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Homosexual Copulations by Male Tree Swallows

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Homosexual copulations by male Tree Swallows.—Homosexual courtship behavior in non-human animals is well known (Ford and Beach 1980) and occurs in a wide variety of taxa. However, homosexual copulations, especially between males, are less well known. In birds, males mounting other males have been observed in the colonially breeding Cattle Egret (*Bubulcus ibis*) (Fujioka and Yamagishi 1981) and Common Murre (*Uria aalge*) (Birkhead et al. 1985, Hatchwell 1988). Neither Fujioka and Yamagishi (1981) nor Birkhead et al. (1985) and Hatchwell (1988) reported whether cloacal contact occurred during their observations of male-male mountings. Here we describe homosexual copulations by male Tree Swallows (*Tachycineta bicolor*) during which cloacal contacts occurred.

In 1993, we studied the social and ecological correlates of the copulation behavior of Tree Swallows that bred in some of the 100 wooden nest boxes mounted on metal poles erected in old fields on the Grand Valley State University campus in Allendale, Ottawa County, Michigan. Nest boxes were arranged in grids, and each nest box was at least 30 m from its nearest neighbor. This spacing was similar to that found in a Canadian population of Tree Swallows using natural cavities as nest sites (Robertson and Rendell 1990).

Swallows were captured using a variety of trapping methods. We identified the sex of captured swallows by noting the presence of a well developed brood patch in females or a cloacal protuberance in males. Each captured swallow was banded with a U.S. Fish & Wildlife Service band and given a unique color mark, using water-proof marking pens and acrylic paints to facilitate individual identification.

At 07:00 EDT on 2 June 1993 we captured, measured, weighed, and color-marked the breeding male from box 42 as he entered the nest box to deliver food to six-day-old nestlings. Because of banding activities, male 42 was released approximately 500 m from box 42 near box 87. Upon his release, male 42 flew directly toward his nest box. As he passed in front of box 86 he was chased by several male swallows. He landed on the top of box 86 which was unoccupied. After male 42 landed, several male swallows attempted to copulate with him. It was clear that these were copulation attempts, because the males were hovering over male 42 and were making the “ticking” vocalizations characteristic of heterosexual copulations in Tree Swallows. At least one male achieved cloacal contact with male 42. After approximately 1 min, male 42 flew from box 86 to box 85, which was also unoccupied, where the males again hovered over his back and attempted to copulate with him. One male was perched on male 42’s back for over 1 min and achieved cloacal contact more than once. All the while, the male held onto the feathers on the back of male 42’s head and neck with his bill. Males commonly grab the backs of female necks and heads during heterosexual copulations in Tree Swallows. It was impossible to count the number of cloacal contacts because of the “cloud” of swallows fluttering around male 42. After several minutes perched on box 85, male 42 flew to box 84 followed by his pursuers. Box 84 was unoccupied as well. Male 42 landed on the top of box 84 and the events at boxes 86 and 85 were repeated. After approximately 1 min on top of box 84, male 42 disappeared in the direction of box 42, pursued by the group of male swallows.

There are several explanations for homosexual behavior in non-human animals. First, it is possible that the pursuers misidentified male 42 as a female because the plumage of after second year female Tree Swallows resembles that of males (Hussell 1983). Mistaken identity is a common explanation for homosexual mountings in insects (Thornhill and Alcock 1983). Both Birkhead et al. (1985) and Hatchwell (1988) concluded that homosexual mountings in the Common Murre were the result of mistaken identity; in their pursuit of extra-pair copulations, male Common Murres attempted to copulate with any individuals that returned to the breeding colony. Common Murres are sexually monomorphic. While mistaken identity

may explain why male 42 was pursued, it does not explain why he did not resist the copulation attempts and cloacal contact. Female Tree Swallows control copulation success (Lifjeld and Robertson 1992) and easily resist copulation attempts from extra-pair males and their mates alike by deflecting their tails preventing cloacal contact or by flying away (Venier et al. 1993; Lombardo, unpubl. data). We are positive that male 42 was a male for several reasons; it had a cloacal protuberance; it did not have a brood patch; its wing chord was 119 mm (Stutchbury and Robertson 1987); and the female at 42 had been marked previously and we had observed her incubating eggs. During observations during the nestling period, we observed male 42 assisting in the feeding of the nestlings in box 42 and defending the nest from our intrusions.

