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A Sexually Selected Paradox in the Pied Flycatcher: Attractive Males are Cuckolded

JAN T. LIFJELD,^{1,4} TORE SLAGSVOLD,² SVEIN DALE,^{2,5} AND HANS ELLEGREN³

¹Zoological Museum, University of Oslo, Sars gate 1, N-0562 Oslo, Norway;

²Division of Zoology, Department of Biology, University of Oslo, Box 1050 Blindern, N-0316 Oslo, Norway; and

³Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, P. O. Box 597, S-751 24 Uppsala, Sweden

Evidence exists from several bird species that females prefer colorful mates (e.g. Hill 1990, Sætre et al. 1994, Sundberg 1995). Because female preferences may be manifested in social mate choice and in extrapair mate choice, one might expect colorful males to have an increased success in obtaining social mates and in achieving intrapair and extrapair fertilizations. There is empirical support for some species that colorful males do better in social and extrapair mate choice (e.g. Sundberg and Dixon 1996) and are cuckolded less frequently (e.g. Burley et al. 1996). In other species, colorful males are favored in social mate choice but are cuckolded to the same extent as are less colorful males (e.g. Hill et al. 1994). Differences among species in this respect may be related to the actual types and strength of costs and benefits relevant to females in the two contexts. In this paper, we examine the relationship between male plumage color and cuckoldry in the Pied Flycatcher (*Ficedula hypoleuca*).

The extensive variation in plumage color of male Pied Flycatchers has generated much research and debate (see Lundberg and Alatalo 1992). Recent studies of our population in Oslo, Norway, have yielded evidence that females have a social mating preference for males with black as opposed to brown plumage (Sætre et al. 1994). Black males are better food providers for nestlings than are brown males (Sætre et al. 1995). Females, therefore, seem to obtain direct reproductive benefits by choosing black males as social mates. Thus, the evolution of black plumage in males is consistent with the good-parent process of sexual selection (Hoelzer 1989). Variation in male plumage color may be maintained by social and reproductive benefits to inferior males of acquiring a brown plumage (Slagsvold and Sætre 1991, Sætre and Slagsvold 1996).

The good-parent process of sexual selection does not require a heritable basis for variance in the preferred trait (Hoelzer 1989). The only necessary condition is that the trait is a true signal of the male's parental ability. Male plumage color in the Pied Flycatcher, however, has a significant heritability component (Lundberg and Alatalo 1992, Slagsvold and Lifjeld 1992). This heritability implies that females might obtain additional, indirect fitness benefits by choosing black males through improved viability of offspring and/or increased attractiveness of their sons. Constraints on female choice caused by monogamy (or weak polygyny) limit the number of females that can pair with black males. Therefore, females paired with inferior brown males might be expected to compensate for a poor initial mate choice by pursuing extrapair copulations with black males.

There are several accounts of extrapair paternity in Pied Flycatchers. In some Swedish and Finnish populations, more than 10% of offspring are sired by extrapair males (Gelter and Tegelström 1992, Rätti et al. 1995). In our Norwegian study population, the level is somewhat lower (i.e. 4 to 7%; Lifjeld et al. 1991, Ellegren et al. 1995). Yet, the phenomenon is poorly understood because few, if any, correlates of extrapair paternity have been detected. Our primary goal is to report an unexpected association between extrapair paternity and male plumage color, namely that cuckolded males are among the blacker, not the browner, males in the population. We also review a number of possible explanations for this relationship.

Methods.—We examined all paternity data currently available for our study population. This includes a sample of 27 broods of 17 males from the 1989 breeding season (Lifjeld et al. 1991) using multilocus DNA fingerprinting, and 18 broods of 18 males from the 1992 season (Ellegren et al. 1995) using microsatellite typing (Ellegren 1992). The plumage color of males was scored on Drost's (1936) seven-point scale, i.e. from 1 (jet black) to 7 (brown and female-like). Males were aged as second year (SY) or older (ASY), and their body mass, wing length, and tarsus length

⁴ E-mail: j.t.lifjeld@toyen.uio.no

⁵ Present address: Department of Biology and Nature Conservation, Agricultural University of Norway, P. O. Box 5014, N-1432 Ås, Norway.

recorded. Data on first-egg dates and clutch sizes also were available for all broods.

