RENESTING BY THE BLACK-BELLIED WHISTLING DUCK[1]

DON DELNICKI AND ERIC G. BOLEN

PRODUCTION of replacement eggs following loss of an initial clutch is important to the population dynamics of many avian species. Renesting enables birds to compensate partially for egg losses in spite of predation, flooding, and other factors that destroy nests. Sowls (1955) was one of the first to deal experimentally with the behavior of hens whose nests were destroyed during incubation. His study, involving five species of common ducks (*Anas* spp.), used individually marked birds, simulated destruction of initial nests, and systematic searches for the renests that might follow. Our work reports similar attempts to study renesting behavior among Black-bellied Whistling Ducks (*Dendrocygna autumnalis*) breeding in southern Texas.

METHODS

Eight study areas were selected within the region bordered by the Aransas River (to the north) and the Rio Grande (south). This region is marked by brushlands, coastal prairies, and marshes. Ranching and farming are important land-use activities. Thomas (*in* Gould 1969) described the climate, vegetation, topography, and edaphic features of the region.

Specific sites consisted of lakes and artificial ponds where predator-proof nesting boxes were erected earlier for various other studies of Black-bellied Whistling Ducks (Bolen 1967a, 1967b, 1970, and others). The sites are somewhat variable in their specific descriptions but, as these features are not critical to our results, further description is not necessary here. Our study of renesting relied on the utilization of predator-proof nest boxes, described elsewhere (Bolen 1967b), which were inspected routinely and a nest history recorded for each set of eggs discovered.

Once incubation began, the adult birds were captured in the nest boxes, banded with USFWS aluminum leg bands and individually marked with various color combinations of quick-drying aerosol spray applied to wing feathers. The large white wingpatch of the Black-bellied Whistling Duck lends itself to this type of temporary marking. As both male and female birds share incubation in this species, repeated visits to the nests usually let us catch both sexes, thus establishing records for known pairs of birds (cf. Bolen 1971).

Nest destruction was simulated by collecting clutches at various stages of incubation; eggs were incubated artificially and the surviving ducklings were banded and released at flying age. Abandonment and other causes of nest failure produced additional renests for study.

Renests were located by further inspection of all nest boxes. No efforts were made to inspect routinely natural tree cavities or ground plots, as earlier studies showed

[1] Welder Contribution No. 171.

that the birds may nest at great distances from water, making additional search for renests impractical (Bolen 1967a, Delnicki and Bolen 1975). Data concerning the persistence of renesting are therefore conservative, as some birds may have renested elsewhere than in the nest boxes. The fieldwork was conducted from May to August 1971 and May to October 1972.

RESULTS

Renesting courtship.—Sowls (1955: 99) reported "renesting courtship" in some species of waterfowl where the pair bond dissolves prior to hatching (e.g. Pintails, *Anas acuta*). Faced with the loss during incubation of her first clutch and abandonment by her drake, a hen must remate for a second nesting attempt, presumably by engaging in a second courtship. We detected no behavior recognizable as courtship among Black-bellied Whistling Ducks after the loss of their initial clutches. In this species the life-long pair bond precludes any need to attract a new mate (Bolen 1971), but we were unsure whether some specialized behavior might foster further copulation to insure fertility of the replacement clutch. None was apparent to us, although the precopulatory behavior in whistling ducks is, in any case, not at all obvious or distinctive (cf. Bolen and Rylander 1973). Copulation is sudden, sometimes beginning even before the female assumes a prone position, and the preceding behavior so closely resembles the unritualized activities of feeding, drinking, or bathing (Johnsgard 1961) that they do not appear as functional displays. Johnsgard later (1965: 24) suggested drinking movements by the male were a precopulatory display, noting that the hen may also perform similar movements.

Location of renests.—Repeated inspection of nest boxes showed that Black-bellied Whistling Ducks renested from 143 to 13,200 feet from the initial nest site. These distances are not significantly different from the year-to-year nest locations (Table 1).

Black-bellied Whistling Ducks thus followed the general pattern established for other waterfowl: birds do not renest at great distances from the original nest site, indicating considerable attachment to local breeding places. In other species mean distances reported between original and second nests were commonly less than 1000 feet (Sowls 1955: 137; Gates 1962; Coulter and Miller 1968: 42). Atwater (1959) found that Canada Geese (*Branta canadensis*) usually renested near their first nest's location, although one pair inexplicably moved 24 miles. Repeated nesting attempts within local areas presumably reflect the same selection process that led to the establishment of the initial nest, thus insuring maintenance of the local population and the full utilization of satisfactory nesting habitat.