Second, homosexual behavior is sometimes seen in the context of reconciliation in primates (e.g., deWaal 1989). Reconciliation between prior antagonists is an unlikely explanation in this case because Tree Swallow sociality is not as complex as that of primates, and because the repeated interactions between individuals that favor reconciliation as a means of settling disputes are uncommon between distantly spaced breeding and relatively short-lived Tree Swallows (Butler 1988).

Third, expressions of dominance, subordination, and appeasement are sometimes manifested as homosexual behavior (e.g., deWaal 1989). Interestingly, male Cattle Egrets that attempted homosexual copulations always ranked higher than, or equal to, the males that were targets of those attempts (Fujioka and Yamagishi 1981). This is a possible explanation for our observations, but it suggests a previously unimagined complexity of Tree Swallow sociality. However, it is of note that nests of the Cattle Egrets studied by Fujioka and Yamagishi (1981) were more closely spaced (average distance between nests of less than 2 m, Fujioka and Yamagishi 1981, Fig. 1) than those of Tree Swallows at our study site, thereby increasing the probability of establishment of dominance hierarchies between Cattle Egrets that have frequent interactions with each other. It is possible that male 42 may have avoided injury from his pursuers by displaying his subordination to them by allowing them to copulate with him. Tree Swallows are capable of inflicting serious injuries on one another during fights (Lombardo 1986).

Fourth, Sauer (1972) hypothesized that homosexual behavior served as an outlet for sexual tension in South African Ostriches (*Struthio camelus*). This is an unlikely explanation for our observations, because we did not observe courtship displays, only chases, copulation attempts, and copulations.

Fifth, sexual play and experimentation are sometimes hypothesized as the explanation for homosexual behavior, especially by juveniles (Ford and Beach 1980). Sexual play and experimentation are unlikely as explanations for what we observed, because all of the males were sexually mature, and the interaction appeared aggressive rather than playful.

Møller (pers. comm.) has suggested that male birds may participate in homosexual copulations as a means of indirectly obtaining extra-pair copulations; sperm deposited by one male in the cloaca of another male could then be passed to the copulation partner of the latter when he copulates with a female. This explanation, while intriguing, is not completely satisfactory, because a stressed bird often defecates, voiding its cloaca of its contents. Male 42 defecated while we handled him, and he was undoubtedly stressed again by the onslaught of the males chasing attempting to copulate with him. We did not record whether he defecated during or after the sequence of events described above.

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Evidence of plural breeding by Red-cockaded Woodpeckers.—The endangered Red-cockaded Woodpecker (*Picoides borealis*) is a cooperatively breeding picid associated with mature pine forests of the southeastern United States (USFWS 1985, Walters 1990). Family groups typically consist of a monogamous breeding pair with one or more of their adult offspring serving as helpers (Ligon 1970, Lennartz et al. 1987, Walters et al. 1988). Helpers, which are almost exclusively male (Walters et al. 1988, Walters 1990), assist with incubation and feeding of nestlings (Lennartz and Harlow 1979). Breeding females typically produce a single clutch of 3–4 eggs (range 1–5) (Ligon 1970, Carter et al. 1983, Walters et al. 1988), although they will often renest if the eggs are lost to predation (Walters 1990). The nest usually is in the roost cavity of the breeding male (Ligon 1970, Walters et al. 1988).

We here report on some unusual nesting behavior exhibited by a group of Red-cockaded