mous 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

BRUCE D. DUGGER,[1] LIA C. BOLLMANN, AND LEIGH H. FREDRICKSON
Gaylord Memorial Laboratory, School of Natural Resources, University of Missouri, Puxico, Missouri 63960, USA

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-

---

[1] Present address: Cooperative Wildlife Research Lab, Southern Illinois University, Carbondale, Illinois 62901, USA. E-mail: bdugger@siu.edu

cupy central positions (Eadie 1989). Eadie (1989) noted that eggs used to experimentally parasitize nests had substantially thinner shells and hypothesized that they broke more frequently than host goldeneye eggs. Thus, rather than being a response to parasitism, egg removal may have occurred in response to broken eggs (Eadie 1989).

The best evidence for host discrimination against parasitic eggs in waterfowl comes from a study of Hooded Mergansers (*Lophodytes cucullatus*) in which parasitic Common Goldeneye (*Bucephala clangula*) eggs were more likely to occupy outside positions in the clutch (Mallory and Weatherhead 1993). Although the cost of brood parasitism to Hooded Mergansers is unknown, Mallory and Weatherhead (1993) hypothesized that the relatively short incubation period of goldeneye eggs increased the risk that the female merganser would leave the nest with the goldeneye ducklings before all of her own eggs hatched. Displacing parasitic eggs to the periphery likely reduces incubation efficiency (Drent 1975), potentially prolonging or preventing successful incubation of the parasitic eggs. Furthermore, Mallory and Weatherhead suggested that the merganser's uniquely shaped egg and the bluish-green color of goldeneye eggs (merganser eggs are white) permitted successful discrimination between the host and parasitic eggs, even in the dark environment of a cavity.

Hooded Mergansers are also known to remove goldeneye and Wood Duck (*Aix sponsa*) eggs from their nests (Mallory and Weatherhead 1993, Dugger et al. 1994), but the frequency and function of such removals are unclear. The influence of brood parasitism on the fitness of Hooded Merganser hosts is unknown. Wood Duck eggs have shorter average incubation periods than do Hooded Mergansers eggs (30 vs. 32 days; Bellrose and Holm 1994, Dugger et al. 1994), which has resulted in female mergansers abandoning their unhatched eggs to tend Wood Duck ducklings (L. H. Fredrickson unpubl. data). Thus, selective pressures may favor egg recognition by female Hooded Mergansers. Alternatively, the spherical shape and exceptionally thick shells of Hooded Merganser eggs (Wood Ducks = 0.32 mm, Hooded Merganser = 0.64 mm; Mallory and Weatherhead 1990) suggest that these eggs should be less prone to breakage in mixed clutches than are Wood Duck eggs (Spaw and Rohwer 1987). If females remove broken eggs, this may account for observed egg losses (Eadie 1989). Currently, no data exist concerning the importance of relative eggshell strength in egg loss from the nests of precocial birds. In this study, we quantified the removal of Wood Duck eggs from Hooded Merganser nests and performed an experiment to test whether egg removal was a specific response to brood parasitism or a response to egg breakage in the nest. We also tested the generality of Mallory and Weatherhead's (1993) conclusions on the position of parasitic eggs within Hooded Merganser clutches using a different interspecific parasite.

Study area and methods.—The study was conducted on the Duck Creek Wildlife Conservation Area and Mingo National Wildlife Refuge in Stoddard and Bollinger counties, southeastern Missouri. Hooded Merganser nests were located from March to June, 1994 and 1995, during periodic checks of artificial nest boxes. We used two egg-addition experiments to help detect and understand egg ejection by female Hooded Mergansers.

To estimate the frequency of interspecific egg loss, fresh Wood Duck eggs were added to a sample of merganser nests. We only added eggs to nests that contained 15 or fewer merganser eggs. However, we did not remove eggs laid by parasites (Wood Duck or merganser) after our experimental egg additions, so final egg totals varied. Nests received either two or five eggs in 1994 and three or six eggs in 1995. Additions of two or three eggs occurred at the same time. To avoid desertion caused by adding large numbers of eggs (Andersson and Eriksson 1982, Eadie 1989), additions of five and six eggs occurred on consecutive nest visits less than one week apart. For similar reasons, no eggs were added while the host was laying; instead, eggs were added during the first two weeks of incubation. All eggs were individually marked.

