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# EMBRYONIC DEVELOPMENT AND NEST ATTENTIVENESS OF WOOD DUCKS DURING EGG LAYING[1]

ROBERT A. KENNAMER AND WILLIAM F. HARVEY IV[2]
*Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29801*

GARY R. HEPP
*Department of Zoology and Wildlife Science, Auburn University, Auburn, AL 36849-5414*

*Abstract.* Waterfowl often begin incubation during egg laying, thus creating developmental asynchrony within clutches. We investigated levels of intraclutch developmental asynchrony (IDA) during early incubation within naturally incubated clutches of Wood Ducks (*Aix sponsa*) in South Carolina. IDA averaged 2.2 ± 1.0 SD days ($n$ = 59) during a 2-year study. A higher average level of IDA in 1988 corresponded with larger average clutch size during that year. Date of nesting did not affect levels of IDA, but larger clutches had increased levels of IDA. In 1988, reduced hatching success was observed in clutches with greater than 3 days of developmental asynchrony, suggesting a cost associated with the early initiation of incubation while still laying eggs.

Nest attendance data collected during the later stages of egg laying indicated that females spent approximately 50% of the day at the nest. Female Wood Ducks engaged in nocturnal nest attendance during egg laying thereby allowing time to meet the nutrient demands of egg synthesis during the diurnal period.

*Key words: Embryonic developmental asynchrony; incubation; nest attendance; Wood Duck;* Aix sponsa; *egg viability; Anatidae.*

## INTRODUCTION

Observations that waterfowl begin incubation during egg laying are common (Breckenridge 1956; Cooper 1978; Afton 1980; Cargill and Cooke 1981; Afton and Paulus, in press). At the termination of laying, significant embryonic development may have occurred as the result of increased attention that some eggs have received from laying females (Prince et al. 1969, Caldwell and Cornwell 1975, Cargill and Cooke 1981). The resulting hierarchy of developing embryos synchronize their hatching (see Davies and Cooke 1983) probably by adjusting developmental rates using intraclutch communication (Vince 1964, 1968).

Reasons for this elaborate incubation strategy are not clear. Arnold et al. (1987) found that viability of unincubated eggs decreased with time, and hypothesized that waterfowl begin incubation during laying in part to maintain high hatchability. Additionally, predation risks (Perrins 1977, Clark and Wilson 1981) and frequency of intraspecific nest parasitism (Clawson et al. 1979, Semel and Sherman 1986) may be sufficiently high in some species to encourage the early initiation of incubation. Previous studies, however, lacked information on levels of developmental asynchrony within naturally incubated clutches.

In this study we quantify the level of developmental asynchrony achieved at the termination of egg laying in a population of box-nesting Wood Ducks (*Aix sponsa*), and relate variation in developmental asynchrony to date of nesting, clutch size, and hatching success. Timing and duration of nest attentiveness by females during laying is also presented.

## METHODS

### NEST-BOX INSPECTIONS

This study was conducted during February–June 1988–1989, on the Department of Energy's Savannah River Site (Aiken and Barnwell County) in west-central South Carolina. Kennamer et al. (1988) and Hepp et al. (1987) provide study area descriptions and population parameters of Wood Ducks using the site, respectively. All nest boxes were constructed of cypress (*Taxodium distichum*) and were of similar dimensions. Boxes ($n$ = 141 and 138, respectively for 1988 and 1989) were checked each week. Nest initiation dates

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[2] Present address: Maryland Department of Natural Resources, Forest, Park, and Wildlife Services, P.O. Box 68, Wye Mills, MD 21679.

were expressed as the days elapsed since initiation of the first nest each year to reduce annual variation in time of nesting. Frequent box checks allowed us to find nests during the laying stage, and therefore we were able to determine egg deposition rates and note when laying had ended. All eggs found in nests during the weekly inspections were numbered to allow individual identification. Clutch size was determined for all nonparasitized nests (i.e., normal nests). Parasitized nests (i.e., dump nests) were identified (Kennamer and Hepp 1987) and excluded from the study, unless eggs were determined to have been dumped in the nest after incubation had begun (see Quantifying Developmental Asynchrony section). These nests were considered the result of laying by a single female (normal nests) after subtracting the number of parasitic eggs from the total clutch size. Females were captured in nest boxes during early incubation (<day 15) and banded if necessary. Nest attempts of breeding females known to have nested earlier within a given year (i.e., known renests) were not used in the study. Successful nests were visited within a week after hatching. Unhatched eggs were identified and known dump eggs were excluded from the determination of hatching success. Hatching success was defined as the proportion of a clutch that hatched and left the box. Counts of membranes from hatched eggs remaining in successful nests often aided in determining hatching success. Complete nest failures resulted from abandonments and predations, and were not used in analyses that included hatching success (see Statistical Methods section).

