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EFFECTS OF BROOD PARASITISM AND NEST-BOX PLACEMENT ON WOOD DUCK BREEDING ECOLOGY[1]

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Abstract. Intraspecific brood parasitism occurs frequently among Wood Duck (*Aix sponsa*) populations nesting in artificial structures. To assess the effects of such parasitism on population ecology, we analyzed 12 years of Wood Duck nesting records (1976–1987) from a study site in northeastern Illinois. Hatchability of eggs (ducklings produced/total eggs laid) was inversely correlated with population density, with the frequency of parasitism, and with the number of eggs laid per nest. The hatchability of all eggs laid in nests that had been parasitized (16–44 eggs) was 57.5% vs. 67.3% for eggs laid in "normal" nests (7–15 eggs). The negative consequences of parasitism were due mainly to nest abandonment, damaged eggs, and eggs laid after the start of incubation, and occurred despite the consistent availability of suitable unused boxes.

The frequency of brood parasitism was strongly affected by box placement. During 1976–1987, parasitism occurred in 49.5% of boxes erected singly in highly visible locations, in 49.5% of boxes erected in highly visible groups, but in only 29.8% of boxes that had been erected singly in visually occluded habitat. Mean clutch sizes for the visible-isolated (15.7 eggs) and visible-clumped (16.3 eggs) boxes were significantly higher ($F = 4.49$, $P = 0.012$) than for the well-hidden boxes (12.4 eggs). Hatchability in successful well-hidden nests was 82.0% vs. ca. 74.0% in successful visible boxes. The data suggest that reduced parasitism and increased hatchability occur when artificial nesting structures are placed in habitats and at densities resembling the natural circumstances in which Wood Ducks evolved. These results have implications not only for the study and management of *A. sponsa* populations, but also for the placement of nest boxes in behavioral and ecological studies of other cavity-nesting birds.

Key words: *Wood Duck;* Aix sponsa; *brood parasitism; hatchability; nest-box placement.*

INTRODUCTION

The use of artificial nesting structures for cavity-nesting birds is a widely accepted management practice and research tool. Boxes provide secure nest sites and additional nesting opportunities in areas where natural cavities are limited. Nest boxes also increase the accessibility of nests to investigators. Given their widespread importance and use, evaluations of the effects of nest boxes themselves on avian breeding behavior and population ecology are warranted.

Nest boxes are commonly used in the management and study of breeding Wood Ducks (*Aix sponsa*). Nest-box programs have contributed to increases in local Wood Duck populations (e.g., McLaughlin and Grice 1952, Bellrose and McGilvrey 1966, Clawson 1975, Zipko 1979), to range expansion (Doty and Kruse 1972, Doty et al. 1984), and to the re-establishment of the species where it had been extirpated (McCabe 1947, Bellrose 1953). Considerable effort has gone into identifying factors that influence nest-box preferences of female Wood Ducks so that box use is maximized (e.g., Webster and Uhler 1964, Strange et al. 1971, Gilmer et al. 1978, Keran 1978, Lacki et al. 1987). Results consistently show that high visibility and clustering of boxes (especially mounting boxes back to back) increase occupancy; thus both practices are widely used (see McGilvrey 1968, Bellrose and Crompton 1972, USFWS 1976, Yoakum et al. 1980).

Grouped, highly visible nest boxes permit Wood Ducks, which typically nest solitarily in widely separated, well-hidden tree cavities (Prince 1965, Robb 1986), to be semicolonial. Intraspecific brood parasitism, undoubtedly a normal

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facet of the nesting biology of Wood Ducks (Andersson 1984) and many other anatids (Weller 1959, Yom-Tov 1980, Andersson and Eriksson 1982, Gauthier 1986), is triggered when females observe conspecifics entering or leaving active nest sites (Heusmann et al. 1980, Semel and Sherman 1986). When boxes are grouped in highly visible locations it becomes impossible for females to visit their nests unobserved. Conversely, in the dense, visually occluded stands of bottomland forest that Wood Ducks favor, it is probably difficult for females to follow conspecifics to active nest sites; moreover, females defend their nests (Bellrose 1986), and this further restricts access to them. Thus the frequency of parasitism in natural cavities is much lower than in densely clumped boxes (reviewed by Semel and Sherman 1986).

When population densities are high, elevated levels of brood parasitism ("dump nesting") occur in nest boxes, leading to various social pathologies, including physical conflicts and behavioral interference with laying females (Bellrose 1986), nest abandonment (McLaughlin and Grice 1952), and drastically reduced hatchability of eggs (Leopold 1951, Grice and Rogers 1965, Jones and Leopold 1967). These well-known but little studied manifestations of dump nesting (see Haramis and Thompson 1985) led us to examine quantitatively (1) how intraspecific brood parasitism affects hatchability, and presumably, Wood Duck demography, and (2) how nest-box placement affects the laying behavior of female Wood Ducks.

STUDY AREA

Fieldwork was conducted at the Max McGraw Wildlife Foundation (MMWF) near Dundee, Kane County, Illinois. Small ponds (n = 33) ranging in size from 0.04 to 3.7 ha and 1 to 7 m deep are scattered throughout the 550-ha site; the total area of water surface is about 27 ha. Mixed woodlands of oaks (*Quercus* spp.), maples (*Acer* spp.), and hickories (*Carya* spp.) are interspersed with the ponds. However, steep embankments and limited emergent vegetation on the ponds provide only marginal Wood Duck habitat (David 1986).

