placement based on prior experience? Animal Behavior 36:1–10.

MAYFIELD, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

MORTON, M. L., K. W. SOCKMAN, AND L. E. PETERSON. 1993. Nest predation in the Mountain White-crowned Sparrow. Condor 95:72–82.

OSBORNE, P., AND L. OSBORNE. 1980. The contribution of nest site characteristics to breeding success among Blackbirds *Turdus merula.* Ibis 122:512–517.

PAYNE, R. B. 1991. Indigo Bunting (*Passerina cyanea*). *In* The birds of North America, no. 4 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

PETERJOHN, B. G., J. R. SAUER, AND C. S. ROBBINS. 1995. Population trends from the North American Breeding Bird Survey. Pages 3–39 *in* Ecology and management of Neotropical migratory birds (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.

ROBERTSON, R. J. 1972. Optimal niche space of the Red-winged Blackbird (*Agelaius phoeniceus*). Part 1. Nesting success in marsh and upland habitat. Canadian Journal of Zoology 50:247–263.

ROBINSON, S. K., F. R. THOMPSON III, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

SAUER, J. R., AND B. K. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival of recovery rates. Journal Wildlife Management 53:137–142.

SCHAUB, R., R. L. MUMME, AND G. E. WOOLFENDEN. 1992. Predation on the eggs and nestlings of Florida Scrub Jays. Auk 109:585–593.

SHERRY, T. W., AND R. T. HOLMES. 1992. Population fluctuations in a long distance Neotropical migrant: Demographic evidence for the importance of breeding season events in the American Redstart. Pages 431–442 *in* Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington D.C.

SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–455.

SUTTON, G. M. 1960. The nesting fringillids of the Edwin S. George Reserve, southwestern Michigan, part IV. Jack-Pine Warbler 38:46–65.

THOMPSON, C. F., AND V. NOLAN, JR. 1973. Population biology of the Yellow-breasted Chat (*Icteria virens*) in southern Indiana. Ecological Monographs 43:145–171.

WESTMORELAND, D., AND L. B. BEST. 1985. The effect of disturbance on Morning Dove nesting success. Auk 102:774–780.

WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214.

WRAY, T. II, AND R. C. WHITMORE. 1979. Effects of vegetation on nesting success of Vesper Sparrows. Auk 96:802–805.

YOUNG, H. 1963. Age-specific mortality in the eggs and nestlings of blackbirds. Auk 80:145–155.

ZIMMERMAN, J. L. 1984. Nest predation and its relationship to habitat and nest density in Dickcissels. Condor 86:68–72.

Received 17 March 1998, accepted 22 June 1998.
Associate Editor: T. E. Martin

The Auk 116(1):264–269, 1999

Floater Males Engage in Extrapair Copulations with Resident Female Tree Swallows

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Floaters are sexually mature yet nonbreeding, nonterritorial individuals (Smith 1978). They are common in many passerine species and avian social systems (see Zack and Stutchbury 1992) but relatively little is known about them. Floating behavior ultimately arises through an excess of sexually mature individuals trying to procure a limited number of nesting sites (Brown 1969, Smith and Arcese 1989). It has been described as an alternative reproductive strategy to territoriality (Austad 1984) and as a behavior based on quality differences among individuals (Smith and Arcese 1989). Floaters are characterized by their frequent intrusions into occupied ter-

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ritories to search for nesting sites (Arcese 1987, Stutchbury 1991) or to attempt extrapair copulations with resident females (Dunbar 1982). In the latter case, males potentially could gain reproductive success without the costs of territory defense and parental care. However, this latter scenario is thought to be unlikely because male floaters typically are deemed to be inferior in quality to resident males (Brown 1969, Smith 1978).

Tree Swallows (*Tachycineta bicolor*) are migratory, secondary cavity nesters and are nest-site limited (Holroyd 1975). Competition for nesting opportunities is intense, and a portion of the population consists of floaters of both sexes (Stutchbury and Robertson 1985, 1987; Barber 1997). Tree Swallows exhibit a high degree of natal dispersal followed by intense breeding-site fidelity (Robertson et al. 1992). Once established as breeders, males typically use the same nest box every year, whereas females usually breed in a different nest box within the same study site (Barber 1997).

