SHORT COMMUNICATIONS

Dynamics of Nest Parasitism in Wood Ducks

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Intraspecific brood parasitism is widespread among waterfowl (Weller 1959, Yom-Tov 1980, Andersson 1984). Often referred to as "dump nesting," the phenomenon is particularly prevalent in Wood Ducks (*Aix sponsa*). In this species more than 50% of the nests may be parasitized, and clutches of 20–40 eggs, far exceeding a female's normal 11–15-egg capacity, are commonly observed (e.g. Grice and Rogers 1965, Morse and Wight 1969, Hansen 1971, Clawson et al. 1979). Although it is clear that supernormal clutches are produced by multiple females, the number of individuals contributing to each nest is unknown. We studied a population of Wood Ducks in southeast Missouri during the spring of 1985 to determine (1) the rate of egg deposition, (2) the minimum number of females laying in each clutch, and (3) behaviors associated with nest searching and laying.

The study was conducted on a reservoir ("Pool 1") located in the Duck Creek Wildlife Management Area in Stoddard and Bollinger counties, Missouri. Pool 1 was created in 1954 when a 718-ha tract of lowland hardwood forest was flooded. Today only scattered bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) trees and stumps remain. In 1955, 55 Wood Duck nest boxes were erected on the area. Since then nesting structures have been added and the Wood Duck population has increased (see Hartman 1972, Clawson 1975). By 1985 there were 103 wood or metal nesting structures on Pool 1; these were attached to living trees, snags, or metal poles, 1–3 m above the water, and 0 m (double boxes) to 500 m apart. The wooden boxes were similar in dimensions and construction (see Webster and Uhler 1964).

The nesting activities of female Wood Ducks were observed from 14 March to 5 April, coincident with the peak of clutch initiations at Duck Creek (see Clawson et al. 1979: fig. 1). To determine rates of egg deposition, a sample of 50 wooden nest boxes was chosen randomly and checked daily between 1000 and 1500, after each day's laying activity had ceased. All eggs were marked individually and dated; increases in egg number and egg disappearances were recorded. To minimize disturbance, we stopped checking a box 2 days after incubation commenced. The first day on which warm, down-covered, symmetrically arranged eggs were observed in the nest bowl was considered the onset of incubation. The accuracy of these criteria was verified by subsequent candling of all the eggs in 5 clutches (Weller 1956). A clutch was considered abandoned if it was never incubated; the date of abandonment was defined as the day after the last egg was laid.

Detailed observations of Wood Duck behavior in the vicinity of 12 of the 50 wooden nest boxes were conducted on 19 days, from first light until all birds had departed (ca. 0900). The boxes under observation were erected during the winter of 1985 in an area of Pool 1 that previously had contained a dense concentration of nesting structures (Hartman 1972: 18). Existing boxes were removed and new ones placed in a semicircle, 5–6 m apart and 10–30 m from a blind; the 12 focal boxes and the blind were connected by a catwalk. Traps consisting of a spring-loaded sliding door and an electrically triggered release mechanism were installed in each box (trap specifications are available from the authors). Twenty-six female Wood Ducks were captured and marked with individually numbered nasal saddles and U.S. Fish and Wildlife Service leg bands. Trapping occurred only after a day's observations had ended.

Nest-box checks.—Of the 50 boxes that were examined daily, 25 (50%) were used by Wood Ducks, 2 (4%) contained mixed clutches of Wood Ducks and Hooded Mergansers (*Lophodytes cucullatus*), and 23 (46%) were unused. Detailed chronologies were obtained for 21 of the 25 Wood Duck nests, in which 361 eggs were laid; egg deposition in the other 4 nests was well advanced at the start of our study. Of the 21 clutches whose development we witnessed, 20 increased by ≥ 2 eggs/day at least once, implying a parasitism rate of 95%. Nine of the 21 nests (43%) were abandoned before incubation (including 2 nests in the 12 observation boxes). For the remainder, the mean interval between clutch initiation and incubation was 12.8 ± 1.4 (SD) days.