A Wood Duck nest-box program was initiated at MMWF in 1967, when 14 boxes were erected (Dillon 1970). Additional boxes were added in subsequent years, so that by 1976 the total was 73. In following years, the number of available boxes ranged between 73 and 64. Most of the structures (ca. 75%) were secured with iron brackets to mature trees (entrance holes ca. 3 m above the ground) adjacent to water; the remaining boxes were placed directly over water on metal posts, 1 to 2 m above the surface. All except five boxes were metal and conical in shape (Bellrose 1953, Webster and Uhler 1964) and all were protected by metal predator guards or mounted on trees with predator-proof supports.

METHODS

BOX PLACEMENT

In 1985, all nest boxes were visited and categorized according to their conspicuousness and proximity to other boxes. Classifications were made during January–March when vegetative cover approximated that encountered by female Wood Ducks during early-season nest-site searches. Four general categories were recognized: (1) visible-isolated (VI), (2) visible-clumped (VC), (3) well-hidden (WH), and (4) "other." VI boxes (n = 11) were attached individually to poles 1–2 m above water; from each one no other artificial nesting structures could be seen. VC boxes (n = 10) were duplexes (boxes mounted back to back) attached to poles 1–2 m above water; each duplex was placed 8–10 m from one other duplex. WH boxes (n = 8) were attached to trees in woodlots 10–20 m from the water; these were difficult to see from the nearest water and females could probably enter or leave them without being observed by conspecifics on the water. Boxes not meeting the VC, VI, or WH criteria (n = 37) were termed "other." In 1986, the "other" boxes were repositioned so that they fit into categories 1–3. During the 12-year period 1976–1987, the total number of boxes available by category were: WH = 102, VI = 157, VC = 118.

NEST-BOX CHECKS

During 1976–1985, all nest boxes were checked weekly beginning the last week of March and continuing until termination of all clutches. Following hatching, egg membranes, unhatched eggs, and dead chicks were counted; thereafter, nest contents were replaced with fresh wood shavings.

In 1986 and 1987, 30 and 66 boxes, respectively, were checked daily. Daily checks were initiated in late March and continued, for active nests, until 2 days after the termination of egg

TABLE 1. Annual Wood Duck nesting summaries for the Max McGraw Wildlife Foundation, Dundee, Illinois, 1976–1987.

Year	Nest starts	Successful nests	Eggs laid	Eggs hatched	Hatchability (%)	Mean clutch size	Nests >15 eggs
1976	40	31	580	380	65.5	14.5	17
1977	31	28	464	341	73.5	15.0	15
1978	40	30	651	397	61.0	16.3	23
1979	56	28	944	362	38.4	16.9	29
1980	41	27	597	346	58.0	14.6	16
1981	41	33	755	421	55.8	18.4	26
1982	47	38	804	505	62.8	17.1	24
1983	44	34	771	466	60.4	17.5	28
1984	26	18	289	197	68.2	11.1	3
1985	21	18	268	206	76.9	12.8	4
1986	29	18	361	221	61.2	12.5	9
1987	32	23	457	315	68.9	14.3	12
Mean	37	27	578	346	59.9	15.1	17
Total	448	326	6,941	4,157	62.5	—	206

deposition. Checks normally were conducted between 11:00 and 15:00, when daily laying activity had ceased. Eggs in each box were numbered sequentially with a felt-tipped pen. Because individual females are not known to lay more than one egg in a 24-hr period (Leopold 1951, Drobney 1980), ≥ 2 eggs deposited in a nest between checks indicated brood parasitism. Periodic checks of completed clutches were conducted in the early morning or late evening, while females were away feeding, to verify clutch size and/or evidence of clutch disturbance. The start of incubation was defined as the first day on which eggs were covered, arranged symmetrically in the nest bowl, and on which a female was present on the nest for >4 hr (i.e., if a female was present during the initial nest check on a given day, the nest was reinspected >4 hr later).

DEFINITIONS

Hatchability was defined as the total number of ducklings leaving a nest box/total number of eggs laid in that box. Clutch size was the maximum number of eggs deposited in a nest (i.e., including any eggs missing from a nest box prior to hatch, such as those removed by a predator). The conventional term "normal" was used to define those clutches with 7–15 eggs (assuming that such nests were not parasitized); by contrast, any nest with >15 eggs was defined as a parasitized or "dump nest" (see Grice and Rogers 1965, Heusmann 1972, Haramis and Thompson 1985). Eggs deposited in nests following the start of incubation were defined as non-term eggs (Morse and Wight 1969). Nests with 1–6 eggs were called drop nests following Morse and Wight (1969); these nests were rarely incubated and never hatched. A successful nest was one from which at least one duckling hatched. Finally, nest-box occupancy rate was the fraction of boxes in which a nest was initiated (i.e., at least one egg was found). Individual boxes often had more than one nest start during a breeding season.

STATISTICAL ANALYSIS

Linear regression, Analysis of variance, Student's t-test, and the nonparametric Kruskal-Wallis and Chi-square tests were performed with the SPSS/PC+ statistical package (Norusis 1986). Exponential curves were developed using the Bivariate Data Program (Texas Instruments 1977).