TABLE 1
COMPARISON AND ANALYSIS OF DISTANCES BETWEEN INITIAL AND RENEST LOCATIONS WITH THE YEAR-TO-YEAR LOCATIONS OF INITIAL NESTS

	No. nests	Mean distance-feet
Year-to-year initial nests	20	4077
Renest locations	12	2328
Pooled df	30	—
Difference of means	—	1749
t value of differences: 0.2836[1]		
t value, $P = 0.05$: 2.042		

[1] Not significant.

Renesting interval.—The elapsed time between the loss of the first clutch and the first egg of the renest is the renesting interval (Sowls 1955: 133). The length of this period no doubt varies with several factors, among them the stage of incubation when the first nest was lost. The farther incubation has progressed, the longer the renesting interval, apparently because of the rapid regression of the hen's reproductive tract after the cessation of laying (Johnson 1961, Phillips and van Tienhoven 1962). The renesting interval was accordingly thought to vary rather directly in proportion to the stage of incubation so that the relationship could be predicted mathematically (cf. Sowls 1955: 134; Grice and Rogers 1965: 48). Coulter and Miller (1968: 49) summarized a larger set of data that proved highly variable, probably reflecting the influence of nutrition, genetics, age, and other population characteristics on the renesting interval. Black-bellied Whistling Ducks have an additional variable involving recrudescence of the male's testes, which regress as he incubates. We have little data concerning gonadal condition in relation to incubation, but hens engaged in laying had follicles nearly 40 mm in diameter—the testes of males accompanying these hens varied from 2–5 cc in volume. In contrast, a male found dead at a nest in the early stages of hatching (ca. 26 days of incubation) had testes 0.37 cc in volume.

Our efforts to calculate the renesting interval for Black-bellied Whistling Ducks were repeatedly thwarted by the high incidence of compound clutches, or "dump nesting." Several hens simultaneously laying in the nest boxes confounded our back-dating renests to determine when they were initiated. Only in a single instance was a renest known to be a clutch laid by one hen. In this case the initial nest was a dump nest abandoned after 15 days' incubation; 10 days later the hen began a second clutch of 12 eggs, which she never incubated. If Sowls' (1955: 134) prediction equation for the renesting interval of puddle ducks is

applied to our single observation, the calculated renesting interval is 12 days, or about 20% greater than actually occurred.

Extent of renesting.—A total of 57 pairs of Black-bellied Whistling Ducks was potentially available for renesting based on the loss of their initial clutches. Of these, 11 pairs (19%) were known to renest. This percentage compares favorably with the extent of renesting in other species. Hunt and Anderson (1966) found that 17% of 110 marked hens of 8 species of game ducks renested and that differential renesting rates exist among the species they studied. Similarly Sowls (1955: 139) earlier found that Pintails commonly renested (30%) whereas Blue-winged Teal (*Anas discors*) did so less often (6%). Coulter and Miller (1968: 47) analyzed data for 544 marked hens of 9 species of ducks (*Anas* and *Aythya* spp.) and found that, overall, 132 (24%) renested. Geis (1956) proposed that 30–40% of the unmarked Canada Geese she studied renested after losing their first clutch, but Atwater (1959) found that only 2 of 12 birds (17%) he marked actually renested. These data are, of course, conservative estimates as some renests undoubtedly were undetected.

Persistence of renesting.—Although some Black-bellied Whistling Ducks did not renest, other individuals persisted in their attempts to nest throughout the season. The second clutch (first renest) was taken from two pairs of birds; both renested a second time that season. Other workers (Sowls 1955, Gates 1962, Coulter and Miller 1968, and others) have also found second and even third renests; a fourth renest (fifth clutch) has been recorded in Mottled Ducks (*Anas fulvigula*) (Engeling 1949). Gates (1962) and Grice and Rogers (1965) each suggested that older females may be the more persistent renesters. When Coulter and Miller (1968: 48) compared 51 hens 2 years old or older with 65 hens of mixed ages, significantly more older birds renested (49%) than did those of mixed ages (31%). Hence the age structure of a waterfowl population seems important to the extent and persistence of renesting behavior, but we did not know the ages of the Black-bellied Whistling Ducks involved in our experiment above.

CHARACTERISTICS OF RENESTS

Bennett (1938: 57–58) and later Low (1945) tried to distinguish renests on the basis of one or more of the following: (1) reduced clutch size, (2) less abundant down in the nest lining and other physical features of the nest, and (3) the date the nest was initiated. These criteria are of little or no use for determining the renests of Black-bellied Whistling Ducks.

TABLE 2

CLUTCH SIZES FOR FIRST AND SUBSEQUENT NESTS OF BLACK-BELLIED WHISTLING DUCKS

Pair[1]	Initial clutch	First renest	Second renest
272 and 097	61	18	22
342 and 343	62	33	40[2]
954 and 375	52	15	
974 and 801	34	15	
985 and 973[3]	44	7	
803 and 817	42	22	
358 and 387	54	34	
429 and 435	22	25	
410 and 412[3]	48	20	
389 and 395[3]	24	7	
439 and 440	18	12	

[1] Designated by the last three digits of the band number.
[2] Additional 24 eggs were collected for other experiments.
[3] Renested after successfully hatching the initial clutch.