To evaluate the potential role of rapid mate switching as an alternative source of extrapair paternity, we also present data on copulation and mate switching during the initial stages of breeding for the years 1989–1993. Methods for monitoring individual females during their mate-sampling and early nest-building stages are reported in detail in Dale et al. (1992) and Slagsvold and Dale (1994). Briefly, females were caught in one area, individually marked, and released into another area where displaying males were monitored continuously by means of video cameras directed at their nest boxes. None of these females was included in the data set used for paternity analysis.

Results and discussion.—In 1989, extrapair paternity accounted for 15% (4/27) of broods and 4% (6/135) of young (Lifjeld et al. 1991). In 1992, the corresponding rates were 17% (3/18) of broods and 7% (7/98) of young (Ellegren et al. 1995). Overall, seven males had one or more unrelated offspring in their brood(s), whereas 28 males had full paternity.

The seven cuckolded males were among the blackest males in the population (Table 1). Cuckolded males were significantly blacker than non-cuckolded males in 1992 and for the entire data set, but the difference was not statistically significant for the 1989 sample analyzed separately (Table 1). Two of the cuckolded males in 1989 were polygynous, i.e. one bigamist and one trigamist. They lost paternity in only one of their broods each. Because the probability of detecting extrapair paternity is likely to increase with the number of broods analyzed, we also used the total data set to calculate a Spearman rank correlation between plumage color score and the relative number of broods with documented extrapair paternity for each male. This analysis confirmed that blacker males were more likely to be cuckolded ($r_s = -0.44$, $n = 35$, $P = 0.01$; corrected for ties).

The identity of three cuckolders (one in 1989 and two in 1992) could be disclosed by the genetic analyses. They were all quite black (color scores 2 and 3), in two cases slightly blacker than the male they cuckolded. Thus, both the cuckolders and the cuckoldees seemed to be rather black.

Because males become blacker with age (Lundberg and Alatalo 1992), it was not surprising that the cuckolded males tended to be older than the non-cuckolded males ($\chi^2 = 2.86$, $df = 1$, $P = 0.09$; corrected for continuity). In fact, all seven cuckolded males were ASY birds. The two categories of males did not differ with respect to body mass, wing length, or tarsus length (Mann-Whitney *U*-tests, all $P_s > 0.10$). Furthermore, egg-laying date and clutch size did not differ between broods with and without extrapair young for each year analyzed separately or for both years combined (all $P_s > 0.10$).

Black males probably are phenotypically superior

TABLE 1. Plumage color scores (1 [black] to 7 [brown]) of male Pied Flycatchers in Oslo, Norway, in relation to extrapair paternity in their broods. Values are $\bar{x} \pm SE$ (n).

Year	Cuckolded males	Non-cuckolded males	P^a
1989 ^b	2.5 ± 0.5 (4)	3.4 ± 0.3 (13)	0.13
1992 ^c	2.5 ± 0.3 (3)	3.7 ± 0.3 (15)	0.047
Both years	2.5 ± 0.3 (7)	3.6 ± 0.2 (28)	0.014

^a Mann-Whitney *U*-test.

^b Paternity data from Lifjeld et al. (1991).

^c Paternity data from Ellegren et al. (1995).

to brown males. On average, they are older (Lundberg and Alatalo 1992), they arrive earlier in spring (Curio 1959, Slagsvold and Lifjeld 1988), and they are larger (Slagsvold and Lifjeld 1988). Black males also have a larger song repertoire than brown males (Lampe and Espmark 1994). Thus, if anything, females seeking genes for viability and/or attractiveness should pursue fertilizations with black males, and extrapair paternity should preferentially occur in broods of brown males. Therefore, our finding that cuckolded males were black is not consistent with the hypothesis that extrapair paternity is caused by females seeking good genes through extrapair copulations. But the possibility cannot be entirely ruled out. All of the identified cuckolders were quite black. Similarly, Rätti et al. (1995) identified one cuckolder in their study, and he also was quite black. If females seek extrapair copulations with black males, it becomes a mystery why females mated to brown males do not perform this behavior. The only possible explanation we can think of is that extrapair copulation is a costly behavior that can be afforded only by the best (e.g. ASY) females. However, extrapair paternity was not associated with female age in the combined data set ($\chi^2 = 0.04$, $df = 1$, $P = 0.85$; corrected for continuity).

Our results suggest that black males are at a selective disadvantage in sperm competition, yet, they are favored in social mate choice. How can this apparent paradox be resolved? Several possible explanations exist, and we will review each of them in turn. The three key elements in our discussion are that: (1) female preferences may differ between the choice of a copulation partner and the choice of a social mate, (2) male-male competition also may influence paternity patterns, and (3) extrapair copulation is not the only behavioral mechanism for extrapair paternity.