RESULTS

FACTORS AFFECTING HATCHABILITY

During 1976–1987, there were 448 nest starts by Wood Ducks at MMWF (Table 1). Of these, 206 (46%) were considered dump nests, 204 (46%) were normal, and 38 (8%) were drop nests. Nest-box occupancy rate varied from 47% to 85%, while nesting success ranged from 50% to 90%. Hatchability averaged 62.5% and ranged from 38% to 77% (Table 1).

As the number of nest starts in 1976–1987 increased, mean clutch size also increased significantly (Fig. 1A). This correlation (r^2 = 0.62, P < 0.01) implied that more intraspecific brood parasitism occurred. Indeed, the number of dump nests was positively correlated with the number of nest starts (r^2 = 0.83, P < 0.001, Fig. 1B).

However, as clutch sizes increased and dump nesting became more prevalent, there was a highly significant decline in hatchability ($r^2 = 0.70$, $P < 0.001$, Fig. 1C). Annual hatchability was also inversely correlated ($r^2 = 0.61$, $P < 0.01$) with the total number of eggs laid in the population each year (Semel et al., in press).

Hatchability of eggs from normal nests (67.3%) was higher than from dump nests (57.5%) for the 12 years combined; this difference was marginally significant ($t = 1.13$, $P = 0.07$). Hatchability increased slightly as mean clutch size increased over the range of 7 to 15 eggs (Fig. 2); this was probably due more to the frequency (35%; $n = 16$) with which 7 to 9-egg clutches were abandoned than to any actual facilitating effect of increased clutch size. Hatchability declined sharply and significantly as the mean clutch size increased from 16 to 44 eggs (Fig. 2).

EFFECTS OF NEST-BOX PLACEMENT ON CLUTCH SIZE

Of the 448 nest starts recorded in our sample, 245 occurred in boxes designated as VI, VC, or WH (Table 2). Clutch sizes were significantly lower ($F = 4.49$, $P = 0.01$) in WH boxes (12.4 eggs) than in either VI (15.7 eggs) or VC (16.3 eggs) boxes. Whereas only 30% of WH boxes were parasitized, 49.5% of both VI and VC were dump nests (Table 2). Significantly fewer ducklings left each WH box than either VI or VC boxes ($t = -2.38$, $P = 0.02$), due to the lower number of eggs deposited in each WH box.

WH boxes were used by the ducks only 46.1% of the times they were available, significantly less often ($\chi^2 = 26.2$, $P < 0.001$) than either VI (66.9%) or VC (78.8%) boxes (Table 2). This is presumably because WH boxes were inconspicuous. Successful WH nests, however, had a slightly higher hatchability (82.0%) than either VI or VC nests: 73.7% and 74.1%, respectively ($F = 1.79$, $P = 0.17$). Rather unexpectedly, clutches in WH boxes were less often successful (59.6%) than those in either VI (78.1%) or VC (73.1%) boxes. However, rates of hatchability were not significantly different by box designation when considering both successful and unsuccessful nests ($F = 1.29$, $P = 0.28$).

RATES OF DAILY EGG DEPOSITION

Seventeen of 30 (57%) and 22 of 66 (33%) boxes selected for intensive study were occupied in 1986 and 1987, respectively. Of the 13 nests in which rates of daily egg deposition indicated that only one female was contributing, the mean clutch size was 10.8 eggs (SD = ±1.0, range = 7–12). This is consistent with mean clutch sizes re-

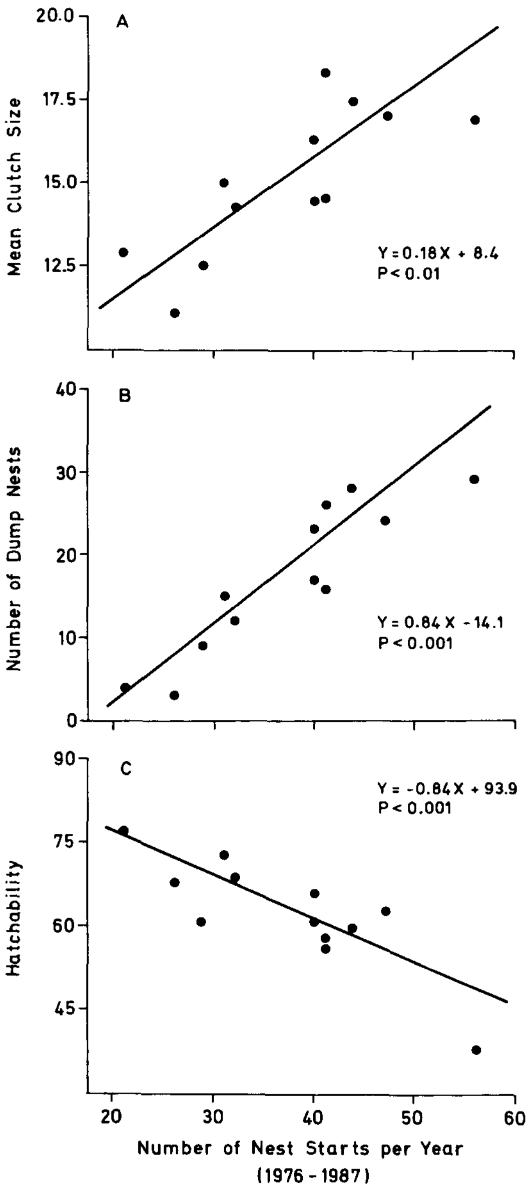

FIGURE 1. Relationship between the annual number of Wood Duck nest starts per year during 1976–1987 at the Max McGraw Wildlife Foundation and (A) average clutch size per box per year, (B) numbers of dump nests (>15 eggs) per year, and (C) hatchability (%) of eggs per box per year. In each panel, the line represents a regression of best fit; the regression equation is also given.

