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Within-pair Copulations: Are Female Tree Swallows Feathering Their Own Nests?

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A variety of hypotheses has been proposed to explain why socially monogamous birds copulate repeatedly with their mates when only a single copulation is necessary to fertilize an entire clutch (Birkhead and Møller 1992, Petrie 1992, Hunter et al. 1993). Petrie (1992) hypothesized that a female should copulate frequently with her mate so as to reduce her mate's involvement in extrapair copulations. By reducing her mate's involvement in extrapair copulations, a female may: (1) avoid the transmission of parasites and sexually transmitted diseases (Hamilton 1990); (2) may avoid sperm depletion by her mate; and (3) may monopolize her mate's paternal care (Petrie 1992).

Whittingham et al. (1994) tested Petrie's (1992) hypothesis on Tree Swallows (*Tachycineta bicolor*). Their results did not support part of Petrie's hypothesis. Whittingham et al. (1994:table I) found that within-pair copulation rates were higher in pairs where a female's mate gained extrapair copulations than in pairs where a female's mate was not involved in extrapair copulations. They concluded that female Tree Swallows copulated frequently with their pair-bond mates so as to assure the fertilization of clutches by mates, especially if the mate was of high quality. In drawing this conclusion, they rejected the hypothesis that, by copulating frequently with their mates, females might gain material benefits such as mate feeding, assistance in nest building, or increased paternal care (Birkhead and Møller 1992, Petrie 1992, Hunter et al. 1993). However, Whittingham et al.'s rejection of the material-benefits hypothesis is premature because they failed to consider an important aspect of Tree Swallow natural history.

It is true that male Tree Swallows do not feed their mates (Robertson et al. 1992), and there appears to be no relationship between within-pair copulation rate and male parental care during the nestling period (Lifjeld et al. 1993, Whittingham et al. 1993). However, Whittingham et al.'s (1994) statement that male Tree Swallows do not assist their mates in nest building is incorrect. Tree Swallows build nests made of a

mat of dry grasses with a nest cup lined with feathers. Females build the grass portion of the nest (Kuerzi 1941, Sheppard 1977, Robertson et al. 1992), but during egg laying and incubation males add many of the feathers that line the nest cup (Sheppard 1977, Cohen 1985, Robertson et al. 1992, Lombardo unpubl. data). Competition between males for feathers is intense (Kuerzi 1941, Cohen 1985, Winkler 1993, Lombardo 1994) and is characterized by long aerial battles and chases between two or more swallows fighting over the ownership of feathers (Winkler 1993, Lombardo 1994). Males go into a feather-collecting "frenzy," rapidly collecting feathers and attempting to steal feathers from other swallows that are carrying feathers back to their nests when feathers are provided to them during egg-laying and incubation periods (Cohen 1985, Lombardo unpubl. data). The amount of feathers lining the cup varies among nests (Lombardo 1994).

Not only do males assist females in nest building by adding feathers, the feathers that males add may make a significant contribution to female reproductive success. Winkler (1993) demonstrated by experiment that nestlings reared in nests with feathers were larger and had fewer ectoparasites when 12 days old, and fledged earlier than nestlings reared in nests from which he removed feathers. However, feathers had no effect on fledging success (Winkler 1993). Lombardo (1994) showed by correlation analyses that nests well insulated with feathers were advantageous early in the season, when ambient temperatures were low and eggs and nestlings needed to be kept warm, but disadvantageous late in the season when it is warmer and nestlings in well-insulated nests were at risk of hyperthermia. Following Winkler (1993), Lombardo et al. (1995) showed by experiment that females that nested in nests with feathers had shorter incubation periods (nests with feathers, $\bar{x} = 12.40 \pm$ SD of 0.84 days, $n = 12$ nests; nests without feathers, 13.21 ± 0.70, $n = 12$; Wilcoxon two-sample test corrected for continuity, $Z = -2.27$, $P = 0.02$) and fledged more young (nests with feathers, 3.60 ± 1.58 fledglings, $n = 12$; nests without feathers, 2.08 ± 1.56 fledglings, $n = 12$; $Z = 2.16$, $P = 0.03$) than females in nests from which we removed feathers. All clutches were standardized to five eggs each before the start of the experiment. Twelve-day-old nestlings reared in nests with feathers had significantly longer right tarsi (nests with feathers, 12.08 ± 1.04 mm, $n = 42$ nestlings; nests without feathers, 11.44 ± 0.66 mm, $n = 28$; $Z = -3.06$, $P = 0.002$) and wing chords of right wings (nests with feathers, 41.05 ± 6.29 mm, $n = 42$ nestlings; nests without feathers, 34.86 ± 9.05 mm, $n = 28$; $Z = -3.01$, $P = 0.003$) and weighed significantly more than nestlings reared in nests from which we removed feathers (nests with feathers, 20.44 ± 2.57 g, $n = 42$ nestlings; nests without feathers, 18.84 ± 3.64 g, $n = 28$; $Z = 2.3$, $P = 0.02$). The results of these studies suggest that feathers lining the nest have a positive influence on Tree Swallow reproductive performance. Thus, feather collecting may be an important component of parental and paternal care in Tree Swallows.