Although Tree Swallows are socially monogamous (both the male and female defend a nest site and feed the young) they are not genetically monogamous (Lifjeld and Robertson 1992, Lifjeld et al. 1993, Barber et al. 1996). Indeed, in some populations as many as 87% of the females obtain extrapair fertilizations (Dunn et al. 1994), and up to 69% of the young are sired by extrapair males (Barber et al. 1996). Resident males sire only 20% of all extrapair young (Dunn et al. 1994); therefore, the majority of extrapair males must be either floaters or birds that breed outside the study population.

Despite this high frequency of extrapair paternity (which is among the highest recorded for any passerine) and the loud, frequent, and conspicuous nature of within-pair copulations (Venier and Robertson 1991), observations of extrapair copulations by Tree Swallows are uncommon (Lifjeld et al. 1993, Venier et al. 1993). The purpose of this study was to examine the behavior of floater males in a breeding population of Tree Swallows and to determine which, if any, individuals gained extrapair copulations and fertilizations with resident females.

Study area and methods.—In 1992, we studied a nest-box population of Tree Swallows breeding in a hayfield located on the Hughson Tract of the Queen's University Biological Station in southeastern Ontario, Canada (44°34'N, 76°19'W). The study grid contains 18 nest boxes in which Tree Swallows have been breeding since 1976. Nest boxes are set up in five rows, with rows 1, 3, and 5 having four nest boxes each, all parallel to each other, and rows 2 and 4 having three nest boxes each, also parallel to each other (Fig. 1). The even numbered rows are staggered from the odd numbered rows such that a box in row 1 is 40 m away from a parallel box in row 3, and a box in row 2 is 28 m away from a diagonal box in row 3. Tree Swallows occupied every box in 1992.

During April and early May, we captured and sexed Tree Swallows on the study site and marked them with unique acrylic paint codes so that they would be easily identified from a distance. Because we did not want to influence copulation patterns, we stopped capturing birds once the first copulation was observed. We conducted daily surveys at each nest box to determine residency status of the marked individuals.

To determine the frequency with which extrapair copulations occurred, we conducted extensive watches of the boxes from 10 to 26 May between 0530 and 1200 EST. These 17 days encompassed the prelaying, laying, and incubation stages. Two people observed breeding pairs at three different nest boxes each for 30 min before rotating through to the next three boxes. Thus, between the two observers, one complete rotation of observations at all 18 nests took 1.5 h, with an additional 30-min watch being conducted to survey the entire grid. We did 2.75 to 3 rotations every morning, resulting in 5.5 to 6 hour-long daily watches. The between-day watches were staggered such that we started with a different set of nest boxes every day over a four-day period. We noted every copulation and attempted copulation (within-pair and extrapair) that occurred and also noted the participating individuals, the solicitor, the time of occurrence, the number of cloacal contacts, and the general behavior of the birds involved. By definition, a "copulation" occurred when a male made successful cloacal contact at least once with a female, and an "attempt" occurred when a male attempted to alight on a female's back while making copulatory sounds (Venier et al. 1993), but failed to make cloacal contact. We observed birds for 192 h (between two people) in the mornings, 5 h one afternoon, and 5.5 h during four evenings, resulting in a total of 202.5 h of observation.

We conducted DNA fingerprinting (Lifjeld et al. 1993, Barber et al. 1996) on 15 families. Unfortunately, we were unable to obtain blood from three families whose nests failed (Fig. 1). The first nesting attempt at box B4 failed when the female disappeared early in the incubation period, but the male subsequently renested successfully with another female.

Nestlings were considered to be extrapair if: (1) their band-sharing coefficient (Wetton et al. 1987) was less than 0.40 with the social male or female, and (2) they had more than four novel bands for both the *per* (Shin et al. 1985) and Jeffreys' 33.15 (Jeffreys et al. 1985) probes combined (see Lifjeld et al. 1993, Barber et al. 1996). All extrapair young were genetically related to the social female.