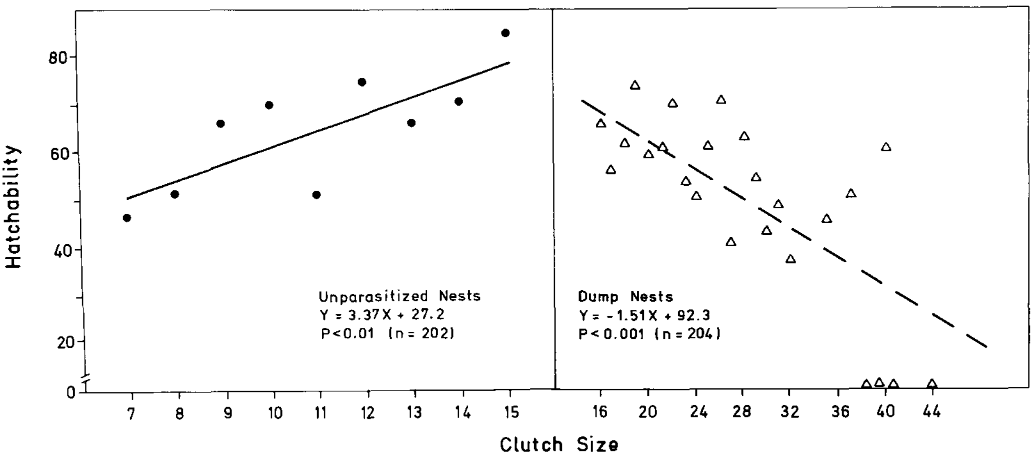

FIGURE 2. Relationship between mean clutch size and hatchability (eggs hatched/eggs laid per box) of Wood Duck eggs at the Max McGraw Wildlife Foundation during 1976–1987. Solid dots represent mean hatchability for all "normal" (i.e., unparasitized) nests (7–15 eggs), while the open triangles represent mean hatchability of dump nests (16–44 eggs). The ascending line is the best fitting regression for normal nests and the descending line depicts the best fitting regression for dump nests (sample size is in parentheses).

ported for unparasitized nests elsewhere (e.g., Bellrose 1953, Hansen 1971, Drobney and Fredrickson 1985).

Daily nest-box checks revealed highly variable daily egg deposition rates in parasitized nests (Fig. 3) like those reported for Wood Ducks in Missouri by Semel and Sherman (1986). Following nest initiation, 75% of the females (n = 27) skipped a day before laying a second egg. Although clutches typically were initiated by a single female (i.e., only one egg appeared on the first day in 97% of nest starts), eggs were laid parasitically at all stages thereafter, even until 10 days after incubation had begun (e.g., Fig. 3C). Nest-box checks in 1987 also revealed that many eggs (n = 36) which failed to hatch in successful nests had been deposited after the start of incubation.

Box visibility strongly affected the incidence of parasitism. Whereas no more than two females nested in any WH box, at least three females laid in some VC boxes and as many as five females laid in a single VI box (Fig. 4). Visible boxes (VI and VC, combined) received significantly more multiple female clutches than WH boxes (Kruskal-Wallis H = 7.87, P = 0.02).

Daily nest-box checks defined more clearly the incidence of parasitism than counting the total number of eggs per box. Of the 39 nests included in our sample, 15 (38.5%) contained >15 eggs. Daily egg-deposition rates, however, revealed that

TABLE 2. Summary of Wood Duck nesting success in various nest-box designations at the Max McGraw Wildlife Foundation, 1976–1987.

	Box designation		
	Well hidden	Visible isolated	Visible clumped
Available boxes	102	157	118
Mean clutch size	12.4	15.7	16.3
No. boxes used (% occupancy)	47 (46.1)	105 (66.9)	93 (78.8)
Frequency of nest parasitism (>15 eggs)	29.8	49.5	49.5
Range	2–24	1–41	1–44
No. of successful nests (% successful)	28 (59.6)	82 (78.1)	68 (73.1)
No. eggs hatched/laid in all nests (% hatchability)	332/583 (56.9)	1,042/1,644 (63.4)	867/1,517 (57.2)
No. eggs hatched/laid in successful nests (% hatchability)	332/405 (82.0)	1,042/1,413 (73.7)	867/1,170 (74.1)
Mean no. ducklings leaving nest	7.1	9.9	9.3

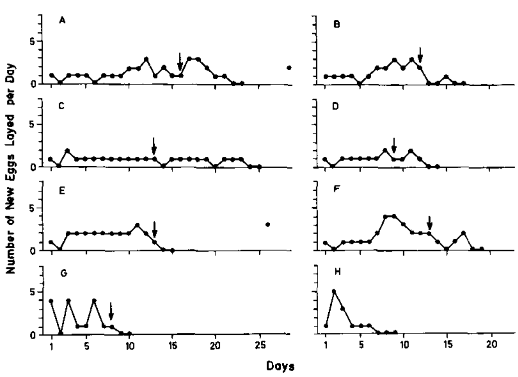

FIGURE 3. Daily rates of egg deposition for eight parasitized nest boxes used by Wood Ducks at Max McGraw Wildlife Foundation during 1986–1987. For all panels, "Day 1" is the first day on which an egg was found in a nest. Arrows indicate the day on which incubation began. Some eggs were found during nest inspections following the last day of daily box checks, and these are depicted as unconnected dots.

