dergraduate Research Program to R. M. Bosman and me from Grand Valley State University.

LITERATURE CITED

BIRKHEAD, T. R., AND A. P. MØLLER. 1992. Sperm competition in birds. Evolutionary causes and consequences. Academic Press, London.

COHEN, R. R. 1985. Capturing breeding male Tree Swallows with feathers. N. Am. Bird Bander 10: 18–21.

HAMILTON, W. D. 1990. Mate choice near or far. Am. Zool. 30:341–352.

HUNTER, F., M. PETRIE, M. OTTRONEN, T. R. BIRKHEAD, AND A. P. MØLLER. 1993. Why do females copulate repeatedly with one male? Trends Ecol. & Evol. 8:21–26.

KUERZI, R. G. 1941. Life history studies of the Tree Swallow. Proc. Linn. Soc. N.Y. 52–53:1–52.

LIFJELD, J. T., P. O. DUNN, R. J. ROBERTSON, AND P. T. BOAG. 1993. Extra-pair paternity in monogamous Tree Swallows. Anim. Behav. 45:213–229.

LOMBARDO, M. P. 1994. Nest architecture and reproductive performance in Tree Swallows. Auk 111: 814–824.

LOMBARDO, M. P., R. M. BOSMAN, C. A. FARO, S. G. HOUTTEMAN, AND T. S. KLUISZA. 1995. Effects of feathers as nest insulation on incubation behavior and reproductive preformance of Tree Swallows (*Tachycineta bicolor*). Auk 112:973–981.

PETRIE, M. 1992. Copulation frequency in birds: Why do females copulate more than once with the same male? Anim. Behav. 44:790–792.

ROBERTSON, R. J., B. J. STUTCHBURY, AND R. R. COHEN. 1992. Tree Swallow. *In* The birds of North America, No. 11 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

SHEPPARD, C. D. 1977. Breeding in the Tree Swallow, *Iridoprocne bicolor*, and its implications for the evolution of coloniality. Ph.D. thesis, Cornell Univ., Ithaca, New York.

VENIER, L. A., AND R. J. ROBERTSON. 1991. Copulation behaviour of Tree Swallows, *Tachycineta bicolor*: Paternity assurance in the presence of sperm competition. Anim. Behav. 42:939–948.

WHITTINGHAM, L. A., P. O. DUNN, AND R. J. ROBERTSON. 1993. Confidence of paternity and male parental care: An experimental study in Tree Swallows. Anim. Behav. 46:139–147.

WHITTINGHAM, L. A., P. O. DUNN, AND R. J. ROBERTSON. 1994. Do female Tree Swallows guard their mates by copulating frequently? Anim. Behav. 47:994–997.

WINKLER, D. W. 1993. Use and importance of feathers as nest ling in Tree Swallows (*Tachycineta bicolor*). Auk 110:29–36.

Received 21 March 1995, accepted 29 June 1995.

The Auk 112(4):1079–1080, 1995

Do Males Exchange Feathers for Copulations in Tree Swallows?

LINDA A. WHITTINGHAM[1], PETER O. DUNN[1], AND RALEIGH J. ROBERTSON
Department of Biology, Queen's University, Kingston K7L 3N6, Canada

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

[1] Present address: Museum of Natural Science, 119 Foster Hall, Louisiana State University, Baton Rouge, Louisiana 70803, USA.

within-pair copulation rate and the beneficial effects of feathers. As a result, we expect a positive relationship between within-pair copulation rate and the number of feathers only for females that nest early in the breeding season when they are beneficial. Later in the breeding season, when ambient temperatures are higher, nest feathers are actually harmful because nestlings are at greater risk of hyperthermia (Lombardo 1994). If copulation rate is related to the beneficial effects of feathers, then we expect copulation rate to decrease with laying date. This prediction is not upheld in Tree Swallows because within-pair copulation rate is not related inversely to laying date (attempted copulations, $r^2 = 0.01$, $P = 0.62$; cloacal contacts, $r^2 = 0.02$, $P = 0.53$, $n = 21$; data from Dunn et al. 1994).

In support of his hypothesis, Lombardo (1995) argued that males will not cheat on their mates even though there is a substantial delay between the timing of copulations (prior to egg laying) and the time when nest feathers are provided (during egg laying and incubation). This is because males risk negatively affecting their own reproductive success if they do not provide feathers. Inherent in this argument is the assumption that a higher frequency of within-pair copulations is related positively to the male's certainty of paternity. However, in Tree Swallows, within-pair copulation rate is not related to paternity (Lifjeld et al. 1993) or to the male's confidence of paternity (Whittingham et al. 1993). In our experiment, even though males were removed during large portions of the female's fertile period, they did not adjust their level of parental care in terms of feeding nestlings or intensity of nest defense (Whittingham et al. 1993). Thus, male Tree Swallows provided high levels of parental investment regardless of their prior within-pair copulation rate. As Lombardo (1995) pointed out, providing feathers for nest lining is just another form of male parental investment and, thus, he proposed that one form of parental investment (feather lining) should be related to the within-pair copulation rate, even though other forms of parental investment (feeding and defending young) are not related.

Lombardo's hypothesis essentially states that females may successfully coerce their mate into providing feathers for nest lining by copulating more frequently with him. However, if feathers influence positively the male's reproductive success, then it is unclear why females should need to coerce males into providing feathers. Furthermore, it is unlikely that male Tree Swallows will need to be coerced into providing one form of parental care (feathers) when males provide high levels of other forms of parental care (feeding nestlings and nest defencse) regardless of their within-pair copulation rate or paternity.

Literature Cited

Dunn, P. O., R. J. Robertson, D. Michaud-Freeman, and P. T. Boag. 1994. Extra-pair paternity in Tree Swallows: Why do females copulate with more than one male? Behav. Ecol. Sociobiol. 35: 273–281.

Lifjeld, J. T., P. O. Dunn, R. J. Robertson, and P. T. Boag. 1993. Extra-pair paternity in monogamous Tree Swallows. Anim. Behav. 45:213–229.

Lombardo, M. P. 1994. Nest architecture and reproductive performance in Tree Swallows. Auk 111: 814–824.

Lombardo, M. P. 1995. Within-pair copulations: Are female Tree Swallows feathering their own nests? Auk 112:1077–1079.

Robertson, R. J., B. J. Stutchbury, and R. R. Cohen. 1992. Tree Swallow. *In* The birds of North America, No. 11 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Whittingham, L. A., P. O. Dunn, and R. J. Robertson. 1993. Confidence of paternity and male parental care: An experimental study in Tree Swallows. Anim. Behav. 46:139–147.

Whittingham, L. A., P. O. Dunn, and R. J. Robertson. 1994. Do female Tree Swallows guard their mates by copulating frequently? Anim. Behav. 47:994–997.

Received and accepted 17 November 1995.