

# EFFECTS OF MATE REMOVAL ON INCUBATION BEHAVIOR AND REPRODUCTIVE SUCCESS OF FEMALE WOOD DUCKS<sup>1</sup>

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**Abstract.** Breeding Wood Ducks (*Aix sponsa*) maintain pair-bonds later into the incubation period than most other species of North American ducks. We tested whether being paired was beneficial to females during incubation by comparing incubation constancy, incubation period, changes in female body mass, and reproductive success in a mate removal experiment. Females were assigned randomly to one of two treatments: paired controls ( $n = 24$ ) or widowed ( $n = 21$ ). Mates of females were removed early in incubation ( $\bar{x} = \text{day } 5$ ), and nests of paired and widowed females were equipped with temperature data loggers to record the presence and absence of incubating females. Paired and widowed females did not differ significantly with respect to incubation constancy, incubation period, body mass, or nesting and hatching success. Paired females, however, tended to produce second broods more often than widowed females. Being paired did not result in advantages to incubating females, but longer attendance by male Wood Ducks may benefit both sexes where breeding seasons are long and future reproductive opportunities (i.e., second broods) are more likely to occur.

**Key words:** *Aix sponsa*, incubation, mate removal, pair-bonds, reproductive success, Wood Duck.

## INTRODUCTION

Wood Ducks (*Aix sponsa*) differ from most species of North American ducks in that males generally remain with females throughout incubation (Leopold 1951, Bellrose 1980, Fredrickson 1990). Longer attendance by breeding males may increase foraging efficiency of females during incubation by decreasing harassment by other males and allowing females to feed undisturbed (Ashcroft 1976). However, males also may remain with females to participate in breeding opportunities later in the season (Hipes and Hepp 1993, Bellrose and Holm 1994). Wood Ducks breeding at southern latitudes are not subject to the same time constraints as ducks breeding at more northerly locations (Hepp et al. 1989). Renesting is common after failed nesting attempts, and females in southern populations frequently produce two broods in a single season (Kennamer and Hepp 1987, Moorman and Baldassarre 1988).

In this study we test whether attendance of male Wood Ducks during incubation results in advantages to their mates. Mates of some females were removed early in incubation, and incubation behavior, body mass, and reproductive

success of paired and widowed females were compared. We predicted that paired females would lose less weight during incubation, spend more time incubating, and have shorter incubation periods resulting in greater nest success and hatching success than widowed females.

## METHODS

The study was conducted during January–June 1996 and 1997, at the Bradley Unit of Eufaula National Wildlife Refuge in southwestern Georgia (32°N, 85°W). Moorman and Baldassarre (1988) provided descriptions of the study area. Nest boxes were maintained for Wood Ducks in 1996 ( $n = 43$ ) and in 1997 ( $n = 38$ ). Nest boxes were placed on posts over water at several impoundments on the refuge. All nest boxes were wooden and of similar size. They were checked weekly during the breeding season to monitor nesting activity. All eggs were counted and numbered during weekly inspections. Date of nest initiation was estimated by subtracting the number of eggs in the nest when it was first found from the Julian date that the nest box was checked (Hepp and Kennamer 1993). Day of incubation was estimated by candling eggs (Hanson 1954). Because variation in clutch size may affect incubation patterns (Gloutney 1996) and length of incubation (Hepp et al. 1990), clutch size was reduced during late egg-laying and early incubation ( $\leq \text{day } 4$ ) so that all nests con-

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tained approximately the same number of eggs (adjusted clutch size = 12 eggs). Nesting females were captured during early incubation ( $\leq$  day 10) and anesthetized using methoxyflurane to help reduce nest abandonment (Rotella and Ratti 1990). Females were weighed (nearest 5 g), banded with a U.S. Fish and Wildlife Service leg band, and aged as yearling or adult using methods of Harvey et al. (1989). Females were recaptured and weighed during late incubation ( $\geq$  day 25). Nests were considered successful if at least one duckling hatched and left the box. Successful nests were inspected within a week after hatching to record hatching success. In most instances, parasitic females laid additional eggs to previously reduced clutches. These unnumbered eggs were included in final clutch size determinations, but were excluded from the determination of hatching success. Because final clutch size was similar between paired and widowed females (see Results), the effect of mate removal on hatching success could be evaluated. Hatching success was defined as the percentage of eggs that hatched. Renesting and second nest attempts were determined by capturing previously banded females during incubation of nests initiated later in the season.