### QUANTIFYING DEVELOPMENTAL ASYNCHRONY

All eggs were field candled within 8 days ($\bar{x}$ = 3.0 ± 1.98 SD days) after the end of laying (Weller 1956). Stage of embryonic development of each egg was determined to the nearest day using Hanson's (1954) guide for aging incubated Wood Duck eggs. We assumed that developmental rate was constant for all eggs between the end of laying and the time that we candled the eggs.

We were alerted to the presence of some parasitic eggs in clutches during candling. Typically, an average of 44% of a clutch was at the greatest stage of development within the clutch. The remaining eggs were at successive declining stages of development. Breaks in the declining sequence of development of greater than 1 day indicated that the least developed egg/eggs were parasitically laid. Such eggs were not used when determining developmental asynchrony within clutches.

For each nest, intraclutch developmental asynchrony (IDA) was defined as the difference (in days) between the most developed and least developed eggs within a clutch. Independent estimates of IDA in 23 clutches (267 eggs) were made by two observers in 1988. Observer differences were minimal and nonsignificant (mean difference = 0.30 days, paired $t$ = 1.91, $P$ = 0.07) with a high degree of correlation ($r$ = 0.79, $P$ = 0.0001). In subsequent analyses, one observer's estimate of IDA was used for all nests.

### FEMALE NEST ATTENDANCE

During 1988, we monitored nest attendance during the egg-laying period for three nests. Three miniature cantilever beam load cells (11.34 kg capacity) were mounted to the inside bottom of each nest box. Plexiglas (235 × 220 × 6 mm) was attached to the load cells providing a platform for nest materials. A basket made of fiberglass screen material was stapled to the inside walls of the box. The basket contained contents of the nests (i.e., wood chips, eggs, and feather down) and was located on top of the Plexiglas platform. Eighteen-gauge wire connected the load cells to a Campbell Scientific CR21X micrologger and power source. Two 12-V batteries were placed in parallel to power the load cells, and one additional battery powered the micrologger system. Data from load cells were recorded by the micrologger every minute and weight changes detected at the nest provided information on female attendance.

### STATISTICAL METHODS

We used the Statistical Analysis System (SAS) to complete statistical summaries and analyses (SAS Institute 1985). Hatching success proportions were arcsine-transformed before performing analyses. No serious cases of collinearity among the independent variables were identified during diagnostic procedures. Two-tailed $t$-tests were used to test for yearly differences in clutch size and hatching success. The general linear models procedure (GLM) was used to perform an analysis of covariance (ANCOVA) that tested the simultaneous effects of year, time of nesting, and

TABLE 1. Sample size ($n$), mean ($\bar{x}$), and standard deviation (SD) of date of nesting, clutch size, hatching success, and level of intraclutch developmental asynchrony (IDA) in Wood Ducks.

| | Date of nesting[a] | | | Clutch size | | | Hatching success[b] | | | IDA | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | $n$ | $\bar{x}$ | SD | $n$ | $\bar{x}$ | SD | $n$ | $\bar{x}$ | SD | $n$ | $\bar{x}$ | SD |
| 1988 | 24 | 41.3 | 27.5 | 24 | 11.6 | 2.1 | 17 | 88.3 | 11.8 | 24 | 2.6 | 1.02 |
| 1989 | 35 | 44.2 | 25.2 | 35 | 10.4 | 2.3 | 28 | 86.7 | 16.0 | 35 | 2.0 | 0.97 |

[a] Date of nesting expressed as the number of days elapsed since the initiation of the first nest each year.
[b] Hatching success is the percentage of eggs hatching and leaving the nest.

clutch size on IDA. Since IDA is a range and may be sensitive to sample size (i.e., clutch size) we also performed the ANCOVA on log standard deviations (SD) of within-clutch egg development. Results of analyses using IDA or log SD as dependent variables were similar. We report results based on IDA for simplicity. Estimates of IDA from females sampled in both years of the study ($n$ = 7) were treated as independent, because residuals from the ANCOVA for these individuals were uncorrelated between years ($r_s$ = 0.00, $P > 0.95$) (Draper and Smith 1966). Sample means are presented ±1 SD and results are considered significant at the $P \leq 0.05$ level.