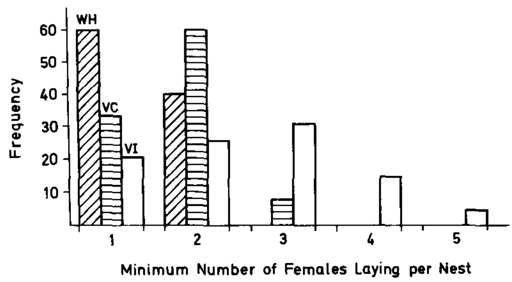

FIGURE 4. Frequency histogram of the minimum number of Wood Duck females laying eggs in each box (i.e., as indicated by the maximum daily egg accumulation; see Fig. 3) separated by nest-box designation: WH = well-hidden, VC = visible-clumped, and VI = visible-isolated. Data are from daily nest-box checks at the Max McGraw Wildlife Foundation during 1986–1987 (n = 5WH, 15 VC, and 19 VI nest starts in the sample).

26 of the 39 nests (66.7%) had actually been parasitized. In other words, clutch-size counts alone underestimated the frequency of parasitism by 42%. Few WH boxes in our sample were parasitized (40%), while 80% and 67% of VI and VC boxes, respectively, received ≥2 eggs/day at least once. Therefore, daily nest-box checks strengthened the conclusion that increased parasitism is associated with high box visibility.

DISCUSSION

COSTS AND BENEFITS OF BROOD PARASITISM IN WOOD DUCKS

Female birds that lay eggs in the nests of others potentially gain reproductive benefits without incurring the physiological costs or the dangers associated with incubation and parental care (Payne 1977, Andersson 1984). For Wood Ducks, the risk of predation is extreme in natural cavities. For example, nest success ranges from 22% (Robb 1986) to 52% (Sousa and Farmer 1983), and the greatest mortality among nesting female Wood Ducks occurs during incubation (Bellrose et al. 1964). Parasitism also benefits females who cannot find a suitable nest cavity of their own, since they can thereby gain at least some reproduction; in precocial species there is probably little risk that a few extra eggs will jeopardize the success of an entire clutch. Finally, by dispersing eggs into more than one nest females may eliminate the possibility of a failed clutch jeopardizing all their reproductive output (Brown and Brown 1988). Payne (1977) provides data suggesting that when nesting success is low, survival of at least one egg is more than twice as high when a clutch is dispersed into multiple nests than if all the eggs were deposited in a single nest. For these reasons, it is not surprising that brood parasitism is common in hole-nesting, precocial anatids (Yom-Tov 1980, Andersson 1984, Gauthier 1986).

Interestingly, at low levels, intraspecific brood parasitism may also benefit the host. For example, the "parasites" might be closely related individuals (daughters or sisters; Bellrose 1976, p. 187) who could not find a nest site of their own; laying in the nest of a close relative may have positive effects on the inclusive fitness of both (Andersson 1984). Even when host and parasite are unrelated, if a small number of eggs are laid parasitically, this could increase the survival rate of the host female's own eggs due to either a predator dilution or a "selfish herd" effect (Hamilton 1971): the chances of a predator removing one of the incubating female's own offspring is reduced by the presence of foreign eggs (Yom-Tov 1980, Andersson 1984). Because broods hatching from larger clutches (dump nests) do not experience greater rates of predation than small broods (Heusmann 1972), the selfish herd effect may extend through brood development as well.

In light of these considerations, it seems at first surprising that Wood Duck brood parasitism apparently occurs at low frequencies in natural cavities. We located clutch size data for 28 natural

TABLE 3. Hatchability rates for normal nests and dump nests in Wood Ducks at eight study locations.

		Normal nests			Parasitized nests		
Location	Reference	No. eggs hatched	Hatch-ability all nests	Hatch-ability success-ful nests	No. eggs hatched	Hatch-ability all nests	Hatch-ability success-ful nests
Illinois	This study	1,567	67.3	83.0	2,585	57.5	74.0
Louisiana	Davis (1978)	754	—	71.9	2,878	—	66.5
Louisiana	Moore (1981)	1,017	—	75.2	3,816	—	51.1
Massachusetts	Heusmann (1972)	1,341	—	87.8	1,562	—	76.8
Missouri	Clawson et al. (1979)	2,121	47.1	77.9	4,196	39.5	62.9
New Jersey	Zipko (1979)	6,309	33.6	65.1	7,308	26.0	57.6
New York	Haramis and Thompson (1985)[a]	617	46.0	61.9	1,425	39.9	58.6
Oregon	Morse and Wight (1969)	586	68.9	92.4	1,033	52.9	75.7

[a] 1974 excluded from data set. Actual nesting efficiency was not available for this year due to human disturbance.

Wood Duck nests (Semel and Sherman 1986). Of these, 20 (71%) contained less than 16 eggs and only 8 (29%) were clearly parasitized. Similarly, Robb (1986) reported a mean clutch size of 10.3 for 12 nests found in natural cavities, and no instances of clutches larger than 15 eggs.