#### MATE REMOVALS

Nests were assigned randomly to one of two treatments each year: paired controls or widowed. Males of nests assigned to the widow treatment were shot early in the incubation period ( $\leq$  day 10) as they returned with their mate to the nest box following an incubation recess. Nests initiated during the same time period, but in which males were not removed, were used as controls. Nests of five widowed females in 1997 were observed later in incubation to determine whether they paired with another male or remained widowed.

#### FEMALE NEST ATTENDANCE

Nests were equipped with temperature data loggers (Stowaway<sup>®</sup>, Onset Computer Corp., Pocasset, Massachusetts) to record the presence and absence of incubating females. Data loggers were installed in nests during late egg-laying and early incubation (at the time clutches were reduced), and were programmed to record nest temperatures at 6.4-min intervals for 35 days. When installing data loggers, contents of the nest were removed and a platform containing a

single wooden egg was placed in the nest box. A thermistor was embedded in each wooden egg, and wooden eggs were securely fastened to each platform with lag bolts (10 cm) to prevent females from moving them. The tip of the thermistor was exposed on top of the egg to ensure contact with the brood patch of the incubating female; a cable (61 cm) connected the thermistor to the data logger. Wood chips and eggs were returned to the box after installing the platform. Wooden eggs were positioned in the center of the clutch, and data loggers were placed beneath wood chips.

Data loggers were removed from nests after ducklings departed from the box, and data were downloaded. A rise or drop in temperature of 2.0°C was used to estimate times that females returned to or departed nests. If the rise or drop of 2.0°C was not maintained for two successive time periods (elapsed time = 13 min), then we considered the female to be involved in a comfort movement within the nest box. Incubation constancy was defined as the average percent of time spent on the nest per day (Skutch 1962), and incubation period was defined as the number of days from onset of incubation to hatching. Data loggers revealed the date that ducklings exited the nest box, and hatch date was assumed to be the previous day.

#### STATISTICAL ANALYSES

Laying date, final clutch size (determined post-hatching), incubation period, and hatch date were log-transformed to normalize data. Hatching success was arcsine-transformed before analysis. We used two-way ANOVAs (Type III SS) with year and treatment as independent variables to test for differences in nest initiation dates, final clutch size, and hatching success (GLM; SAS Institute 1988). Data from one paired female were excluded from analyses (i.e., an outlier) of hatching success, because temperatures fell well below 0°C during egg-laying and many eggs cracked resulting in an almost complete nest failure. We tested for differences in incubation constancy and incubation period between paired and widowed females using ANCOVA (Type III SS) with hatching date and final clutch size as covariates. In the most general models, we included all two-way interactions between factors and covariates, and then eliminated interaction terms that did not explain a significant amount of variation in the dependent

TABLE 1. Means ( $\pm$  SE) of nest initiation date (1 = 31 January 1996; 1 = 12 January 1997)<sup>a</sup>, clutch size at hatch, early incubation body mass, late incubation body mass, and rate of body mass change during incubation of experimental female Wood Ducks.

	Paired females		Widowed females	
	$\bar{x} \pm$ SE	<i>n</i>	$\bar{x} \pm$ SE	<i>n</i>
Nest initiation date	53.7 $\pm$ 6.6	24	59.3 $\pm$ 7.2	21
Clutch size	15.7 $\pm$ 1.0	21 <sup>b</sup>	16.5 $\pm$ 1.0	21
Initial body mass (g)	573.7 $\pm$ 9.8	24	570.2 $\pm$ 10.8	21
Final body mass (g)	557.0 $\pm$ 7.2	19 <sup>c</sup>	549.4 $\pm$ 6.9	21
Body mass change (g day <sup>-1</sup> )	0.5 $\pm$ 0.3	19 <sup>c</sup>	0.8 $\pm$ 0.3	21

<sup>a</sup> Date of first nests in a given year.

<sup>b</sup> Final clutch size of three nests could not be determined due to nest failures.

<sup>c</sup> Final body mass of five females could not be determined due to nest failures and early hatches.

variable. We compared least-squares means (LSM  $\pm$  SE) using *t*-tests when sample sizes were unequal (PDIFF option, SAS Institute 1988), and used Tukey's studentized range test to compare unadjusted means when sample sizes were equal (Sokal and Rohlf 1981). Frequency of second broods and nest success of paired and widowed females were compared using a *G*-test of independence with Williams' correction (Sokal and Rohlf 1981). Values presented are means  $\pm$  SE.