## RESULTS

We candled 643 eggs from 59 Wood Duck nests during the 2-year study. Initiation dates of nests ranged from 19 February to 29 May. Forty-five of 59 nests (76%) produced ducklings, and the percentage of eggs hatching from successful nests averaged approximately 87% (Table 1). Hatching success did not differ between years of study ($P > 0.7$). Overall, IDA averaged 2.2 ± 1.0 days (range = 0–5 days) and was moderately variable (CV = 46%) within the population. Greater levels of IDA in 1988 ($t$ = 2.22, $P$ = 0.03) corresponded with significantly larger clutch sizes ($t$ = 2.04, $P$ = 0.05) during the same year (Table 1).

IDA was significantly related to clutch size (Table 2), with large clutches showing greater levels of developmental asynchrony. Date of nesting approached significance in covariance model (Table 2). All first-order interactions were nonsignificant ($P > 0.20$). In 1988, reduced hatching success was observed in clutches with greater than 3 days of developmental asynchrony, but this trend was not apparent in 1989 (Fig. 1).

During the later stages of egg laying, three female Wood Ducks spent an average of 50% of the day at their nests (Table 3). They entered nest boxes in the early evening and remained throughout the night, leaving the next morning (Table 3). Females spent the diurnal period away from the nest.

## DISCUSSION

Caldwell and Cornwell (1975), studying incubation in captive Mallards (*Anas platyrhynchos*), reported that temperatures sufficient for egg development occurred as early as the sixth egg in a final clutch of 10 to 12 eggs. But, because of periodic warming of the eggs as females attended nests, embryos within clutches differed in age by only 1 to 2 days. The degree of developmental asynchrony in Mallard clutches is within the range of values that we found for Wood Ducks. Caldwell and Cornwell (1975) and Afton (1980) showed that female ducks spent approximately 50% of the day on the nest when 80 to 90% of the clutch was completed. Northern Shovelers (*A. clypeata*), for example, spent more time on the nest with each egg that was laid (Afton 1980). Female Wood Ducks engaged in nocturnal incubation during egg laying and spent the daytime away from nests. Similar patterns of nest attendance during egg laying in Wood Ducks have been reported by Leopold (1951) and Breckenridge (1956). In contrast, neither Mallards nor Northern Shovelers began nocturnal nest attendance until the clutch was completed (Caldwell and Cornwell 1975, Afton 1980). Wood Ducks obtain protein for egg production by feeding on protein-rich foods (Drobney and Fredrickson 1979) and not by using endogenous protein reserves (Drobney 1980). Nocturnal attendance at nests would allow females time during the diurnal period to meet nutrient demands of egg synthesis, and thereby reduce the cost of beginning incubation before clutches are complete.

For altricial and semiprecocial species that are nidicolous to varying degrees, the risk of predation may be adequate to explain the evolution

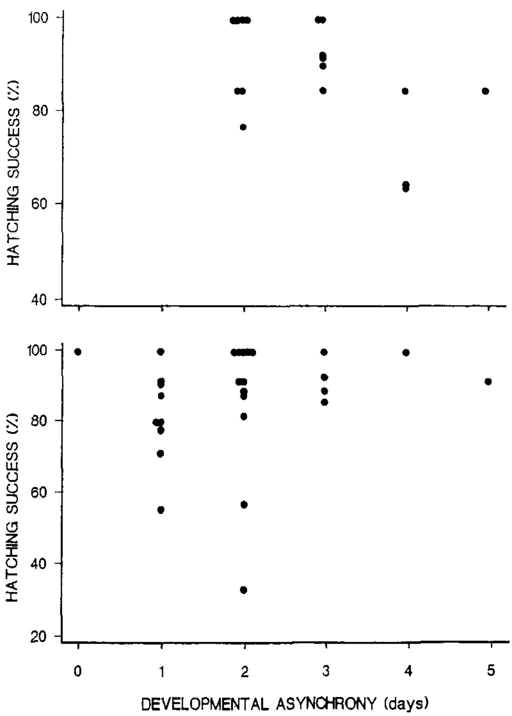


FIGURE 1. Relationship between intraclutch developmental asynchrony (IDA) and hatching success in 1988 (top) and 1989 (bottom) Wood Duck nests.

