The Condor 95:220–222

EFFECT OF MATE REMOVAL ON NEST SUCCESS OF FEMALE WOOD DUCKS[1]

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Key words: Aix sponsa; *Anatidae; mate removal; nest success; pair bonds; Wood Duck.*

North American ducks in the subfamily Anatinae are monogamous, but males provide no direct care for young and usually leave their mates in early incubation (Palmer 1976, Bellrose 1980). Species in this subfamily have male-biased sex ratios (Bellrose et al. 1961), and strong competition for mates may not allow males to acquire more than one female (Wittenberger and Tilson 1980). Rohwer and Anderson (1988), however, suggested that these ducks are monogamous because pair formation occurs away from breeding areas, and female-biased natal philopatry and breeding-site fidelity make it virtually impossible for males to pair and return to breeding areas with more than one female.

The breeding range of Wood Ducks (*Aix sponsa*) in eastern North America is extensive, stretching from Nova Scotia to Florida (Haramis 1990). Nesting seasons (initiation of first nests to hatching of last nests) at southern latitudes may begin in January and continue through July. Southern populations of Wood Ducks do not have the same time constraints during the breeding season as do northern populations and other species of waterfowl nesting at northern latitudes (Hepp et al. 1989). Wood Ducks, for example, are unique among North American anatids because long breeding seasons enable some females to produce two broods in one season (Kennamer and Hepp 1987, Moorman and Baldassarre 1988). Pair bonds also are maintained longer than in other North American Anatinae (Fredrickson 1990); males escort females throughout incubation and possibly into the brood-rearing period (Leopold 1951, Bellrose 1980). However, as the breeding season progresses males abandon their mates at earlier periods in incubation (Fredrickson 1990; D. Hipes, pers. obs.). Males of other species leave their mates shortly after completion of the clutch (Palmer 1976).

Contribution of males to reproduction is well documented for nidicolus species where male parental care is more apparent (review in Bart and Tornes 1989). Relatively few studies have addressed the effects of male parental care on reproductive success in nidifugous species (Martin et al. 1985, Martin and Cooke 1987, Schneider and Lamprecht 1990). Longer attendance by male Wood Ducks may facilitate uninterrupted foraging of females during incubation by preventing harassment from other males (e.g., Ashcroft 1976), thereby helping females maintain body condition which may increase present and future reproductive success (Kennamer and Hepp 1987, Hepp et al. 1990). However, males simply may remain with their mates because the probability of obtaining future breeding opportunities (i.e., renests and second nests) is greater than finding another female. In this study, we tested whether removal of mates during egg-laying and early incubation influenced the nest success of female Wood Ducks at a southern breeding site.

METHODS

Data were collected at Eufaula National Wildlife Refuge in southwestern Georgia (32°N, 85°W). Nest boxes ($n = 87$) were checked for nesting activity from 3 March–29 June 1991. Clutch size and hatching success of all nests were recorded, and day of incubation was estimated by candling eggs (Hanson 1954). Nests were classified as successful if at least one duckling hatched and exited the box. Hatching success was defined as the percentage of eggs in the clutch producing ducklings that left the nest. Male Wood Ducks were collected by shooting during 20 March–1 May, a period in the breeding season when females were accompanied by males late into incubation. Males were removed as they returned with their mate to the nest box either just prior to completion of clutches ($n = 6$) or early ($\leq$ day 6) in the incubation period ($n = 3$). Nests initiated during the same time period, but in which males were not removed, were used as a control group ($n = 25$). These boxes were not shot over. Females in both groups were captured on the nest during late incubation, banded with a U.S. Fish and Wildlife Service leg band, and individually marked with a nasal saddle. Nest success of widowed and non-widowed females was compared using a G-test of independence with Williams' correction (Sokal and Rohlf 1981). Clutch size and hatching success of the two groups were compared with Mann-Whitney tests (Zar 1984).

RESULTS

Clutch size and hatching success of widowed and paired females did not differ (Table 1). Nest success of widowed females (77.8%, $n = 9$) and paired females (84.0%, $n = 25$) also did not differ ($G_{adj} = 0.14$, df = 1, $P > 0.50$). It is not thought that shooting influenced abandonment. The two widowed females that abandoned nests had their mates removed while laying their third and fourth egg while others in the group had laid ten

[1] Received 28 May 1992. Accepted 9 September 1992.

or more eggs or were incubating. Of paired females that nested unsuccessfully, three abandoned nests during egg-laying, and one nest was destroyed by a rat snake (*Elaphe obsoleta*) during incubation. We observed five of the seven widowed females that nested successfully returning to their nest boxes without male escorts, and assumed that all widowed females remained unpaired. Checks of nest boxes later in the breeding season revealed that none of the females, either widowed or paired, produced more than one brood.

TABLE 1. Mean clutch size and hatching success of paired and widowed female Wood Ducks.

	Paired $n = 21$	Widowed $n = 7$	Mann-Whitney U
Clutch size	14.4	16.1	90.75 NS[a]
Hatching success (%)	83.4	77.3	55.50 NS

[a] $U_{0.05(1)7,21} = 106$ (Zar 1984).

