mate (Westneat and Sherman, 1993).

These considerations help explain why paternal provisioning is independent of paternity in so many socially monogamous passerines (e.g., MacDougall-Shackleton and Robertson, 1998; Wagner et al., 1996; Whittingham and Lifjeld, 1995; Whittingham et al., 1993; Yezerinac et al., 1996). However, in some birds males do adjust nestling provisioning or nest-defense efforts to the whole brood according to their likelihood of paternity (reviewed by Möller and Cuervo, 2000). Such ad-
justments have been documented in species in which males have a reliable behavioral cue about certainty of paternity. For example, in polygynous or polygynandrous mating systems, males often use the time spent alone with the female when she was receptive (i.e., the male’s perceived effectiveness at mate guarding; Burke et al., 1989; Lifjeld et al., 1998; Sheldon et al., 1997; Sheldon and Ellegren, 1998; Weatherhead et al., 1994).

**Males seek EPCs**

Now assume that males seek EPCs. If so, frequencies of extrapair activities will be affected by trade-offs with other reproductive behaviors and responses of females.

**Trade-offs with other reproductive behaviors**

In socially polygynous species, paired males can increase their reproductive success by staying on their territory and advertising for additional social mates. This is not an option for males in socially monogamous species: they can only increase their mating success by leaving their territory to seek EPCs. Thus males in socially polygynous species can potentially enhance their mating success while simultaneously maintaining mate guarding efficacy, whereas males in socially monogamous species must sacrifice mate guarding for gallivanting (or else wait until their mate is no longer fertile). The result is a higher frequency of EPCs and EPY in socially monogamous species.

**Responses of females**

When extrapair suitors appear, females may either accept or physically resist their copulation attempts (e.g., by struggling or fleeing; Westneat, 1987, 1990; Westneat et al., 1990). Resistance is more likely in socially polygynous than in monogamous species because a greater proportion of females can pair with attractive (i.e., preferred) males. These females gain by avoiding dilution of the sperm of their high-quality mate. In addition, by protesting, females may attract the attention of their social mate and receive his protection, as well as avoiding retaliation for perceived infidelity. Finally, males in socially polygynous species may be large enough relative to females that they can force extrapair copulations on females that have mated with other males (Møller and Birkhead, 1991). If these retaliatory extrapair matings give the paired males’ sperm an advantage, frequencies of EPY would be reduced despite frequent EPCs.

In socially monogamous species, in contrast, there is a greater chance that an extrapair suitor will be of higher quality than a female’s social mate. If so, females should be less likely to protest his sexual advances. Moreover, because males of socially monogamous species are about the same size as their mate, they are presumably less able to force retaliatory extrapair copulations and also less able to physically punish their mate for copulating with other males.

**Conclusion**

Our analyses indicate that social mating systems of passerines have important effects on their genetic mating systems. The most likely explanation is that females control copulations and sperm usage, and they choose to be more faithful to their pair-bonded mate in socially polygynous than in monogamous species. This is probably because benefits of engaging in EPCs are lower and costs are higher than in socially monogamous species. Thus, the female choice hypothesis best explains the relationship between social mating systems and EPY among passerine species; however, the male trade-off hypothesis may apply within some species (see Figure 3; Dunn and Robertson, 1993; Soukup and Thompson, 1997).

Of course, other environmental and social factors, such as breeding synchrony, density, or female condition also may affect the frequency of extrapair activities (Gowaty, 1996; Møller and Birkhead, 1993b; Stutchbury, 1998a,b). However, our results imply that social mating systems should henceforth be included as an important variable in attempts to understand the factors underlying differences in extrapair sexual activities among populations and species of passerine birds.

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**REFERENCES**


Burke T, Davies NB, Bruford MW, Hatchwell BJ, 1989. Parental care...