Clutch size.—Sowls (1955: 130) found that the average number of eggs in first clutches is statistically greater than the average number in renests, but the difference was not large enough to tell first clutches from renests. Other workers have reported similar results, although clutch sizes were often the same or larger than in the initial nest. The prevalence of dump nesting in Black-bellied Whistling Ducks again precluded any study of clutch size in relation to renesting, as shown in Table 2. The same problem limited determination of average clutch size in initial nests for this species although Bolen (1967a) estimated this as 13.4 eggs ($N = 58$, $S_d = 2.1$ eggs).

Abundance of down.—This criterion, including other physical features of the nest, is useless for determining renests as Black-bellied Whistling Ducks do not pluck or accumulate down as a nest material. As the nests are usually in tree cavities, the birds have no opportunity for varying the construction or degree of concealment. The utilization of nest boxes further eliminated nest concealment as a criterion in our study.

Date of nesting.—Waterfowl adapted to cool temperature zones tend to have early and rather well-defined breeding seasons so that when some nests are in fact begun later than normal, it may reasonably be assumed that these are renesting attempts. At the latitude of Delta, Manitoba Sowls (1955: 140) set 20 May as the date arbitrarily marking the beginning of renesting activities for Mallards (*Anas platyrhynchos*) and Pintails. Renesting may be of such magnitude (i.e. 10–50%) that a second peak of nesting occurs each season. For species adapted to warm temperate or tropical zones early nesting has no selective value because of the relatively long period for rearing broods (Weller 1964). Nesting seasons in such species may accordingly be long and without peaks of activity; Bolen (1967a) reported the average length of the nesting season

for Black-bellied Whistling Ducks as 109 days in southern Texas with no peak activity periods.

RENESTING AFTER NESTING SUCCESS

Although waterfowl are single brooded, instances of renesting following successful hatching of a brood are known to occur. Barnes (1948) reported a Wood Duck (*Aix sponsa*) hen that renested when her first brood was unable to leave a nesting box; Grice and Rogers (1965: 45) and McGilvrey (1966) likewise noted a second brood in Wood Ducks as have Errington (1934) and Bjarvall (1969) in Mallards and Sowls (1955: 136) in Pintails. For Black-bellied Whistling Ducks Johnson and Barlow (1971) reported the laying of a second clutch after an earlier clutch elsewhere in the same tree had successfully produced ducklings, but their case involved three unmarked birds, so what they believed to be a second nest may actually have been the first clutch of a second pair. Nonetheless such incidents, plus the species' extended nesting season, have promoted the notion that Black-bellied Whistling Ducks might annually raise two broods (Bent 1925: 270; Kortright 1942: 376).

Our records include three instances of renesting following successful hatches. Each involved at least one marked bird of each pair. In one case, the pair renested about 6 weeks after their first nest hatched. In another, about 8 weeks elapsed between hatching of the first nest and the start of the second clutch. The interval could not be estimated in the third case. The fates of the broods in these three cases are unknown. We believe that these renestings were induced by the loss of the first brood as the young otherwise remain with their parents for at least 6 months after hatching. Such occurrences are of course rare but further illustrate the persistence of renesting in Black-bellied Whistling Ducks. Moreover, the long renesting intervals between the loss of a brood and the successful production of young from a renest again reflect the long favorable nesting period in southern Texas for Black-bellied Whistling Ducks. Late nesting in this species, including a brood hatched after 15 September has been documented by Cottam and Glazener (1959).

ACKNOWLEDGMENTS

Several landowners, among them S. Fry, M. Wright, J. Hailey, R. West, and J. Maurin, generously granted permission to erect and inspect nest boxes on their property. The refuge manager at Santa Ana National Wildlife Refuge, Wayne Shifflett, and his assistant, Cruz Martinez, were helpful with various aspects of the fieldwork, as were Barbara Mason and students at the Welder Wildlife Foundation. The late Clarence Cottam, Director, and W. C. Glazener, then Assistant Director, of the Foundation administered financial support of the study. We are grateful to all for their assistance.

Summary

Renesting in Black-bellied Whistling Ducks was stimulated by removing initial clutches during incubation; abandonment and other nest losses added to our sample. Each pair of incubating birds was marked and banded prior to removing the initial clutch.

No distinctive courtship behavior was noted between the loss of the first nest and the second laying. Distances between first nests and renests were not significantly different than the year-to-year locations of first nests by the same pair, indicating considerable attachment for local breeding grounds. Attempts to calculate the renesting interval were repeatedly thwarted by the incidence of dump nests.