Results.—We observed 17 extrapair copulations and copulation attempts (eight extrapair copulations, eight extrapair attempts, and one unknown whether copulation or attempt) during 202.5 h of observation (Table 1, Fig. 1). All but one (male D6 with female C7; Table 1) occurred during the female's fer-

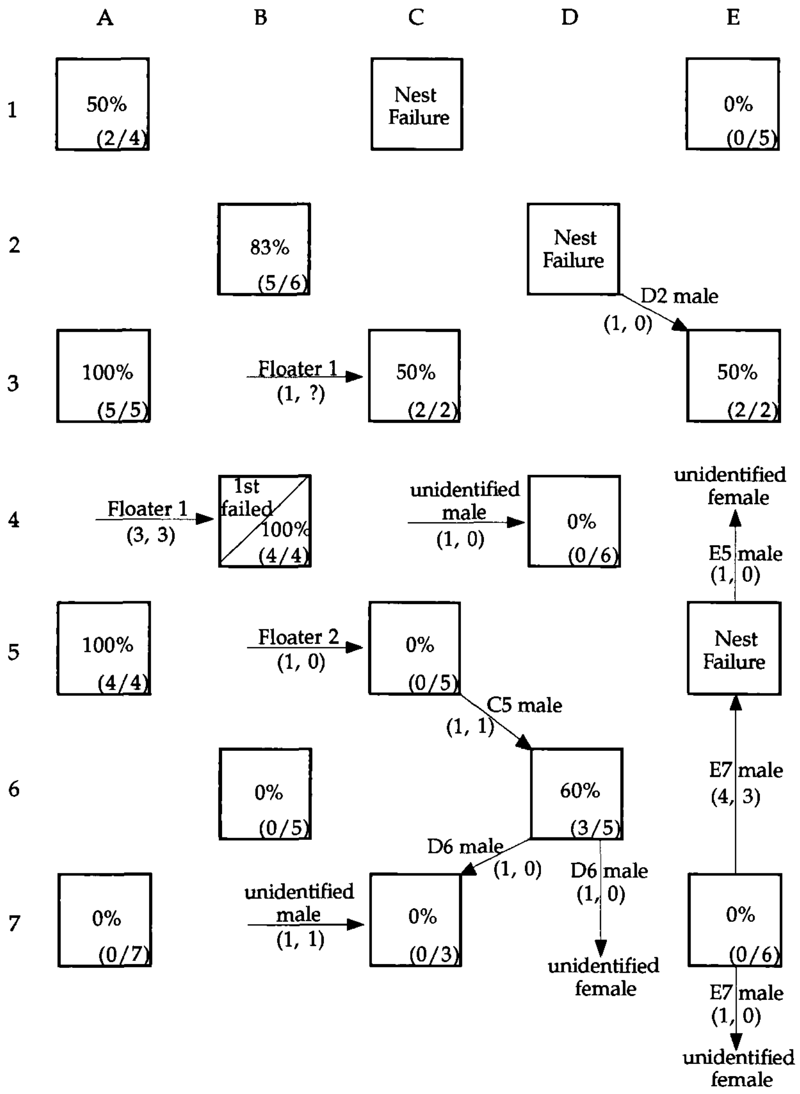

FIG. 1. Schematic representation of extrapair attempts and copulations in Tree Swallows. Boxes represent nest boxes; the percentage of extrapair young is shown in center of each box; the number of extrapair young per brood is shown in parentheses in the right-hand corner of box. Arrows indicate extrapair attempts and extrapair copulations by floater males (1 and 2), resident males (shown by their nest box), and unidentified males with resident females (arrows point to female's nest box) or unidentified females. Unidentified males and females were extrapair. Numbers in parentheses by arrows indicate the number of extrapair attempts and successful extrapair copulations, respectively.

tile period (i.e. the period from eight days prior to the first egg through laying of the penultimate egg; Birkhead 1988). Resident males were no more successful than floaters in gaining actual copulations with resident females (4/10 vs. 3/4, respectively; Fisher's exact test, $P = 0.56$). About one-third (5/17) of the extrapair copulations and copulation attempts were achieved by two floater males (both of whom had been marked with a paint code). We believe they were floaters because they were sexually mature and appeared to be nonterritorial (i.e. they did not reside on any of our other study sites). Other floater males were seen on the study site but were never observed in extrapair matings. Five of the 18 resident males accounted for 10 other extrapair copulations/attempts. The male(s) involved in two of the extrapair copulations/attempts could not be identified, but they were not the social mates of the resident fe-

TABLE 1. Summary of extrapair copulation attempts and successful extrapair copulations observed in Tree Swallows in 1992. NSM = not social mate.