Nests were visited periodically between the time of egg additions and hatching to record the presence and position of individually marked eggs. We recorded the position of each egg in the clutch as either peripheral (i.e. at least one side of the egg against the nest-box wall) or central (i.e. surrounded on all sides by other eggs). If female Hooded Mergansers discriminated against Wood Duck eggs, we predicted that more Wood Duck eggs than expected would be located on the nest periphery. To avoid confounding our egg-loss results, we did not purposefully place eggs in specific locations (e.g. central or peripheral) nor move eggs on subsequent nest checks as did Mallory and Weatherhead (1993).

To determine the function of egg removals, we added three natural Wood Duck eggs (control) and three Wood Duck eggs that had been coated with clear urethane (treatment) to a sample of merganser nests in 1995. The urethane coating increased eggshell strength without markedly changing the appearance and mass of the egg. The urethane was applied by dipping the eggs using a wire egg holder. A small spot at the air-pocket end of the egg was left uncoated to prevent gas buildup in the egg. Each addition of three eggs contained a mixture of coated and non-coated eggs. After additions, nests were checked as in the first experiment. If relative eggshell strength is an important determinant of egg loss from waterfowl nests (Eadie 1989), we predicted that coated (stronger) eggs would be lost less often (i.e. because they would be less likely to break and be removed). However, if egg removal was a specific response to parasitism, we predicted that egg loss would be similar for coated and uncoated eggs.

We used individual nests as our sample units during analysis. We compared observed egg loss with expected egg loss to test if Wood Duck eggs were lost in proportion to their abundance in the nest. We calculated expected values by multiplying the proportion of the total clutch (sum of merganser and Wood Duck eggs) lost from a nest by the total number of Wood Duck eggs added to the nest. For example, if five Wood Duck eggs were added to a merganser clutch of 15 eggs, and four eggs of either species were lost from the nest, the expected number of Wood Duck eggs lost would be 1.0 (i.e. [4/20] × 5).

Although our egg additions were not specifically designed to compare the loss of interspecific versus conspecific parasitic eggs, we tested this idea by calculating a second expected value using only eggs we attributed to brood parasites (i.e. our added Wood Duck eggs + eggs added by Hooded Merganser brood parasites). Because we were unable to definitively assign merganser eggs to either host or parasite, we estimated the number of parasitic merganser eggs by subtracting 13 (i.e. the maximum clutch size attributed to a single female; Dugger et al. 1994) from the total merganser clutch size. Thus, in the example cited previously, two eggs were attributed to conspecific brood parasitism (i.e. 15 − 13), and the expected number of Wood Duck eggs lost from the nest would be 2.9 (i.e. [4/7] × 5). This calculation assumes that all merganser eggs reported missing belonged to parasites. This, plus the fact that we underestimated the number of eggs added by conspecific brood parasites (e.g. nests with 15 merganser eggs may have had more than two parasitic eggs present), meant that our analysis was a conservative test that more Wood Duck eggs were lost from nests than were parasitic merganser eggs (i.e. expected values were biased high).

Analysis of egg-position data differed from egg removals because several visits to a nest were available for testing an individual female's response. For each visit, we calculated the expected number of Wood Duck eggs that should occupy central positions if egg placement was random (i.e. the proportion of the total clutch occupying central positions multiplied by the total number of Wood Duck eggs in the nest). Because the response of individual females was of interest, we then summed the sign values (expected − observed) for all visits to a specific nest to generate a single value for each nest. We compared expected to observed values for all experiments using sign tests. P-values for all tests except the egg-coating experiment were two-sided.