TABLE 2. Results of analysis of covariance relating levels of intraclutch developmental asynchrony to nest characteristics in Wood Ducks.

| Source | df | $F^a$ | $P$ |
|---|---|---|---|
| Year | 1, 55 | 1.56 | 0.217 |
| Date of nesting | 1, 55 | 3.36 | 0.072 |
| Clutch size | 1, 55 | 11.32 | 0.001 |

[a] Calculated using Type III sums of squares.

of developmental asynchronies (Clark and Wilson 1981), but may be less important to precocial nidifugous species (Perrins 1977). Furthermore, predation risks may exert even less selective pressure on reproductive tactics of cavity nesters (e.g., Wood Ducks) due to low predation rates and greater nesting success (Lack 1968, Perrins 1977, Bellrose 1980).

Alternatively, the evolution of developmental asynchrony in some nidifugous species may be connected to levels of intraspecific parasitism. It obviously would be maladaptive for parasitizing conspecifics to deposit eggs in the nests of hosts that are already incubating. For parasitism to be a successful reproductive strategy, eggs must be deposited in hosts' nests during laying or early incubation to assure hatching. Investigators studying intraspecific nest parasitism in Wood Ducks have shown that as many as 80% of parasitically laid eggs are deposited during the laying stage of the host female (Clawson et al. 1979). In addition, female hosts, while laying or incubating, occasionally have been observed to repulse intruding conspecifics (Clawson et al. 1979, Semel and Sherman 1986), thus reducing the likelihood of parasitic laying after incubation commences. Consequently, the increased time that females spend attending nests as laying progresses could serve to reduce opportunities for parasitic females. The resulting developmental asynchronies may be a cost of nest defense rather than the purpose of early incubation. Nest attendance, however, does not necessarily imply incubation as Haftorn and Reinertsen (1985) demonstrated in their study of Blue Tits (*Parus caeruleus*). Our nest attendance data suggest that during the later stages of egg laying, female Wood Ducks spend only the nocturnal period attending nests. Since Wood Ducks generally lay eggs during the morning hours (Bellrose 1980), it therefore seems unlikely that embryonic developmental asynchrony in Wood Ducks is a consequence of nest defense from parasitic conspecifics.

Recently, Arnold et al. (1987) proposed that clutch size in dabbling ducks and other precocial species may be influenced by egg hatchability. The first-laid eggs of species with relatively large clutches must remain viable until incubation begins in order to maintain high hatching success. They demonstrated that hatchability was affected by the length of preincubation delay and suggested that waterfowl initiate incubation during egg laying in part to reduce egg-viability losses while continuing to produce eggs. But, increasing nest attentiveness (i.e., increasing developmental asynchrony) during the laying period would increase hatchability only if embryos are able to synchronize hatching despite greater developmental asynchrony. In 1988, our results suggest that there may be an effective limit on the level of developmental asynchrony since hatching success was reduced in clutches with greater than 3 days of developmental asynchrony. Further evidence of a limitation to hatching synchronization has been demonstrated in other precocial species

TABLE 3. Timing and duration of nest attentiveness by female Wood Ducks during egg laying in 1988.

| Band number | Clutch size (nest type)[a] | n[b] | Minimum percentage of clutch completed[c] | Average time spent on the nest: Begin (hr)[d] | End (hr)[d] | Total time (min) | Percentage of day |
|---|---|---|---|---|---|---|---|
| 865-94625 | 14 (P) | 3 | 57.4 | 19:31 ± 18 | 06:53 ± 32 | 668 ± 39 | 46.4 ± 3.5 |
| 865-94725 | 19 (P) | 5 | 42.1 | 19:07 ± 53 | 09:44 ± 59 | 877 ± 41 | 60.9 ± 2.9 |
| 865-94735 | 8 (N) | 2 | 75.0 | 19:50 ± 6 | 06:08 ± 2 | 618 ± 8 | 43.0 ± 0.5 |
| Mean | | | 58.2 | 19:29 ± 21 | 07:30 ± 117 | 721 ± 138 | 50.1 ± 9.5 |

[a] P = parasitized; N = not parasitized (see Methods).
[b] Number of consecutive days during egg laying that nests were monitored.
[c] Percentage of the final clutch size that was present on the first day that female attentiveness data were collected.
[d] Standard deviation expressed as minutes.

(Davies and Cooke 1983, Ockleford and Vince 1985). Davies and Cooke (1983), for example, experimentally created developmental asynchrony in nests of female Lesser Snow Geese (*Chen caerulescens caerulescens*). They found that no eggs delayed more than 4 days hatched successfully. A trade-off between increasing levels of intraclutch developmental asynchrony to assure viability of first-laid eggs and the possibility of reduced hatching success of last-laid eggs may result in a constraint of the most productive clutch size in precocial species capable of laying relatively large clutches.

