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FREQUENCY AND TIMING OF SECOND BROODS IN WOOD DUCKS

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ABSTRACT.—Occurrence of second broods in Wood Ducks (*Aix sponsa*) was studied during 1982–1986. Successful second nests comprised 7.6% (21 of 275) of all nesting attempts in which females were identified and 9.6% (21 of 219) of successful nestings. Length of the nesting season averaged 157 days. Average initiation dates of the first and second nests of double-brooded females were 14 February and 16 May, respectively. Mean interval between hatching of first nests and initiation of second nests was 47 days. Minimum age of females that produced two broods was 2.3 years. Mean egg mass, clutch size, clutch mass, and body mass of females were greater for first nests than for second nests. We compared first nests of double-brooded females with nests of single-brooded females that initiated nests during the same time period (20 January–4 March). There were no differences in mean egg mass, clutch size, clutch mass, body mass, and age between single-brooded and double-brooded females. Females producing one brood, however, lost a greater percentage of body mass during incubation than did double-brooded females. *Received 4 Nov. 1986, accepted 10 Apr. 1987.*

Reports of Wood Ducks (*Aix sponsa*) having two broods in a single nesting season are common (Odom 1970, Fredrickson and Hansen 1983). Little, however, is known about the factors that contribute to an individual's ability to rear two broods. Other species of North American anatids do not usually nest successfully more than once in a breeding season, and some species rarely renest if the first nest is destroyed (Bellrose 1980). In Wood Ducks and other species of ducks, it seems likely that length of the breeding season influences the probability of producing a second brood. Fredrickson and Hansen (1983), for example, reported that Wood Duck populations nesting at northern latitudes have second broods much less often than do populations at southern latitudes where the breeding season is longer. Drobney (1982) hypothesized that production of second broods by female Wood Ducks also may be related to their use of exogenous protein during laying and incubation, which conserves endogenous protein and may shorten the time needed to reach prebreeding condition again. In addition, annual variations in climate (e.g., precipitation and temperature), and its influence on the acquisition and maintenance of nutrient reserves, may affect the frequency of second broods at the population level.

In this paper, we report the frequency and timing of second broods in a southern Wood Duck population during five breeding seasons. Mean

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egg mass, clutch size, and clutch mass are compared between first and second nests. We also relate female age, length of the breeding season, and weight loss during incubation to the probability of producing a second brood.

STUDY AREA AND METHODS

The study was conducted on the Department of Energy's Savannah River Plant (SRP) in west-central South Carolina (33.1°N, 81.3°W). Wood Duck nest boxes were erected on the SRP during the mid-1970s (Fendley 1978). In 1982–1986 nest boxes generally were checked weekly during the nesting season (January–July). We used data on second broods from this 5-year period. Length of the nesting season was the number of days between initiation of the first nest and hatching of the last nest.

Wood Duck nests were determined to be the result of one (normal nest) or more (dump nest) females. Identification of dump nests was based on at least one of the following criteria: (1) egg deposition rate exceeded one egg per day, (2) viable nonterm eggs were present at hatching, and (3) clutch size was ≥ 17 eggs (Morse and Wight 1969). Length (L) and breadth (B) of all eggs were measured to the nearest 0.1 mm with vernier calipers. L, B, and fresh mass (M) of 105 Wood Duck eggs were used to predict fresh egg mass from external egg measurements:

$$M = 0.993 + 0.00054\ (LB^2),$$

$P < 0.0001$, $R^2 = 0.97$. Egg mass estimates from this equation were used to calculate mean egg mass and clutch mass of normal nests.

Each year most breeding females were captured in nest boxes and banded with U.S. Fish and Wildlife Service leg bands. We also web-tagged day-old ducklings (Haramis and Nice 1980), and the return of web-tagged females to breed provided a sample of known-age individuals. Our sample of female Wood Ducks consisted of (1) known-age individuals, (2) females that nested and were banded in previous years but were not web-tagged (i.e., exact ages were not known), and (3) females that were neither banded nor web-tagged at time of capture. Nesting females that were not banded or web-tagged were called 1-year-old birds. Mean age of females, therefore, is a minimum estimate. In 1986, mass of females was recorded to the nearest 5 g with 1000-g Pesola spring scales during early (≤ 9 days) and late (≥ 26 days) incubation.