Results.—We added natural Wood Duck eggs to 22 merganser nests. All but three nests were visited at least three times between egg additions and hatching ($\bar{x}$ = 3.8, range 1 to 5). All but one nest successfully hatched ducklings. At least one Wood Duck egg was lost from 82% (18 of 22) of the nests, whereas a merganser egg was missing in only 18% (4 of 22) of these same nests. In all, 43 of the 80 Wood Duck eggs we added were lost from nests. More Wood Duck eggs than expected were missing in 18 of 19 nests (P = 0.0001; Fig. 1). The mean deviation of observed from expected was 1.86 eggs (95% C.I. = 1.42 to 2.3), with 14 of the 18 nests differing by at least one egg. Although small sample sizes precluded analyses, egg loss appeared to be influenced by merganser clutch size and by the number of Wood Duck eggs added to the nests (Table 1). Wood Duck eggs were lost from nests more often than the eggs of conspecific parasitic eggs in 12 of 14 nests (P = 0.013, n = 15; Fig. 1). Seven of the 12 nests differed from expectation by at least one egg ($\bar{x}$ = 1.24, 95% C.I. = 0.75 to 1.51). Data on egg position were collected on 16 nests. Wood Duck eggs were no more likely to occupy central positions as to occupy peripheral positions in the nest (P = 1.00; Fig. 1).

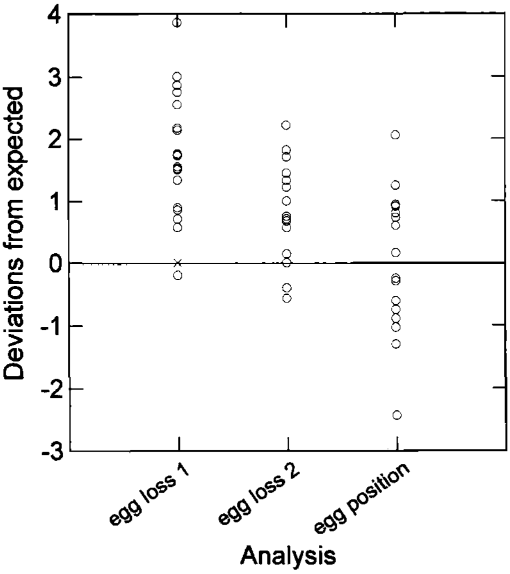

FIG. 1. Deviations of observed versus expected values for analyses of Wood Duck eggs in Hooded Merganser nests. Each circle represents a separate nest; three nests with the same value are represented by an "x." "Egg loss 1" tested that Wood Duck eggs were removed in proportion to their abundance in the nest. "Egg loss 2" compared removal between interspecific Wood Duck eggs and eggs of conspecific brood parasites. "Egg position" tested whether Wood Duck eggs occupied central positions in the clutch in proportion to their abundance.

We added coated and uncoated eggs to 11 merganser nests. Similar to our findings in the first experiment, at least one uncoated Wood Duck egg was

TABLE 1. Probability of Wood Duck egg loss (%) from Hooded Merganser nests relative to Hooded Merganser clutch size and number of Wood Duck eggs added to nest.

Merganser clutch size	No. of Wood Duck eggs added	
	2 to 3	5 to 6[a]
≤13	33 (3)[b]	100 (4)
14 to 16	50 (2)	100 (4)
≥17	83 (6)	100 (3)

[a] Includes one nest with 4 eggs.

[b] No. of merganser nests in parentheses.

missing in 72.7% of the nests. At least one coated egg was lost from 54.5% of nests. Two nests lost no eggs, one nest lost one egg from each group, and seven of the eight remaining nests lost non-coated eggs more often than coated eggs ($P = 0.035$).

Discussion.—Loss of Wood Duck eggs from Hooded Merganser nests was common. Eighty percent of our experimental nests lost at least one egg. Wood Duck eggs were more likely to disappear than were merganser eggs, regardless of how expected values were calculated (Fig. 1), indicating that Wood Duck eggs were removed from merganser nests more often than the eggs of conspecific parasites.