Under natural conditions, however, the density of suitable Wood Duck nest cavities is highly variable, and depends on the structure of the woodland habitat. A literature review indicates that the density of natural nesting cavities suitable for Wood Ducks ranges from 0.5/ha to 7.7/ha, with a mean of about 3 cavities/ha (see Bellrose et al. 1964, Prince 1968, Strange et al. 1971, Haramis 1975, Gilmer et al. 1978, Robb 1986, Soulliere 1988). Wood Duck nest sites thus are widely spaced. They are also typically well concealed in the upper story of the forest, making them difficult for humans and probably Wood Ducks to locate initially (Prince 1965, Weier 1966).

There are likely costs to female Wood Ducks who search out active nest sites to parasitize; these costs include time and energy, and risk of predation. The vegetational complexity of bottomland forests inhabited by Wood Ducks (Bellrose 1976, 1986), the low density of suitable cavities in such sites, and the active role of nesting females in avoiding parasitism (including surreptitious behavior near the nest: Semel and Sherman 1986), reduce the likelihood of a female locating an active nest. Even if an active nest is found, it seems unlikely that a female will be able to lay her entire clutch parasitically because the owner may successfully defend her nest (Clawson et al. 1979, Semel and Sherman 1986). Collectively, these factors reduce the frequency of parasitism in natural cavities.

NEST BOXES AND BROOD PARASITISM

The rarity of natural cavities and the susceptibility of incubating females to predators are often implicated in limiting Wood Duck populations (e.g., Robinson 1958, Bellrose et al. 1964, Grice and Rogers 1965, McGilvrey 1968, Strange et al. 1971, Haramis 1975). Therefore, researchers and wildlife managers often increase nest-site availability by using artificial nesting structures with predator guards. Typically nest boxes are placed at high densities in obvious locations (Bellrose et al. 1964, USFWS 1976), causing the birds to be semicolonial. In such populations, high initial nest success rates, reduced predation on females and eggs, and strong philopatry of young females (Bellrose 1976, Hepp et al. 1987) often result in rapid population growth. However, because brood parasitism is elicited in Wood Ducks (Heusmann et al. 1980, Semel and Sherman 1986) and in several other species (e.g., Common Goldeneye, *Bucephala clangula:* Andersson and Eriksson 1982; Redheads, *Aythya americana:* Weller 1959) when females observe conspecifics entering or leaving nest sites, nest-box proximity and visibility drastically increase the opportunities for dump nesting. In addition, the surreptitious behavior of nesting females becomes ineffectual at concealing the nest (Semel and Sherman 1986). Concentrations of visible nest boxes, therefore, reduce the difficulty associated with searching for active, dispersed nest sites and allow females to lay parasitically with greater frequency (Bellrose 1986; USFWS 1987a, 1987b, 1987c). A similar idea was recently proposed by Gauthier (1986), who suggested that Bufflehead (*B. albeola*) using clustered nest boxes may be particularly susceptible to brood parasitism because the artificial nesting structures are more conspicuous than natural cavities.

EFFECTS OF BROOD PARASITISM ON WOOD DUCK REPRODUCTION

Our results (Figs. 1A, B) demonstrate a strong positive correlation between parasitism and population density. Coupled with this trend, however, is a decrease in hatchability (Fig. 1C). In other words, as parasitism increased, there was also a large increase in the proportion of eggs laid that failed to hatch. A review of the literature (Table 3) revealed that at eight different study areas (i.e., every site for which appropriate data are available) Wood Duck eggs in normal nests had slightly to significantly higher hatchability than those in parasitized nests (Table 3).

Decreased hatchability with increasing clutch size (Fig. 2) results from several factors, including: nest desertion (McLaughlin and Grice 1952, Jones and Leopold 1967, Strange et al. 1971, Gauthier 1986), inefficient incubation (Grice and Rogers 1965), crushed eggs (Bellrose 1986), disturbance of laying or incubating females by parasitic females (Davis 1978, Bellrose 1986, Semel and Sherman 1986), and the large number of eggs laid nonterm (Moore 1981, Semel and Sherman 1986; Fig. 3). In addition, females often lay eggs in inappropriate places—such as in the water, on top of boxes, or on the ground (Clawson et al. 1979)—after being physically repelled from an attempted parasitism. In extreme circumstances females have even been found to kill each other during attempts to lay in the same box (Bellrose 1986). Nests subject to intense brood parasitism (i.e., three to six eggs daily) early in clutch development are also frequently deserted (Jones and Leopold 1967; Andersson and Eriksson 1982; Haramis and Thompson 1985; Semel, unpubl. data). Lastly, concentrations of boxes attract nest predators, both avian (e.g., Red-bellied Woodpeckers, *Melanerpes carolinus,* Red-headed Woodpeckers, *M. erythrocephalus,* Common Flickers, *Colaptes auratus*) and mammalian (e.g., raccoons, *Procyon lotor,* and bobcats, *Lynx rufus:* see Bellrose 1953, Strange et al. 1971, USFWS 1987c).