Wilcoxon's signed-ranks test was used to compare characteristics of first and second nests of double-brooded females (Sokal and Rohlf 1981). Comparisons of single-brooded and double-brooded females were based on rank-transformed data (Conover and Iman 1981). Other analyses were made using the Statistical Analysis System (SAS Institute Inc. 1985). Sample means are presented ± 1 SE. We used 2-tailed tests, and statistical significance levels were set at the 0.10 probability level.

RESULTS

Second brood frequency and timing.—In 1982–1986, Wood Ducks initiated 429 nests; of these, 275 (64.1%) nesting females were captured. A total of 219 (51.1%) nests was successful in producing at least one duckling, and we captured the female in 210 (95.9%) successful nests. Hens with second broods comprised 7.6% (21 of 275) of all nests in which females were identified and 9.6% (21 of 219) of successful nests. One female had

TABLE 1

NESTING SEASON LENGTH AND THE OCCURRENCE OF SECOND BROODS IN WOOD DUCKS ON THE SAVANNAH RIVER PLANT, 1982–86

	Length of nesting season[a]	Successful nests	No. of females captured/No. of nesting attempts	No. of double-brooded females
1982	145	34	34/67	1[b] (2.9[c], 2.9[d])
1983	172	46	58/99	4 (8.7, 6.9)
1984	156	48	65/101	5 (10.4, 7.7)
1985	134	30	36/57	0
1986	179	61	82/105	11 (18.0, 13.4)
All years	157 ± 8.3[e]			
Totals		219	275/429	21 (9.6, 7.6)

[a] Length of the nesting season is the number of days from initiation of the first nest to hatching of the last nest.
[b] Number of double-brooded females.
[c] Percentage of successful nests that were successful second nests.
[d] Percentage of all nests in which females were captured that were successful second nests.
[e] $\bar{x}$ ± SE.

second broods in two different years. In 1986, two additional females produced and incubated second clutches, but these nests were abandoned before the eggs hatched.

Length of the nesting season on the SRP averaged 157 days (Table 1). Second broods were not produced during the shortest nesting season (1985), but occurred most frequently in the longest season (1986) (Table 1). Mean initiation date of first nests for female Wood Ducks that produced two broods was 14 February ± 3 days (N = 21; range = 20 January–4 March). Mean earliest initiation date for all females during the 5-year period was only 10 days earlier. Average initiation date of second nests for females producing two broods was 16 May ± 4 days (N = 21; range = 9 April–13 June). The mean interval between hatching of first nests and initiation of second nests was 47 ± 4 days (N = 21; range = 19–92 days).

Characteristics of first and second nests.—Double-brooded females were known-age individuals (N = 4), females that nested and were banded in previous years but were not web-tagged (N = 11), and females that were neither banded nor web-tagged at the time of capture (N = 5). Mean minimum age of all females that produced two broods was 2.3 ± 0.3 years (N = 20; range = 1–5). Four known-age females averaged 2.3 years, and one of these individuals was a yearling.

A comparison of double-brooded females' first and second nests showed that mean egg mass, clutch size, and clutch mass were greater ($P < 0.05$) for first nests (Table 2). Body mass of females in early incubation also was greater for first nests than for second nests (Table 2). Females, how-

TABLE 2
MATCHED-PAIRS COMPARISON OF THE FIRST AND SECOND NESTS OF DOUBLE-BROODED WOOD DUCKS, 1982–1986[a]

Variable	N	First nest[b]	Second nest[b]	*P*
Mean egg mass (g)	9	43.9	41.7	<0.01
Clutch size	9	13.0	10.0	<0.01
Clutch mass (g)	9	610.5	412.3	<0.01
Female body mass (g)[c]	8	632.5	572.5	<0.01
Percent change in body mass during incubation	6	−6.5	−3.6	N.S.