We assumed that all missing eggs were removed directly by host mergansers. An alternative explanation is that egg predators (in our case, black rat snakes [*Elaphe o. obsoleta*]) preferred Wood Duck eggs over merganser eggs (and presumably uncoated over coated Wood Duck eggs). This was unlikely because even in years of high snake depredation, rates never exceeded 29% (80% of our nests lost eggs), and we had no indication that rat snakes preferred Wood Duck eggs (Hansen and Fredrickson 1990).

In the absence of differential egg predation, we suggest that egg removal occurred either as a defense against brood parasitism or as a response to eggs broken in the nest during incubation. Uncoated Wood Duck eggs were more likely to disappear than were coated Wood Duck eggs, which is consistent with the hypothesis that relative eggshell strength influences survival of parasitic eggs in nests (Spaw and Rohwer 1987). We observed that four of our added Wood Duck eggs were broken and subsequently removed from the nest (more frequent nest checks likely would have detected more). Although specific experiments were not conducted to demonstrate that female Hooded Mergansers actively removed broken eggs (see Kemal and Rothstein 1988), observations of cracked eggs (even cracked host eggs) disappearing from the nests of other duck species are common (Joyner 1976, Eadie 1989, Dugger 1996, Sorenson 1997). Furthermore, broken eggs were more common in parasitized nests in several studies (Joyner 1976, Eadie 1989, Sayler 1996, Sorenson 1997). Together, this suggests that the relatively small and thin-shelled Wood Duck eggs were removed more often because they were more prone to breakage in mixed clutches.

Some coated eggs were removed from nests. This indicates either that some coated eggs were not impervious to being broken, or that females selectively ejected a proportion of the parasitic eggs. Furthermore, if Hooded Mergansers are puncture-ejectors, we cannot dismiss the possibility that the urethane coating prevented females from ejecting eggs they recognized as parasitic and "wanted" to remove (although we think it unlikely). However, if this were true, we would have expected females to at least displace these eggs to the nest periphery, as they reportedly do to goldeneye eggs (Mallory and Weatherhead 1993). Because coated eggs were not displaced to the nest periphery (Fig. 1), we suggest that most parasitic eggs were removed after breaking and not in response to brood parasitism.

Unlike Mallory and Weatherhead (1993), we found no evidence that female Hooded Mergansers displaced interspecific eggs to the clutch periphery (Fig. 1). Differences between studies may indicate that the bluish-green goldeneye eggs were easier for mergansers to recognize than were the off-white Wood Duck eggs in the dark environment of cavities (Mallory and Weatherhead 1993). Alternatively, differences between the two studies in how (naturally vs. experimentally) and when (unknown vs. during laying) parasitic eggs were added to nests could have elicited different host responses (Sorenson 1997). For example, if females recognized that eggs added during incubation will not hatch, we would not predict hosts to react to parasitic eggs in our study. However, additional experiments are needed to ensure that differences between our studies resulted from different host response and were not inadvertent outcomes of another factor like relative egg size (goldeneye > Hooded Merganser > Wood Duck). Experiments adding Wood Duck eggs during laying or Wood Duck eggs colored like goldeneye eggs are needed to distinguish between these explanations. Importantly, all of these explanations for differences in egg-placement results are inconsistent with the notion that egg removal is an antiparasite behavior.

We have demonstrated that Wood Duck egg loss from Hooded Merganser nests is common. Although our egg-coating experiment yielded results consistent with both incidental egg breakage and antiparasite behavior, we suggest that our egg-loss results in conjunction with egg-position results are more consistent with Eadie's (1989) hypothesis that egg removal is a response to broken eggs in the nest. Research that tests a female's response to broken eggs, and that determines how Wood Duck eggs break in merganser nests, is needed to confirm this interpretation. If the difference in eggshell strength between Wood Ducks and Hooded Mergansers is causing Wood Duck eggs to break in mixed clutches, comparisons of Wood Duck egg breakage in Wood Duck nests parasitized by Hooded Merganser versus nonparasitized nests may help to distinguish antiparasite behavior from incidental egg breakage and removal.