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## LITERATURE CITED

AFTON, A. D. 1980. Factors affecting incubation rhythms of Northern Shovelers. Condor 82:132–137.

AFTON, A. D., AND S. L. PAULUS. In press. Incubation and brood care in waterfowl. *In* B.D.J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.], The ecology and management of breeding waterfowl. Univ. of Minnesota Press, St. Paul.

ARNOLD, T. W., F. C. ROHWER, AND T. ARMSTRONG. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. Am. Nat. 130:643–653.

BELLROSE, F. C. 1980. Ducks, geese, and swans of North America. Stackpole, Harrisburg, PA.

BRECKENRIDGE, W. J. 1956. Nesting study of Wood Ducks. J. Wildl. Manage. 20:16–21.

CALDWELL, P. J., AND G. W. CORNWELL. 1975. Incubation behavior and temperatures of the Mallard duck. Auk 92:706–731.

CARGILL, S. M., AND F. COOKE. 1981. Correlation of laying and hatching sequences in clutches of the Lesser Snow Goose (*Anser caerulescens caerulescens*). Can. J. Zool. 59:1201–1204.

CLARK, A. B., AND D. S. WILSON. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. Q. Rev. Biol. 52:253–273.

CLAWSON, R. L., G. W. HARTMAN, AND L. H. FREDRICKSON. 1979. Dump nesting in a Missouri Wood Duck population. J. Wildl. Manage. 43:347–355.

COOPER, J. A. 1978. The history and breeding biology of Canada Geese at Marshy Point, Manitoba. Wildl. Monogr. 61:39–41.

DAVIES, J. C., AND F. COOKE. 1983. Intraclutch hatch synchronization in the Lesser Snow Goose. Can. J. Zool. 61:1398–1401.

DRAPER, N. R., AND H. SMITH. 1966. Applied regression analysis. John H. Wiley and Sons, New York.

DROBNEY, R. D. 1980. Reproductive bioenergetics of Wood Ducks. Auk 97:480–490.

DROBNEY, R. D., AND L. H. FREDRICKSON. 1979. Food selection by Wood Ducks in relation to breeding status. J. Wildl. Manage. 43:109–120.

HAFTORN, S., AND R. E. REINERTSEN. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living Blue Tit (*Parus caeruleus*). Auk 102:470–478.

HANSON, H. C. 1954. Criteria of age of incubated Mallard, Wood Duck, and Bob-white Quail eggs. Auk 71:267–272.

HEPP, G. R., R. T. HOPPE, AND R. A. KENNAMER. 1987. Population parameters and philopatry of breeding female Wood Ducks. J. Wildl. Manage. 51:399–402.

KENNAMER, R. A., AND G. R. HEPP. 1987. Frequency and timing of second broods in Wood Ducks. Wilson Bull. 99:655–662.

KENNAMER, R. A., W. F. HARVEY IV, AND G. R. HEPP. 1988. Notes on Hooded Merganser nests in the coastal plain of South Carolina. Wilson Bull. 100:686–688.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

LEOPOLD, F. 1951. A study of nesting Wood Ducks in Iowa. Condor 53:209–220.

OCKLEFORD, E. M., AND M. A. VINCE. 1985. Acceleration of hatching in fowl and quail: relationship between artificial and natural stimulus amplitude. Br. Poult. Sci. 26:57–63.

PERRINS, C. M. 1977. The role of predation in the evolution of clutch size, p. 181–191. *In* B. M. Stonehouse and C. M. Perrins [eds.], Evolutionary ecology. Univ. Park Press, Baltimore, MD.

PRINCE, H. H., P. B. SIEGEL, AND G. W. CORNWELL. 1969. Hatchability, clutch position, and hatching sequence in Mallards. Auk 87:762–763.

SAS INSTITUTE. 1985. SAS user's guide: statistics. Version 5. SAS Institute, Cary, NC.

SEMEL, B., AND P. W. SHERMAN. 1986. Dynamics of nest parasitism in Wood Ducks. Auk 103:813–816.

WELLER, M. W. 1956. A simple field candler for waterfowl eggs. J. Wildl. Manage. 20:111–113.

VINCE, M. A. 1964. Social facilitation of hatching in the Bobwhite Quail. Anim. Behav. 12:531–534.

VINCE, M. A. 1968. Retardation as a factor in the synchrony of hatching. Anim. Behav. 16:332–335.