[a] Wilcoxon's signed-ranks test.
[b] Median values.
[c] Body mass of female Wood Ducks in early incubation (≤9 days).

ever, lost a similar percentage of body mass during incubation of both nests (Table 2).

Comparisons of single-brooded and double-brooded females.—Females that produced one brood in 1986 and initiated nests in the same period (20 January–4 March) as females that produced two broods were compared to double-brooded females. Errors in determining nesting status (single-brooded vs double-brooded) of females in 1986 should have been small because all females that nested successfully in nest boxes were captured. Movement of females between nest boxes (first nest) and natural cavities (second nest) may have occurred; however, this movement should have been minimal due to the philopatric behavior of female Wood Ducks (Hepp et al. 1987). There were no differences ($P \geq 0.35$) in mean egg mass, clutch size, clutch mass, and female age between single- and double-brooded females (Table 3). Body mass of single- and double-brooded females also was the same at the start of incubation, but females that produced two broods lost a smaller percentage of body mass during incubation (Table 3).

DISCUSSION

Female Wood Ducks in this study produced second broods more frequently than Wood Ducks at higher latitudes (see review in Fredrickson and Hansen 1983). In general, length of the breeding season for birds in temperate regions is inversely related to latitude (Wynham 1986), and breeding season length may influence the production of second broods by Wood Ducks. For example, average duration of the nesting season for Wood Ducks in South Carolina (SRP) was 60 days longer than Grice and Rogers (1965) reported for Wood Ducks in Massachusetts (157 vs 97

TABLE 3
REPRODUCTIVE PARAMETERS OF SINGLE-BROODED AND DOUBLE-BROODED FEMALE WOOD DUCKS IN 1986[a]

Variable	Single-brooded female	Double-brooded female	*t*	df	*P*
Nest initiation date	16 Feb (2.4)[b]	9 Feb. (4.0)	1.0	10,10	0.35
Mean egg mass (g)	43.6 (1.0)	45.1 (1.0)	−0.8	5,5	0.45
Clutch size	13.3 (0.7)	13.5 (0.4)	−0.1	5,5	0.94
Clutch mass (g)	579.1 (24.7)	607.7 (14.0)	−0.8	5,5	0.45
Female body mass (g)[b]	610.0 (14.3)	617.5 (12.4)	−0.5	10,7	0.61
Percent change in body mass during incubation	−9.4 (1.0)	−4.3 (2.8)	−1.9	8,5	0.08
Female age	2.6 (0.4)	2.4 (0.5)	0.6	10,10	0.49

[a] Data are from first nesting attempts; *t*-tests are performed on rank-transformed data.
[b] $\bar{x} \pm$ SE.
[c] Body mass of female Wood Ducks in early incubation (≤9 days).

days), and approximately 10% of the females in South Carolina that nested successfully had second broods compared with <1% in Massachusetts. Average time between first and second nests in South Carolina was 47 days. The length of time that Wood Duck hens remain with broods during rearing can vary from 30 to 60 days (Grice and Rogers 1965, Ball et al. 1975, Hepp 1977). Time constraints may prohibit females nesting at high latitudes from successfully producing and rearing two broods, molting, and migrating from northern areas before winter.

Frequency of second broods varied annually in South Carolina, and it was related to differences in the timing and duration of the nesting seasons. Second broods were not produced during 1985 when nesting began relatively late and ended early (13 February–26 June; 134 days). Second broods occurred most frequently during 1986 when Wood Ducks nested early, and the nesting season was long (20 January–18 July; 179 days). Annual differences in nesting chronology and length of the breeding season can be caused by variation in the proximate factors that affect food availability (Perrins 1970). Nesting begins late for some prairie-nesting ducks during years of low spring temperatures and drought conditions that negatively affect the invertebrate food base of breeding females (Krapu et al. 1983, Afton 1984). Renesting by female Lesser Scaup (*Aythya affinis*) that have had first nests destroyed is also less frequent during dry years (Afton 1984). Lipid reserves of female Wood Ducks provide 88% of the lipid and energy requirements of an average-size clutch, while protein for eggs is obtained from exogenous sources (Drobney 1982). Female Wood Ducks may delay breeding until they develop a "threshold" level of lipid reserves

(sensu Alisauskas and Ankney 1985). Factors that affect development and maintenance of lipid reserves and acquisition of protein may influence time of nesting and length of the breeding season and thereby influence the occurrence of second broods at the population level. In South Carolina, when breeding conditions were good (i.e., nesting started early and ended late), approximately 18% of female Wood Ducks produced two broods. The ability to produce two broods in a season was not restricted to adult females.