Because feathers can have a positive influence on reproductive success, female Tree Swallows may benefit by copulating frequently with their mates if within-pair copulation rate is positively correlated with the beneficial effects of the feathers males add to the nest. However, testing this hypothesis may not be accomplished simply by examining a straightforward correlation between the number of within-pair copulations and the number of feathers males add to the nest. First, support for the hypothesis does not require that there to be a positive correlation between within-pair copulation rate and the absolute number of feathers that males add to the nest, only that there be a positive correlation between within-pair copulation rate and the beneficial effects of those feathers. For example, a well-insulated nest is more advantageous early in the season than late in the season because of the risks of nestling hyperthermia later in the season when average ambient temperatures are higher (Lombardo 1994). Therefore, the relationship between within-pair copulation rate and number of feathers collected by males may be influenced by the time in the breeding season. Second, determining the relationship between within-pair copulation rates and feather collecting by males may be confounded by male feather collecting experience. The nests of second-year females contain fewer feathers than the nests of after second-year females (Sheppard 1977, Lombardo 1994), and it is possible that skill gained through experience is an important determinant of feather collecting success by males (Lombardo 1994). Additionally, it might be difficult for females to guard against males that "cheat" by copulating frequently, but do not collect feathers because most of the feathers added by males are added during egg laying and incubation, well after the peak in within-pair copulation rate before the first egg is laid (Venier and Robertson 1991). However, cheating on feather collecting may not be a stable male strategy because males that cheat on their mates by not adding feathers to the nest run the risk of negatively affecting their own reproductive success. Despite these potential difficulties, the hypothesis is testable. In summary, Whittingham et al. (1994) prematurely rejected the material-benefits hypothesis as an explanation for the relatively high within-pair copulation frequency in Tree Swallows because they failed to consider the potentially important contributions male Tree Swallows make to nest building by adding feathers.

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Do Males Exchange Feathers for Copulations in Tree Swallows?

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We studied copulation rates in Tree Swallows (*Tachycineta bicolor*) and found that the within-pair copulation rate was related positively to a male's extrapair copulation rate (Whittingham et al. 1994). We concluded that more frequent within-pair copulations were apparently not deterring males from participating in extrapair copulations. In addition, we suggested that it was unlikely that female Tree Swallows copulated frequently with their mate in order to gain material benefits because males do not feed their mates or assist their mates with nest building (Robertson et al. 1992), and the rate at which males feed or defend nestlings is not related to the within-pair copulation rate nor to paternity (Lifjeld et al. 1993, Whittingham et al. 1993). However, male Tree Swallows provide many of the feathers that line the nest cup (Robertson et al. 1992), and the number of feathers varies extensively among nests (Lombardo 1994, pers. obs.). Lombardo (1995) proposed that females copulate with their mates to gain material benefits—specifically, to gain more feathers to line the nest. The obvious prediction from Lombardo's hypothesis is that within-pair copulation rate will be correlated positively with the number of feathers that the male provides to line the nest.

Lombardo (1995) suggested that the expected correlation is not necessarily between within-pair copulation rate and feather number; rather, it is between

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