High levels of parasitism have additional, more subtle negative influences on individual reproductive success. Weller (1959) and Clawson et al. (1979), and Heusmann et al. (1980) described reduced laying by "owning females" in Redheads and Wood Ducks, respectively, when nests were parasitized. Although the mechanism was not identified, the appearance of a full clutch in some way inhibited further laying. Andersson and Eriksson (1982), studying Common Goldeneye, also found that females reduced laying in response to eggs added parasitically. Because hatchability was known to decrease with increasing clutch size in Common Goldeneye, Andersson and Eriksson (1982) suggested that females reduced their own reproductive output to compensate for the additional parasitic eggs in the clutch.

With increasing clutch size, there is a corresponding reduction in the proportion of eggs that are not offspring of an incubating female. At some point it becomes advantageous for the owning female to simply desert the nest (Andersson 1984). Depending on nutrient reserves and the time in the nesting season, it may be beneficial to abandon a heavily parasitized nest and start a new one (Drobney 1982). The close relationship between the number of early nest desertions and high frequency of dump nesting often observed in Wood Ducks (Clawson et al. 1979, Heusmann et al. 1980), coupled with renesting by solitary females later in the season, seems consistent with this hypothesis.

ATTEMPTS TO REDUCE BROOD PARASITISM

Some of the problems associated with intense parasitism that we have highlighted may be alleviated by adding boxes to the periphery of areas in which dump nesting is prevalent because this may allow females to visit such boxes unobserved. As the population continues to grow, however, so will the incidence of dump nesting (e.g., Haramis and Thompson 1985, Gauthier 1986). Moreover, although nest-site limitation following population growth has often been cited as the factor increasing parasitism (Bellrose et al. 1964, Haramis 1975, Zipko 1979), many other studies question this. For example, Morse and Wight (1969) found no relationship between nest-box availability and the frequency of dump nesting when the dynamic events of nesting and renesting were distributed into week-long intervals. The greatest rate of parasitism observed during their study (65%) occurred when only 58% of the nesting structures were in use. Likewise, Semel and

Sherman (1986) reported that 95% of nests were parasitized at Duck Creek, Missouri when there was only 54% box use. At MMWF, during the highest year of total box occupancy (1979: 85%), only 32 of 66 boxes (49%) were in use at any one time and at least 52% of these nests were parasitized. McLaughlin and Grice (1952), Hartman (1972), Clawson (1975), McCamant and Bolen (1979), Heusmann et al. (1980), Andersson and Eriksson (1982), and Andersson (1984) all have rejected nest-site limitation as the cause of intensive brood parasitism.

Experimental manipulation of nest-box proximity and visibility at MMWF did result in a significant reduction in parasitism as indicated by lower mean clutch sizes (Table 2). Fewer clutches in WH boxes were parasitized than in VI or VC boxes. It should be noted that the simultaneous availability of both well-hidden and visible boxes at MMWF may have accounted for some of the reduction in parasitism in WH boxes because VI and VC boxes were much easier than WH boxes for females to find. However, the 30% rate of parasitism for WH boxes is nearly identical to the parasitism rate reported in the literature for natural cavities (29%; Semel and Sherman 1986). Furthermore, our observations of increased clutch size with increased nest-box visibility are similar to those of McLaughlin and Grice (1952) who presented data for artificial structures placed in three habitat types: open water, wetlands, and woodlands. Average clutch sizes in boxes erected over water and in wetlands (i.e., highly visible locations) were 13.1 eggs and 14.2 eggs, respectively, while the mean clutch size in wooded sites (less visible) was 10.6 eggs. Lee (1954) also placed nest boxes in both conspicuous, open-water sites, and in visually occluded, upland forests. He found upland boxes to have lower clutch sizes, higher nesting success, and higher hatchability.

Payne (1977), in reviewing the ecology of brood parasitism, concluded that bird species nesting in open woodlands are more often parasitized than are species nesting in dense forests. This generality also appears to hold for brood parasitism in Wood Ducks nesting in hidden vs. obvious boxes. Perhaps the reason for the apparent generality of Payne's (1977) conclusion is that in all these cases the mechanism underlying brood parasitism is similar (i.e., watching females enter or leave active nest sites).

CONCLUSION

Data we present suggest that to retain the advantages of using nest boxes to study and manage Wood Ducks, but to minimize the behavioral pathologies associated with dump nesting and high population densities, artificial nesting structures should be placed in visually occluded sites and at densities approximating those in which the species evolved. This simple suggestion is also germane to other cavity-nesting species. For example, high frequencies of brood parasitism and associated density strife have been recorded in at least one other cavity-nesting anatid, the Black-bellied Whistling Duck (*Dendrocygna autumnalis*), when clusters of easily located nest boxes were provided (Delnicki et al. 1976, McCamant and Bolen 1979).

It is also possible that box visibility may increase the frequency of parasitism among hole-nesting passerines. Perhaps the surprisingly high frequency of "multiple-maternity" reported for Eastern Bluebirds (*Sialia sialis*) by Gowaty and Karlin (1984) was due, in part, to the investigators' placement of boxes in highly visible sites and in proximity to other boxes. Similar nest-box programs have resulted in communal nesting in Tree Swallows (*Iridoprocne bicolor*; Sheppard 1977, Muldal et al. 1985) and European Starlings (*Sturnus vulgaris,* Stouffer et al. 1988). Quinney (1983), who also reported multiple-female clutches in Tree Swallows, predicted that communal nesting would increase whereas hatchability and nest success would decrease when boxes were placed at high densities and in obvious locations. These considerations and the results of our study suggest that judicious placement of artificial nesting structures would be prudent in studying the breeding biology of any cavity-nesting avian species.