Mean egg mass, clutch size, clutch mass, and body mass of double-brooded females were smaller for second nests than for first nests. Fredrickson and Hansen (1983) also reported that clutch size and female body mass of double-brooded Wood Ducks declined between the first and second nests. Clutch sizes of renesting ducks generally are smaller than first nests, and smaller clutches of Mallards (*Anas platyrhynchos*) are correlated with smaller lipid reserves of breeding females (Krapu 1981). Female ducks apparently do not establish lipid reserves prior to renesting, as they do for first nests, but depend on exogenous nutrients at the breeding site for egg production (Krapu 1981, F. Rohwer, pers. comm.). Dependence on exogenous sources for both the energy and nutrient demands of renesting attempts may limit clutch size and egg size (Krapu 1981). Hohman (1986) proposed that the nutrient status of breeding Ring-necked Ducks (*Aythya collaris*) varied annually and that smaller lipid reserves of prebreeding females caused a greater reliance on exogenous nutrients during reproduction, resulting in delayed breeding and reduced clutch size in some years. During second nests, body mass of double-brooded females was smaller than during first nests, and they produced smaller clutches and eggs. Smaller body mass of female Wood Ducks indicated that they may have had less lipid reserves at the beginning of second nests and, hence, were dependent more on exogenous nutrients for clutch development. Smaller clutch size and egg mass of Wood Duck second nests, therefore, simply may reflect reduced lipid reserves of females and a greater reliance by females on unpredictable exogenous nutrients for egg production, as reported in other species of waterfowl. Without experimental studies, however, we cannot rule out the possibility that seasonal reductions in clutch size were the result of ultimate (e.g., average amount of food available to the hen and young) rather than proximate factors as proposed by Batt and Prince (1979).

We found no differences in egg mass, clutch size, and clutch mass of first nests of double-brooded females and nests of single-brooded females that nested during the same period of time (20 January–4 March 1986). Female Wood Ducks that produced two broods, therefore, did not appear to expend less energy on first clutches than females that produced only

one brood. Age and body mass of single-brooded and double-brooded females also did not differ. Single-brooded females lost a greater percentage of body mass (9.4%) during incubation than double-brooded females (4.3%). Mass loss during incubation averaged 26.5 g for the first nest of double-brooded females and 57.3 g for females that produced one brood. For other species of waterfowl mass loss during incubation is greater (12–32% of initial body weight) than it is for Wood Ducks (see review in Gatti 1983). Drobney (1980, 1982) reported that female Wood Ducks had an average of 31 g of fat at the end of laying and used about 17 g during incubation; there was no loss of carcass protein during incubation. Assuming that females in this study started to incubate with similar levels of lipids, then single-brooded females depleted all lipid reserves and probably also used some endogenous protein to meet the energy costs of incubation. Lipid reserves of double-brooded females, however, were not exhausted during incubation of first nests. We suggest that high weight loss during incubation may affect the probability of producing a second brood in either of two ways: First, by depleting lipids and using some endogenous protein to help meet the energy demands of incubation, hens may need more time to replenish these reserves, thereby increasing the renesting interval and decreasing renesting ability. Second, nutritional status of birds is known to affect reproductive development (Huxley 1976, Ottinger 1983). Bluhm et al. (1983), for example, showed that environmental stressors can affect hormonal characteristics of Mallards, thereby blocking reproduction. Greater incubation weight loss of single-brooded female Wood Ducks may have been sufficiently stressful to depress gonadal function and terminate reproductive activity.

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