Male	Female	No. attempts	No. successful	No. cloacal contacts	Offspring sired by extrapair male?
Floater 1	B4	3	3	17	No data (nest B4 failed)
Floater 1	C3	1	Unknown	Unknown	No
Floater 2	C5[a]	1	0	0	No (interrupted by social male)
C5	D6	1	1	3	No
D2	E3	1	0	0	No
D6	NSM[b]	1	0	0	Unknown
D6	C7[b]	1	0	0	No
E5	NSM	1	0	0	Unknown
E7	E5[a,b]	4	3	10	No data (nest E5 failed)
E7	NSM[b]	1	0	0	Unknown
NSM	C7	1	1	2	No
NSM	D4	1	0	0	No

[a] Copulation was solicited by female.

[b] Female was unreceptive (snapped at male or flew away); females cooperated in all other cases.

males. Similarly, two females could not be identified but were residents on the study site.

Floater 1 obtained at least three and maybe four extrapair copulations, whereas Floater 2 did not succeed in his one extrapair attempt (Table 1). Floater 1 was successful in copulating with two of the resident females. He did not, however, sire either of the two extrapair young in the C3 brood (band-sharing coefficients of the two extrapair young with Floater 1 were 0.17 and 0.16, and the numbers of novel bands were 15 and 15, respectively). Unfortunately, the nesting attempt of the other female with whom he copulated (B4) failed, so we could not determine if he gained paternity in this brood. Floater 1 eventually settled at box C1 (paired with the resident female) after the resident male disappeared, but only after numerous fights with the B2 male, who also "wanted" this nest box in addition to his own. The C1 female had just laid her fourth egg when Floater 1 settled. She laid her fifth egg three days later, but the nest failed during hatching.

Of the five resident males observed attempting or actually procuring extrapair copulations, the most successful male, E7, accounted for half (5/10) of these observations; he also had no extrapair young in his own brood (Fig. 1). We were unable to determine whether he sired young in his extrapair mate's nest (E5) because it failed during incubation owing to the disappearance of one of the residents. The male from C5 also had an extrapair copulation with the female at D6, but he did not gain paternity through it (band-sharing coefficients of the three extrapair young with this male were 0.22, 0.28, and 0.25, and the numbers of novel bands were 19, 18, and 16, respectively). The C5 male sired all of the young in his own brood (Fig. 1). The male from D2 attempted an extrapair copulation with the female residing at E3 but did not achieve cloacal contact. His own nest eventually failed. Extrapair young were present in E3, but it is unknown if they were sired by the D2 male because we were unable to obtain blood from him. The D6 male made two different attempts at extrapair copulations but was unsuccessful; 60% of his own brood consisted of extrapair young.

The number of observed extrapair copulations and copulation attempts varied from 0 to 4 for females and from 0 to 5 for males, but the distribution was not significantly skewed for either sex (tested against Poisson distribution; females, $\chi^2 = 0.72$, df = 1, $P = 0.40$; males, $\chi^2 = 2.74$, df = 1, $P = 0.10$). Of the resident females that did not attempt or engage in extrapair copulations during our observations, 50% (4/8) still had extrapair young within their broods (Fig. 1). Surprisingly, the C7 female was observed engaging in one successful extrapair copulation and rejecting another such attempt (Table 1), yet she did not have any extrapair young in her brood (Fig. 1).

Discussion.—Whether males were residents or floaters did not affect the frequency with which they obtained extrapair copulations with resident females. This result is somewhat surprising given that: (1) past studies of various species typically have considered floaters to be lower in quality or subordinate compared with residents (Brown 1969, Smith 1978), and (2) floaters have not been observed engaging in extrapair copulations (Buitron 1983, Arcese 1987, Morton et al. 1990). Additionally, detectable differences among residents and floaters have been noted. Smith and Arcese (1989) found that floater male Song Sparrows (*Melospiza melodia*) typically were first-year breeders. Similarly, a significantly higher proportion of younger (i.e. second-year) male Red-winged Blackbirds (*Agelaius phoeniceus*) were present in the "deep floater" group (i.e. males who replaced the replacement males) than in the owner or replacement male groups (Shutler and Weatherhead 1991). Barber et al. (1998) found that a significantly higher proportion of floater male Tree Swallows were new to the study site than were resident males. Floaters also had significantly smaller wing chords than the early settling resident males, suggesting that they were younger.