Within each box, rates of egg deposition were erratic (Fig. 1). Clutches could increase by 7–8 eggs in a single day (Fig. 1b, e), or fail to increase on one or more days (Fig. 1a, b). Most nests (76%) were initiated by one female (i.e. only one egg appeared on the first day of laying in 13 of the 17 nests in which the first egg was recorded), and the heaviest parasitism occurred during the latter half of the laying period (Fig. 1a–f). Eggs were laid parasitically at all stages, however, from clutch initiation (Fig. 1f, h) through incubation (Fig. 1a–g). Most nests had one or two days of peak parasitism when the rate of egg deposition increased 2- to 4-fold (Fig. 1b–f). The variances in the daily rates at which eggs appeared were homogeneous among nests ($\chi^2 = 19.7$, df = 17, $P = 0.4$, Bart-

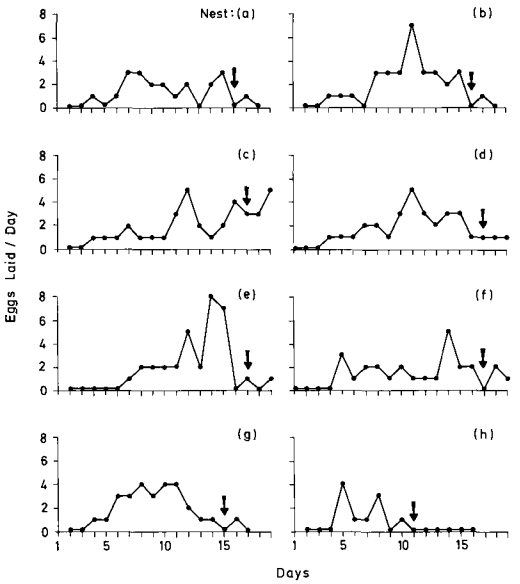

Fig. 1. Daily clutch-size increases (new eggs laid/day) in 8 boxes used by Wood Ducks during the spring of 1985 at Duck Creek, Missouri. The 8 nests depicted are among those with the most complete chronologies, beginning before clutch initiation and continuing to incubation or abandonment. For all panels, day 1 = 16 March; arrows indicate the start of incubation (a–g) or the date of abandonment (h).

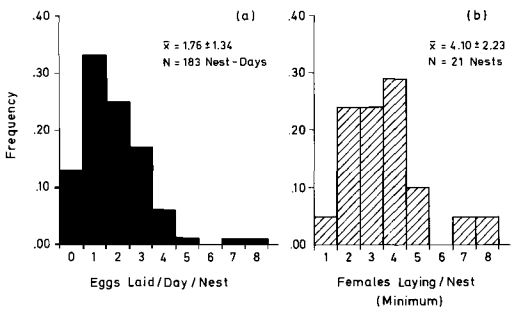

Fig. 2. (a) Rates of egg laying in 21 Wood Duck nests during the spring of 1985 at Duck Creek. Nests were examined daily until 2 days after incubation started or until abandonment (see text); data from all 183 checks of the focal nests are presented. The "0" category indicates a skip: a nest containing eggs and to which eggs subsequently were added failed to increase on a given day (e.g. days 5 and 13 in Fig. 1a). (b) Minimum number of hens that contributed eggs to each of the 21 focal nests, based on the maximum daily egg accumulation in each box (e.g. day 11 in Fig. 1b, or day 12 in Fig. 1c).

lett's test; Sokal and Rohlf 1981: 403), suggesting that irregular egg deposition rates were the norm rather than the exception.