DISCUSSION

Hatching success and nest success of widowed and paired females were not different. Similar results have been found in other nidifugous species. Martin et al. (1985) reported that widowed Lesser Snow Geese (*Anser caerulescens*) were able to hatch as many offspring as paired females. Martin and Cooke (1987) found no differences between paired and widowed Willow Ptarmigans (*Lagopus lagopus*) either in the number of chicks raised to fledging, or their survival to the next breeding season. In both studies, mate retention for future reproductive opportunities in subsequent years was suggested as the reason that males remained with their mates through the brood rearing period. Male Wood Ducks may remain with their mates for a similar reason. Extended pair bonds early in the breeding season would allow males to insure paternity of a second clutch in the event of nest failure, or of a second nesting attempt. Male-biased sex ratios and long-term courtships associated with ducks (Bellrose 1980), make securing a second female after completion of the initial clutch unlikely. As the breeding season progresses opportunity for second nests becomes less likely (G. Hepp, pers. observ.). Therefore, males may have less to gain by remaining with their mates and abandon them earlier in incubation as the season progresses.

Male parental care can influence reproductive success of some species of nidifugous birds. Female Barheaded Geese (*Anser indicus*) accompanied by their mate experience fewer brooding interruptions and have higher offspring survival to fledging than single females (Schneider and Lamprecht 1990). Male Wood Ducks do not take part in any obvious parental care activities, but benefits may be derived from their presence. Female Wood Ducks escorted by males during incubation recesses may feed more efficiently (e.g., Ashcroft 1976). Improved foraging by incubating females may help them complete incubation in good physical condition; females ending incubation with high body mass are more likely to initiate and hatch a second clutch (Kennamer and Hepp 1987) and survive to the next breeding season (Hepp et al. 1990). More efficient feeding also may help to shorten the time females spend away from the nest. Shorter and fewer incubation recesses may reduce cooling of eggs. Low egg temperature lengthens the incubation period (White and Kinney 1974), which may increase predation risk (Lima 1987) and increase energy expended by developing embryos (Booth 1987), thereby reducing the amount of nutrient reserves of hatchlings (Peach and Thomas 1986). Shortened periods away from nests during incubation also may reduce opportunities for intraspecific nest parasitism; eggs frequently are added to nests by parasitic females after incubation has started and sometimes results in lower hatching success (Clawson et al. 1979, Semel and Sherman 1986). As the breeding season progresses, warmer temperatures and declines in the frequency of dump nesting (Haramis 1990) may make timing of incubation recesses less critical.

Results do not support the idea that male attendance during incubation increases reproductive success of females, but it is possible that effects of male attendance were subtle and difficult to detect with the small sample of this study. We suggest that further studies are needed to address the significance of male parental care in Wood Ducks.

This study was funded by the Alabama Agricultural Experiment Station, the Birmingham Chapter of Safari Club International, and Auburn University. We are grateful to Daniel Drennen and the rest of the staff at Eufaula National Wildlife Refuge for their assistance. We also thank Troy Best, Nick Holler, Joe Renden and two anonymous reviewers for their helpful comments. This is article 15-923234 of the Alabama Agricultural Experiment Station.

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The Condor 95:222–225

SURVIVAL AND PRE-FLEDGING BODY MASS IN JUVENILE EMPEROR GEESE[1]

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Key words: Body mass; Chen canagicus; *Emperor Goose; migration; physiological condition; survival.*

A positive relationship exists between fledgling body mass and juvenile survival for some altricial (Krementz et al. 1989, Magrath 1991, Linden et al. 1992) and precocial (Owen and Black 1989, Longcore et al. 1991, Francis et al. 1992) species. Because the energetic demands of migration are high, physiologic condition may be a proximate determinant of juvenile survival in geese. Owen and Black (1989) found that pre-fledging body mass of Barnacle Geese (*Branta leucopsis*) was positively related to juvenile survival to winter. First-year survival in Lesser Snow Geese (*Chen caerulescens caerulescens*) was also affected by pre-fledging body mass (Francis et al. 1992). It is not clear, however, when such mass-related mortality occurs. Both species migrate >3,000 km to wintering areas, but make use of fall staging areas while en route (Owen 1980, Francis and Cooke 1992). Survival of geese between fledging and staging areas has not been addressed. Measurement of survival during this interval could provide insight to the timing of juvenile mortality in arctic geese.

In contrast to Snow Geese and Barnacle Geese, Emperor Geese (*Chen canagicus*) have relatively short migrations (Owen 1980). Emperor Geese breed principally on the Yukon-Kuskokwim Delta (YKD) in Alaska (Eisenhauer and Kirkpatrick 1977). Virtually all Emperor Geese stage on the Alaska Peninsula during spring and fall migrations. They then disperse in winter throughout the Aleutian Islands, on the south coast of the Alaska Peninsula, and on Kodiak Island. Emperor Geese thus migrate 600–750 km between breeding and

[1] Received 23 June 1992. Accepted 12 October 1992.