The two floater males made many intrusions into territories throughout the course of the breeding season and appeared to actively seek nest sites, not just access to fertile females. It is unlikely that these males nested in nearby natural cavities. Floater 1, after intrusions into various territories, eventually procured a nest box, settled, and paired with the resident female. In an experimental study where male resident Tree Swallows were removed from their nest box immediately before the female fertile period (Barber et al. 1998), floater males rapidly filled the vacancies and paired with the resident females. Because all floaters settled at a vacant nest box when given the opportunity, floating behavior in Tree Swallows does not appear to be an alternative strategy to residency in nest cavities.

Presumably, floating behavior is costly to overall reproductive success. In male Song Sparrows, floaters had low reproductive success over their lifetime (Smith and Arcese 1989). Tree Swallows are estimated to have an annual mortality rate of 40 to 60% (Chapman 1955, De Steven 1980), resulting in a high loss of reproductive success for any year in which they do not breed. Nevertheless, floater males would be able to increase their reproductive success if they obtained extrapair fertilizations with resident females.

Despite suggestions that floater males engage in effective extrapair copulations with resident females (Flood 1985, Weatherhead and Boag 1995), no such evidence has existed. We observed floater male Tree Swallows engaging in extrapair copulations with resident females, although these copulations did not result in fertilizations. Our sample size was small, and it remains possible that floater male Tree Swallows are responsible for at least some of the as yet unassigned extrapair young. Our results clearly show that floater male Tree Swallows do gain sexual access to resident females (at least occasionally) and also suggest that floaters are not necessarily the inferior individuals they were once thought to be.

Acknowledgments.—We are grateful to Mark Hovorka and Kelvin Conrad for their assistance with the field work. We thank everyone at the Queen's University Biological Station for providing a great atmosphere in which to work. Jim Briskie, Wally Rendell, John Eadie, and two anonymous reviewers provided constructive suggestions on previous drafts of the manuscript. Funding was provided by an NSERC grant to RJR, and grants to CAB from the North American Bluebird Society, the Animal Behavior Society, the Society of Canadian Ornithologists (Taverner Award), the Frank M. Chapman Memorial Fund, the Sigma Xi Scientific Research Society, and the School of Graduate Studies and Research at Queen's University.

LITERATURE CITED

ARCESE, P. 1987. Age, intrusion pressure and defence against floaters by territorial male song sparrows. Animal Behaviour 35:773–784.

AUSTAD, S. N. 1984. A classification of alternative reproductive behaviors and methods for field-testing ESS models. American Zoologist 24:309–319.

BARBER, C. A. 1997. Determinants of extra-pair paternity in the socially monogamous Tree Swallow, *Tachycineta bicolor.* Ph.D. thesis, Queen's University, Kingston, Ontario.

BARBER, C. A., R. J. ROBERTSON, AND P. T. BOAG. 1996. The high frequency of extra-pair paternity in Tree Swallows is not an artifact of nest boxes. Behavioral Ecology and Sociobiology 38:425–430.

BARBER, C. A., R. J. ROBERTSON, AND P. T. BOAG. 1998. Experimental mate replacement does not increase extra-pair paternity in Tree Swallows. Proceedings of the Royal Society of London Series B 265:1–4.

BIRKHEAD, T. R. 1988. Behavioral aspects of sperm competition in birds. Advances in the Study of Behavior 18:35–72.

BROWN, J. L. 1969. Territorial behavior and population regulation in birds: A review and re-evaluation. Wilson Bulletin 81:293–329.

BUITRON, D. 1983. Extra-pair courtship in Black-billed Magpies. Animal Behaviour 31:211–220.

CHAPMAN, L. B. 1955. Studies of a Tree Swallow colony. Bird-Banding 26:45–70.

DE STEVEN, D. 1980. Clutch size, breeding success, and parental survival in the Tree Swallow (*Iridoprocne bicolor*). Evolution 34:278–291.

DUNBAR, R. I. M. 1982. Intraspecific variations in mating strategy. Pages 385–431 *in* Perspectives in ethology (P. P. G. Bateson and P. H. Klopfer, Eds.). Plenum Press, New York.

DUNN, P. O., R. J. ROBERTSON, D. MICHAUD-FREEMAN, AND P. T. BOAG. 1994. Extra pair paternity in Tree Swallows: Why do females mate with more than one male? Behavioral Ecology and Sociobiology 35:273–281.