Among the sampled nests, the largest clutch contained 37 eggs and the two smallest contained 1 egg apiece (all three eventually were abandoned). On average, nests increased by 1.76 eggs/day (Fig. 2a), and the number of eggs added per nest each day was random (i.e. the distribution of egg deposition rates did not differ significantly from a Poisson: $\chi^2 = 4.8$, df = 7, $P = 0.5$). Because each female lays no more than 1 egg/day (Leopold 1951, Drobney 1980), the maximum daily egg accumulation in a nest yields a minimum estimate of the number of females that laid in it. In our sample, at least 4 different females typically contributed to each clutch (range: 1–8; Fig. 2b). These estimates, however, are unquestionably conservative. For example, direct observations revealed that a minimum of 6 different females (5 marked, ≥1 unmarked) laid in one nest to which no more than 3 new eggs were added on any one day (see Fig. 1a). Furthermore, three times when a closely observed nest increased by only 1 egg/day, the egg was laid by a female other than the one that eventually incubated the clutch (i.e. at least 2 females laid in each of these 3 nests).

Occasionally, eggs disappeared from nests. In 18 of 20 cases (90%) a missing egg was known to have been damaged before its disappearance. Eggs were sometimes cracked by the ducks themselves ($n = 6$), especially on days of peak parasitism when many females entered and exited a box in quick succession. More frequently ($n = 12$), Red-bellied Woodpeckers (*Melanerpes carolinus*) entered unattended boxes, pecked a hole in an egg, and ate some of the contents. We directly observed the fate of damaged eggs five times. In every case a female Wood Duck carried the damaged egg from a box to the water in her bill, broke it open, and quickly ate the contents.

Behavioral observations.—During our unobtrusive observations ($n = 62$ h) we saw how rapid clutch development occurred. Soon after sunrise each day, pairs of Wood Ducks began appearing near boxes. Pairs arrived singly, usually from different directions, and remained apart. If one female entered or left a box, however, a group of pairs quickly coalesced and more females sought to enter that nest. Pairs often flew considerable distances (e.g. 0.5–1.0 km) from vantage points high in trees to boxes where such activity was occurring. Soon the chosen box was surrounded by many birds (e.g. in one case 8 pairs), either on the water or perched on stumps or adjacent boxes.

Groups of paired birds changed frequently in size and composition as females entered and exited the chosen box, then departed the area followed by their mates. Investigations of nest boxes by females typically occurred rapidly, and because many of the birds laid eggs, clutches could develop quickly. For example, 5 different females entered and left one box

in 21 min; 4 of them laid eggs. Intense activity around recently occupied boxes contrasted with the birds' relative lack of interest in nearby nests (regardless of whether they contained eggs) and suggests that the mechanism underlying parasitism involves following and observing conspecifics entering or leaving nest sites. Similar observations were made by Heusmann et al. (1980) for Wood Ducks and by Andersson and Eriksson (1982) for Common Goldeneyes (*Bucephala clangula*).

Female Wood Ducks attempted to evade nest parasitism in two ways. First, they behaved surreptitiously in the vicinity of their box and avoided approaching or entering it when conspecifics were nearby. For example, we observed the arrival of marked female Gr-4 to the nest she eventually incubated on 8 mornings (0630–0730). On 4 days no other females were visible to us when she arrived, and Gr-4 entered the box 12.4 ± 5.7 min after we first sighted her. In contrast, on the 4 days when at least one other female was visible to us, Gr-4's latency to enter the box was 68.5 ± 18.4 min ($P < 0.01$, t-test). Second, females attempted to thwart parasitism by aggressively excluding intruders from their nests. On 9 occasions we saw a female try to enter a box when it was occupied; in 7 of these cases, involving 4 different nest "owners," there was a struggle and the intruder was repelled (similar aggressive defense of nests was reported by Clawson et al. 1979).

There was a striking lack of box fidelity among laying females. For example, one marked bird laid 4 eggs in one box (over a 6-day period), then disappeared, and a different female laid 8 eggs and incubated the entire clutch. Another female laid 3 eggs in one box (over 5 days) and 1 in a second box, and two females laid 1 egg in each of two different boxes before disappearing. Twice, females that we saw repulsed by nest owners entered a nearby empty box, laid an egg, and abandoned it. In addition, freshly laid eggs were found on the catwalk ($n = 1$), on top of a box ($n = 1$), and on the shore near boxes ($n = 4$).