First, females may discriminate against black males as copulation partners. Although there is little evidence to suggest that black males are genetically inferior to brown males, black males may be more subject to temporal reductions in fertility, e.g. due to sperm depletion (Birkhead 1992). If females engage in extrapair copulations primarily to ensure fertility (Sheldon 1994), then one would expect females paired with black males to have more extrapair offspring and

a reduced hatching success of their eggs. Indeed, when combining the data sets for both years (including nests not analyzed for paternity), resident males at nests with one or more unhatched eggs were nearly significantly blacker ($\bar{x} = 3.1$) than at nests where all eggs hatched ($\bar{x} = 3.5$; Mann-Whitney *U*-test, $Z = -1.96$, $n_1 = 30$, $n_2 = 57$, $P = 0.051$). This finding seems consistent with the fertility hypothesis, but we emphasize that the pattern may be confounded with other factors that influence hatching success (cf. Lifjeld 1994). A detailed analysis of the occurrence of unhatched eggs seems worthwhile (see Birkhead et al. 1995).

Second, the relationship between paternity and plumage color also could arise through an extrapair copulation mechanism if paternity is determined by male, not female behavior. For example, black males would be expected to spend less effort on mate guarding, and more effort on mate attraction than brown males if there is a tradeoff between mate guarding and mate attraction. A similar reasoning has been applied to explain the higher frequency of cuckoldry among older versus younger males in other species (Westneat 1987, Sherman and Morton 1988). The problem with this explanation is that we have seen no evidence of mate guarding, or of any other paternity-guarding strategies, in our population (Lifjeld et al. 1991, Chek et al. 1996). Hence, a tradeoff between mate attraction and paternity protection does not seem to exist.

The third possible explanation is that extrapair paternity arises through rapid mate switching (Birkhead and Møller 1992). Females that initially mate with an inferior (i.e. brown) male may be expected to divorce him if they find an unmated superior (i.e. black) male in the neighborhood. Because females prefer black males (Sætre et al. 1994), it seems plausible that black males would be more likely to attract females that have actively divorced their first mate. But for cuckoldry to occur in such cases, females must have been inseminated by the first mate, and the sperm stored in their reproductive tract must have been viable until the eggs were fertilized. In some passerines, females can store viable sperm for more than a week (Birkhead et al. 1989, Birkhead 1992).

Our data suggest that rapid mate switching does occur. Among 125 marked females that were experimentally released and that subsequently obtained a male, at least 22% continued to visit other males after the females had initiated nest building. Seven females (i.e. 6% of the total number that settled) left their initially chosen male after they had started nest building and bred with another male in the area. The distance between the two nest boxes averaged 231 m (range 137 to 575 m). However, there was no tendency for females to switch from a browner male to a blacker male. In three cases females switched to a blacker male, in three cases they switched to a browner male, and in one case the two males had similar plumage color scores.

The video recordings also revealed that copulations occur at this early stage. All seven copulations that were recorded occurred between 10 min and 2 h 38 min ($\bar{x} = 48$ min) after the first visit to the male. The number of copulations obviously underestimates the true frequency because the video cameras recorded only the activity at the nest box itself. It is, however, questionable whether these early copulations result in fertilizations, because egg-laying normally is initiated about seven days (minimum four days) after the start of nest building (Lifjeld and Slagsvold 1989). Recent paternity analyses of females subjected to experimental mate switching revealed that copulations that result in fertilization take place no earlier than two days before the first egg is laid (Lifjeld et al. 1997). Hence, early copulations do not seem to function in fertilization, although they may play a role in pair formation. Therefore, we conclude that rapid mate switching as observed near the time of nest initiation is unlikely to explain the observed association between plumage color and cuckoldry.

Quite frustratingly, we are left without an adequate explanation for the apparent paradox that black (i.e. attractive) male Pied Flycatchers are more likely to be cuckolded than are brown (i.e. less attractive) males. Our findings contrast with those of a recent study in Finland that found no association between cuckoldry and male plumage color in Pied Flycatchers (Rätti et al. 1995), but the way extrapair paternity arises is not known for that population either. At present, the evidence suggests that fertility assurance plays a role, but further studies are needed. In particular, we need detailed observations during the fertile period of females with extrapair offspring to determine whether they have engaged in extrapair copulations or mate switching. It also is essential to know which sex initiates the actual behavior.

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