At least 19% (N = 11 of 57) of the whistling ducks were known to renest, a percentage not unlike that for some other species of waterfowl. The persistence of renesting in Black-bellied Whistling Ducks was suggested when the renests of two pairs were collected and they again renested, thus producing a third clutch for the year. Black-bellied Whistling Duck renests cannot be recognized on the basis of a reduced clutch size, abundance of down, or by the time of year they are initiated. Black-bellied Whistling Ducks also renested after the presumed loss of a brood, illustrating both the persistence of renesting and the long period of favorable nesting conditions for this species in southern Texas.

Literature Cited

Atwater, M. G. 1959. A study of renesting in Canada Geese in Montana. J. Wildl. Mgmt. 23: 91–97.

Barnes, W. B. 1948. Unusual nesting behavior of a Wood Duck. Auk 65: 449.

Bennett, L. J. 1938. The Blue-winged Teal. Ames, Iowa, Collegiate Press.

Bent, A. C. 1925. Life histories of North American wild fowl. U.S. Natl. Mus. Bull. 130.

Bjarvall, A. 1969. Unusual cases of renesting Mallards. Wilson Bull. 81: 94–96.

Bolen, E. G. 1967a. The ecology of the Black-bellied Tree Duck in southern Texas. Unpublished Ph.D. dissertation, Logan, Utah State Univ.

Bolen, E. G. 1967b. Nesting boxes for Black-bellied Whistling Ducks. J. Wildl. Mgmt. 31: 794–797.

Bolen, E. G. 1970. Sex ratios in the Black-bellied Tree Duck. J. Wildl. Mgmt. 34: 68–73.

Bolen, E. G. 1971. Pair bond tenure in the Black-bellied Tree Duck. J. Wildl. Mgmt. 35: 385–388.

Bolen, E. G., and M. K. Rylander. 1973. Copulatory behavior in *Dendrocygna*. Southwestern Naturalist 18: 348–350.

Cottam, C., and W. C. Glazener. 1959. Late nesting of water birds in south Texas. Trans. North Amer. Wildl. Conf. 24: 382–395.

Coulter, M. W., and W. R. Miller. 1968. Nesting biology of Black Ducks and Mallards in northern New England. Bull. 68–2, Montpelier, Vermont Fish and Game Dept.

DELNICKI, D. E., AND E. G. BOLEN. 1975. Natural nest site availability for Black-bellied Whistling Ducks. Southwestern Naturalist, in press.

ENGELING, G. A. 1949. The Mottled Duck—a determined nester. Texas Game and Fish 7: 6–7, 19.

ERRINGTON, P. L. 1934. Second broods in the Mallard Ducks. Auk 51: 78–80.

GATES, J. M. 1962. Breeding biology of the Gadwall in northern Utah. Wilson Bull. 74: 43–67.

GEIS, M. B. 1956. Productivity of Canada Geese in the Flathead Valley, Montana. J. Wildl. Mgmt. 20: 409–419.

GOULD, F. W. 1969. Texas plants—a checklist and ecological summary, revised ed. College Station, Texas A&M Agr. Exp. Station.

GRICE, D., AND J. P. ROGERS. 1965. The Wood Duck in Massachusetts. Boston, Bull. Massachusetts Div. Fisheries and Game.

HUNT, E. G., AND W. ANDERSON. 1966. Renesting of ducks at Mountain Meadows, Lassen County, California. California Fish and Game 52: 17–27.

JOHNSGARD, P. A. 1961. The taxonomy of the Anatidae—a behavioral analysis. Ibis 103: 71–85.

JOHNSGARD, P. A. 1965. Handbook of waterfowl behavior. Ithaca, Cornell Univ. Press.

JOHNSON, A. R., AND J. C. BARLOW. 1971. Notes on the nesting of the Black-bellied Tree Duck near Phoenix, Arizona. Southwestern Naturalist 15: 394–395.

JOHNSON, O. W. 1961. Reproductive cycle of the Mallard Duck. Condor 63: 351–364.

KORTRIGHT, F. H. 1942. The ducks, geese, and swans of North America. Harrisburg, Stackpole Co.

LOW, J. B. 1945. Ecology and management of the Redhead (*Nyroca americana*) in Iowa. Ecol. Monogr. 15: 35–69.

MCGILVREY, F. B. 1966. Second nesting of the Wood Duck. Auk 83: 303.

PHILLIPS, R. E., AND A. VAN TIENHOVEN. 1962. Some physiological correlates on Pintail reproductive behavior. Condor 64: 291–299.

SOWLS, L. K. 1955. Prairie ducks. Harrisburg, Stackpole Co.

WELLER, M. W. 1964. Distribution and migration of the Redhead. J. Wildl. Mgmt. 28: 64–103.

Rob and Bessie Welder Wildlife Foundation, Sinton, Texas 78387. Present address of first author: P.O. Box 156, Challenge, California 95925. Accepted 7 March 1975.