## RESULTS

Data were collected for 19 females (11 paired controls, 8 widows) in 1996, and 26 females (13 paired controls, 13 widows) in 1997. Females were widowed in early incubation ( $\bar{x}$  = day 5; range = 1–10 days), and none of the widowed females abandoned their nests. To help determine whether widowed females remained unpaired, we observed five widowed females in 1997 during mid-incubation ( $\bar{x}$  = day 20) as they

returned to the nest box following morning recesses. Observations were recorded an average of 14 days (range = 7–22 days) after females were widowed. Three females returned alone and two were accompanied by more than one male. However, breeding behaviors of males and widowed females indicated that they were not paired.

Date of nest initiation and final clutch size did not differ (*P*s > 0.05) between widowed and control females (Table 1). Incubating females were monitored for an average of 29 days (range = 20–34 days). Incubation constancy, incubation period, body mass, hatching success, and nest success of females did not differ between years (*P*s > 0.05), therefore data were combined across years for further analyses. Body mass in late incubation was positively related to initial body mass ( $F_{1,37} = 27.2$ ,  $P < 0.001$ ), but final body mass did not differ ( $F_{1,37} = 0.6$ ,  $P = 0.45$ ) between paired and widowed females (Table 1). Rate of body mass change also was positively related to initial body mass ( $F_{1,37} = 16.9$ ,  $P < 0.001$ ), but did not differ ( $F_{1,37} = 0.5$ ,  $P = 0.49$ ) between paired and widowed females (Table 1).

Incubation constancy was not related to final clutch size or hatching date, and did not differ between widowed (86.4  $\pm$  0.9%,  $n = 20$ ) and paired females (88.1  $\pm$  0.9%,  $n = 21$ ; Table 2). Incubation period decreased as the breeding season advanced, but final clutch size had little affect on incubation period (Table 2). After statistically controlling for variation in clutch size and hatching date, there was a slight tendency for widowed females (31.1  $\pm$  1.0 days,  $n = 20$ ) to have longer incubation periods than paired females (30.5  $\pm$  1.0 days,  $n = 21$ ), but the difference was not significant (Table 2).

TABLE 2. Results of ANCOVAs (Type III SS) that test for differences in incubation constancy and incubation period between paired and widowed female Wood Ducks. Final clutch size and hatch date are covariates. All *df* = 1, 37.

	Incubation constancy		Incubation period <sup>a</sup>	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Treatment	1.8	0.19	3.7	0.06
Final clutch size <sup>b</sup>	0.1	0.74	0.5	0.50
Hatch date	0.7	0.41	18.9	0.00

<sup>a</sup> Data from one widowed female were excluded from this analysis (i.e., an outlier). We captured and weighed this female on four different occasions during incubation. All other females ( $n = 41$ ) were weighed an average of 2.2 times during incubation. Therefore, we believe this female's incubation period (36 days) may have been influenced by excessive handling.

<sup>b</sup> Final clutch size included eggs that were laid parasitically after clutches were reduced to 12 eggs.

Hatching success did not differ between treatments ( $F_{1,37} = 0.05$ ,  $P > 0.5$ ). Mean hatching success for both treatments combined was  $83.6 \pm 2.5\%$  ( $n = 41$ ). Differences in nest success of widowed females (100%,  $n = 21$ ) and paired females (87.5%,  $n = 24$ ) approached significance ( $G_{\text{adj}} = 3.39$ ,  $df = 1$ ,  $P = 0.06$ ). Of paired females that nested unsuccessfully ( $n = 3$ ), two females abandoned nests during late incubation, and one nest was destroyed by a raccoon (*Procyon lotor*) during incubation.

In 1996, 1 of 54 (2%) females that successfully produced one brood, returned to initiate a second nest. In 1997, mild temperatures and abundant rainfall provided better habitat conditions, and 9 of 63 (14%) females returned to produce a second brood. Five of nine double-brooded females were experimental birds (4 paired and 1 widowed). In 1997, no female having a successful first nest that was initiated after 6 March returned to produce a second brood. Therefore, in testing whether mate loss influenced the frequency that females produced a second brood, we limited our comparison to experimental females that initially nested  $\leq 6$  March ( $n = 6$  paired females,  $n = 6$  widowed females). Frequency of double brooding did not differ ( $G_{\text{adj}} = 2.88$ ,  $df = 1$ ,  $P = 0.09$ ) between paired and widowed females; however, paired females tended to produce more second broods ( $n = 4$ ; 67%) than widowed females ( $n = 1$ ; 17%).