Effects of nest boxes on parasitism.—Our data (Figs. 1 and 2) reveal that (1) clutch sizes increased erratically and sometimes explosively, (2) daily egg deposition rates were random among nests, and (3) many different females contributed to each clutch. Although similar phenomena have been described previously in Wood Ducks (e.g. Grice and Rogers 1965, Hartman 1972, Heusmann et al. 1980), this is the first time they have been quantified. Interestingly, nearly every nest we studied (95%) was parasitized despite an abundance (46%) of empty boxes that had been used in previous years (J. Ware unpubl. data). This supports the contention that brood parasitism in *A. sponsa* is not caused solely by a scarcity of suitable nest sites (Morse and Wight 1969, Haramis 1975, Andersson 1984).

Naturally occurring tree cavities in which Wood Ducks nest are typically widely spaced and difficult for humans, and perhaps potentially parasitic females, to locate (Weier 1966, Prince 1968). Although nest parasitism can occur under natural conditions (e.g. Sampson 1901, Bellrose et al. 1964), its frequency is apparently lower and the size of clutches is smaller than in man-made nesting situations. For example, we located clutch-size data in the literature from 28 nests in natural cavities (Bent 1923, Dixon 1924, Prince 1965, Bolen and Cottam 1967). Of these, 71% ($n = 20$) contained ≤16 eggs (range: 7–16), likely laid by one female, while 29% (8) clearly were parasitized (range: 19–31 eggs). In contrast, 76% ($n = 19$) of our 25 occupied nest boxes contained ≥19 eggs, and clutch sizes ranged as high as 37. Furthermore, dump nests containing 45–50 eggs have been observed at Duck Creek (Clawson et al. 1979, L. H. Fredrickson pers. comm.) and elsewhere (e.g. Oregon: Morse and Wight 1969).

We hypothesize that proximity and visibility of nest boxes facilitates the development of supernormal clutches (i.e. dump nesting). The grouping of artificial structures forces Wood Ducks, which normally nest solitarily, into semicoloniality. This causes the surreptitious behavior of females, which probably helps conceal nest-site locations in natural situations (and so reduces parasitism), to become ineffectual. In other words, the placement of boxes at high densities and in obvious places (a standard management practice) makes it difficult for females to visit their nests undetected. If the local population density rises due to successful reproduction and female philopatry (Bellrose et al. 1964, Doty and Kruse 1972), the effect is exacerbated (e.g. Jones and Leopold 1967, Haramis and Thompson 1985), making it nearly impossible for females to hide their nest sites or to repel increasing numbers of potentially parasitic conspecifics.

Female birds that lay eggs in others' nests potentially achieve reproductive success without incurring the physiological costs or the dangers associated with incubation and parental care (Payne 1977, Andersson 1984). However, extreme parasitism rates, explosive increases in clutch size, frequent nest abandonment, and parasitic egg laying at inappropriate times (e.g. during incubation) and places (atop boxes, on the ground, or in the water; see Clawson et al. 1979) together suggest that nesting interference may have reached a pathologically high level in *A. sponsa* at Duck Creek and perhaps elsewhere (e.g. Massachusetts: Heusmann et al. 1980). If so, dump nesting may have become reproductively disadvantageous for females laying parasitically as well as for birds incubating clutches, due to drastically reduced hatchability (e.g. Haramis and Thompson 1985). Under these artificial ecological and social conditions, it is impossible to quantify either the "normal" frequency of brood parasitism or its costs and benefits for individual females (e.g. Emlen and Wrege 1986). Evaluating hypotheses concerning the evolution or adaptive significance of brood parasitism in *A. sponsa* (e.g. the

kinship component: Andersson 1984), as well as the implications of dump nesting for Wood Duck population biology and its management, will require detailed comparisons under more natural nesting situations.

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