FLOOD, N. J. 1985. Indices of polygyny and extra-pair copulation in the Northern Oriole. Auk 102:410–412.

HOLROYD, G. L. 1975. Nest site availability as a factor limiting population size of swallows. Canadian Field-Naturalist 89:60–64.

JEFFREYS, A. J., V. WILSON, AND S. L. THEIN. 1985. Hypervariable 'minisatellite' regions in human DNA. Nature 314:67–73.

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

LIFJELD, J. T., AND R. J. ROBERTSON. 1992. Female control of extra-pair fertilizations in Tree Swallows. Behavioral Ecology and Sociobiology 31:89–96.

MORTON, E. S., L. FORMAN, AND M. BRAUN. 1990. Extra-pair fertilizations and the evolution of colonial breeding in Purple Martins. Auk 107:275–283.

ROBERTSON, R. J., B. J. STUTCHBURY, AND R. R. COHEN. 1992. Tree Swallow (*Tachycineta bicolor*). *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.

SHIN, H-S., T. A. BARGIELLO, B. T. CLARK, F. R. JACKSON, AND M. W. YOUNG. 1985. An unusual coding sequence from a *Drosophila* clock gene is conserved in vertebrates. Nature 317:445–448.

SHUTLER, D., AND P. J. WEATHERHEAD. 1991. Owner and floater Red-winged Blackbirds: Determinants of status. Behavioral Ecology and Sociobiology 28:235–241.

SMITH, J. N. M., AND P. ARCESE. 1989. How fit are floaters? Consequences of alternate territorial behaviors in a non-migratory sparrow. American Naturalist 133:830–845.

SMITH, S. M. 1978. The underworld in a territorial sparrow: Adaptive strategy for floaters. American Naturalist 112:571–582.

STUTCHBURY, B. J. 1991. Floater behaviour and territory acquisition in male Purple Martins. Animal Behaviour 42:435–443.

STUTCHBURY, B. J., AND R. J. ROBERTSON. 1985. Floating populations of female Tree Swallows. Auk 102:651–654.

STUTCHBURY, B. J., AND R. J. ROBERTSON. 1987. Behavioral tactics of subadult female floaters in the Tree Swallow. Behavioral Ecology and Sociobiology 20:413–419.

VENIER, L. A., P. O. DUNN, J. T. LIFJELD, AND R. J. ROBERTSON. 1993. Behavioural patterns of extra-pair copulation in Tree Swallows. Animal Behaviour 45:412–415.

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

WEATHERHEAD, P. J., AND P. T. BOAG. 1995. Pair and extra-pair mating success relative to male quality in Red-winged Blackbirds. Behavioral Ecology and Sociobiology 37:81–91.

WETTON, J. H., R. E. CARTER, D. T. PARKIN, AND D. WALTERS. 1987. Demographic study of a wild House Sparrow population by DNA fingerprinting. Nature 327:147–149.

ZACK, S., AND B. J. STUTCHBURY. 1992. Delayed breeding in avian social systems: The role of territory quality and "floater" tactics. Behaviour 123:194–219.

Received 13 November 1997, accepted 22 June 1998.
Associate Editor: J. M. Eadie

The Auk 116(1):269–273, 1999

Response of Female Hooded Mergansers to Eggs of an Interspecific Brood Parasite

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Brood parasitism is a common feature of the breeding biology of many precocial birds like waterfowl (Eadie et al. 1988, Rohwer and Freeman 1989, Sayler 1992), yet relatively little is known about how host females respond to parasitic eggs. Two potential responses are to remove them from the nest (Eadie 1989) or displace them to the clutch periphery (Mallory and Weatherhead 1993). Although such responses have been relatively well documented in passerines (Rothstein 1975) and in one precocial species (Ostrich [*Struthio camelus*]; Bertram 1979), most reports of discrimination against the eggs of brood parasites by waterfowl hosts are anecdotal (e.g. Weller 1959). The few studies that looked for host responses reported potentially conflicting results. Canvasbacks (*Aythya valisineria*) did not remove Redhead (*A. americana*) eggs from their nests or displace them to the outside of the clutch (Sayler 1996, Sorenson 1997). In contrast, parasitic eggs were lost significantly more often in both naturally and experimentally parasitized goldeneye (*Bucephala* sp.) nests (Eadie 1989). However, within goldeneye clutches, parasitic eggs were, if anything, more likely to oc-

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