## DISCUSSION

A possible advantage to Wood Ducks of maintaining pair-bonds through incubation is that females may experience greater foraging efficiency during recesses because mates defend them from intruding males (Anderson and Titman 1992, Bellrose and Holm 1994). If this is true, then paired females should be in better physical condition, and hence, spend more time incubating, and have shorter incubation periods than females without mates. However, we found no differences in body mass at the end of incubation, incubation constancy, and incubation period between paired and widowed females. These results strongly suggest that maintenance of pair-bonds by Wood Ducks is not needed for females to meet the costs of incubation.

Similar findings have been reported for other species of precocial birds. Body mass at hatch of Ross' Geese (*Chen rossii*; LeSchack et al.

1998), nest attendance of Lesser Snow Geese (*Chen caerulescens caerulescens*) and Ross' Geese (Martin et al. 1985, LeSchack et al. 1998), and incubation constancy and length of incubation of Canada Geese (*Branta canadensis interior*; Paine 1992) did not differ between paired and widowed females. In Snow Buntings (*Plectrophenax nivalis*), an altricial species in which males regularly feed their mates during incubation, removal of males resulted in reduced nest attentiveness and increased length of incubation (Lyon and Montgomerie 1985). These results help to confirm that if males play an important role during incubation, their absence should result in predictable changes to female incubation behaviors.

Because incubation of female Wood Ducks was not affected by mate attendance, it is not surprising that nest success and hatching success of paired and widowed females also did not differ. These results support those of an earlier study (Hipes and Hepp 1993) where reproductive success also did not differ between paired and widowed females. However, effects of male parental care on reproductive success in other precocial species are variable. Nests of Western Sandpipers (*Calidris mauri*), for example, failed if either parent was removed during incubation (Erckmann 1983). Nest success of Willow Ptarmigan (*Lagopus lagopus*) (Martin and Cooke 1987), Canada Geese (Paine 1992), Lesser Snow Geese and Ross' Geese (LeSchack et al. 1998), and hatching success of Lesser Snow Geese and Ross' Geese (Martin et al. 1985, LeSchack et al. 1998) did not differ between paired and widowed females. Some of these studies suggest that the reproductive effort of males can be significant, but often male attendance during incubation does not necessarily benefit females in terms of current reproductive success.

Testis mass of male Wood Ducks did not decline until after late incubation (Hipes and Hepp 1995). This would be expected if longer attendance by male Wood Ducks increased future breeding opportunities in the event that first nests fail or females initiate first nests early enough to produce two broods. Studies of Mallards (*Anas platyrhynchos*) found that after initial nests were destroyed, most females re-united with familiar mates (Humburg et al. 1978, Ohde et al. 1983). Losito and Baldassarre (1996) suggested that longer pair-bonds may maximize the opportunity for male Mallards to remain active

on the breeding grounds. In our study, nine females successfully hatched second broods in 1997, and paired females tended to initiate and hatch second broods more frequently than widowed females. We suggest that duration of pair-bonds in Wood Ducks corresponds to the probability of future breeding opportunities.

Maintenance of long pair-bonds involves trade-offs. Bellrose and Holm (1994) suggested that there probably is a latitudinal effect on pair-bond duration, because Wood Ducks breeding at northern latitudes have a relatively short time to nest and rear offspring (Grice and Rogers 1965). However, southern populations of Wood Ducks are not subject to the same time constraints as ducks breeding at more northerly locations (Hepp et al. 1989). There would be little advantage to males of leaving their mate early in incubation to prepare for fall migration because southern breeding Wood Ducks migrate relatively late (Beshears 1974) and travel short distances (Hepp and Hines 1991). Costs of remaining paired are probably low for Wood Ducks, thus facilitating maintenance of longer pair-bonds.

In summary, our study indicates that pair-bonds maintained by Wood Ducks during incubation do not result in benefits to incubating females. Longer attendance by males may be advantageous where breeding seasons are long and females are likely to initiate multiple nests.

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