Acknowledgments.—Funding was provided by Gaylord Memorial Laboratory. We thank the staffs at Mingo NWR and Duck Creek WCA for allowing us to use their nest boxes, and D. E. Burhans, K. M. Dugger, J. M. Eadie, R. D. Sayler, and three anonymous reviewers for helpful comments on the manuscript. This is Missouri Agricultural Experiment Station Project 183, Journal Series Number 12,664.

LITERATURE CITED

ANDERSSON, M., AND M. O. G. ERIKSSON. 1982. Nest parasitism in Goldeneyes *Bucephala clangula*: Some evolutionary aspects. American Naturalist 120:1–16.

BELLROSE, F. C., AND D. L. HOLM. 1994. Ecology and management of the Wood Duck. Stackpole Books, Mechanicsburg, Pennsylvania.

BERTRAM, B. C. R. 1979. Ostriches recognize their own eggs and discard others. Nature 279:233–234.

DRENT, R. H. 1975. Incubation. Pages 333–407 *in* Avian biology, Vol. 5 (D. S. Farner and J. R. King, Eds.). Academic Press, New York.

DUGGER, B. D. 1996. The impact of brood parasitism on host fitness in Common Pochards and Tufted Ducks. Ph.D. dissertation, University of Missouri, Columbia.

DUGGER, B. D., K. M. DUGGER, AND L. H. FREDRICKSON. 1994. Hooded Merganser (*Lophodytes cucullatus*). *In* The birds of North America, no. 98 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

EADIE, J. M. 1989. Alternative reproductive tactics in a precocial bird: The ecology and evolution of brood parasitism in goldeneyes. Ph.D. dissertation, University of British Columbia, Vancouver.

EADIE, J. M., F. P. KEHOE, AND T. D. NUDDS. 1988. Prehatch and post-hatch brood amalgamation in North American Anatidae: A review of hypotheses. Canadian Journal of Zoology 66:1709–1721.

HANSEN, J. L., AND L. H. FREDRICKSON. 1990. Black rat snake predation on box nesting Wood Ducks. Pages 251–254 *in* The 1988 North American Wood Duck Symposium (L. H. Fredrickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, Eds.). St. Louis, Missouri.

JOYNER, D. E. 1976. Effects of interspecific nest parasitism by Redheads and Ruddy Ducks. Journal of Wildlife Management 40:33–38.

KEMAL, R. E., AND S. I. ROTHSTEIN. 1988. Mechanisms of avian egg recognition: Adaptive responses to eggs with broken shells. Animal Behaviour 36: 175–183.

MALLORY, M. L., AND P. J. WEATHERHEAD. 1990. Effects of nest parasitism and nest location on eggshell strength in waterfowl. Condor 92:1031–1039.

MALLORY, M. L., AND P. J. WEATHERHEAD. 1993. Responses of nesting mergansers to parasitic Common Goldeneye eggs. Animal Behaviour 46: 1226–1228.

ROHWER, F. C., AND S. FREEMAN. 1989. The distribution of conspecific nest parasitism in birds. Canadian Journal of Zoology 67:239–253.

ROTHSTEIN, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

SAYLER, R. D. 1992. Ecology and evolution of brood parasitism in waterfowl. Pages 290–322 *in* Ecology and management of breeding waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

SAYLER, R. D. 1996. Behavioral interactions among brood parasites with precocial young: Canvasbacks and Redheads on the Delta Marsh. Condor 98:801–809.

SORENSON, M. D. 1997. Effects of intra- and interspecific brood parasitism on a precocial host, the Canvasback. Behavioral Ecology 8:153–161.

SPAW, C. D., AND S. ROHWER. 1987. A comparative study of eggshell thickness in cowbirds and other passerines. Condor 89:307–318.

WELLER, M. W. 1959. Parasitic egg-laying in the Redhead (*Aythya americana*) and other North American Anatidae. Ecological Monographs 29:333–365.

Received 1 December 1997, accepted 22 June 1998.
Associate Editor: J. M. Eadie