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LITERATURE CITED

ANDERSSON, M. 1984. Brood parasitism within species, p. 195–227. *In* C. J. Barnard [ed.], Producers and scroungers: strategies of exploitation and parasitism. Croom Helm, London.

ANDERSSON, M., AND M. G. ERIKSSON. 1982. Nest parasitism in Goldeneyes *Bucephala clangula*: some evolutionary aspects. Am. Nat. 120:1–16.

BELLROSE, F. C. 1953. Housing for Wood Ducks. Ill. Nat. Hist. Surv. Circ. 45.

BELLROSE, F. C. 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, PA.

BELLROSE, F. C. 1986. The breeding ecology of Wood Ducks at Nauvoo Flats, Illinois. Ill. Nat. Hist. Surv. Report to IDOC and Private Contributors.

BELLROSE, F. C., AND R. CROMPTON. 1972. Nest houses for Wood Ducks. Ill. Nat. Hist. Surv., Springfield.

BELLROSE, F. C., K. L. JOHNSON, AND T. U. MEYERS. 1964. Relative value of natural cavities and nesting houses for Wood Ducks. J. Wildl. Manage. 28: 661–676.

BELLROSE, F. C., AND F. B. MCGILVREY. 1966. Characteristics and values of artificial nesting cavities, p. 125–131. *In* J. B. Trefethen [ed.], Wood Duck management and research: a symposium. Wildl. Manage. Inst. Washington, DC.

BROWN, C. R., AND M. B. BROWN. 1988. A new form of reproductive parasitism in Cliff Swallows. Nature 331:66–68.

CLAWSON, R. L. 1975. The ecology of dump nesting in Wood Ducks. M.Sc.thesis. Univ. of Missouri, Columbia.

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.

DAVID, P. 1986. Survival and movements of Wood Duck broods in northern Illinois. M.Sc.thesis. Univ. of Wisconsin, Madison.

DAVIS, D. J. 1978. The utilization of artificial nest cavities by Wood Ducks. M.Sc.thesis. Louisiana State Univ., Baton Rouge.

DELNICKI, D. E., E. G. BOLEN, AND C. COTTAM. 1976. An unusual clutch size of the Black-bellied Whistling Duck. Wilson Bull. 88:347–348.

DILLON, S. T. 1970. Response of Wood Ducks to nest boxes at the Max McGraw Wildlife Foundation. Proc. 32nd Midwest Fish and Wildl. Conf. Winnipeg, Manitoba. Abstract.

DOTY, H. A., AND A. D. KRUSE. 1972. Techniques for establishing local breeding populations of Wood Ducks. J. Wildl. Manage. 36:428–435.

DOTY, H. A., F. B. LEE, A. D. KRUSE, J. W. MATTHEWS, J. R. FOSTER, AND P. M. ARNOLD. 1984. Wood Duck and Hooded Merganser nesting on Arrowwood NWR, North Dakota. J. Wildl. Manage. 48:577–580.

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

DROBNEY, R. D. 1982. Body weight and composition changes and adaptations for breeding in Wood Ducks. Condor 84:300–305.

DROBNEY, R. D., AND L. H. FREDRICKSON. 1985. Protein acquisition: a possible proximate factor limiting clutch size in Wood Ducks. Wildfowl 36:122–128.

GAUTHIER, G. 1986. The use of nest boxes by Buffleheads and other cavity nesting birds. Siala 8: 123–128.

GILMER, D. S., I. J. BALL, L. M. COWARDIN, J. E. MATHISEN, AND J. H. RIECHMANN. 1978. Natural cavities used by Wood Ducks in north-central Minnesota. J. Wildl. Manage. 42:288–298.

GOWATY, P. A., AND A. A. KARLIN. 1984. Multiple maternity and paternity in single broods of apparently monogamous Eastern Bluebirds (*Sialia Sialis*). Behav. Ecol. Sociobiol. 15:91–95.

GRICE, D., AND J. P. ROGERS. 1965. The Wood Duck in Massachusetts. Mass. Div. Fish. and Game, Fed. Aid Wildl. Restor. Rep. W-19-R.

HAMILTON, W. D. 1971. Geometry for the selfish herd. J. Theoret. Biol. 31:295–311.

HANSEN, J. L. 1971. The role of nest boxes in management of the Wood Duck on Mingo National Wildlife Refuge. M.A.thesis. Univ. of Missouri, Columbia.

HARAMIS, G. M. 1975. Wood Duck (*Aix sponsa*) ecology and management within the green-timber impoundments at Montezuma National Wildlife Refuge. M.Sc.thesis. Cornell Univ., Ithaca, NY.

HARAMIS, G. M., AND D. Q. THOMPSON. 1985. Density-production characteristics of box-nesting Wood Ducks in a northern greentree impoundment. J. Wildl. Manage. 49:429–436.

HARTMAN, G. W. 1972. The biology of dump nesting in Wood Ducks. M.A.thesis. Univ. of Missouri, Columbia.

HEPP, G. R., R. T. HOPPE, AND R. A. KENNAMER. 1987. Population parameters and philopatry of breeding female Wood Ducks. J. Wildl. Manage. 51:401–404.

HEUSMANN, H. W. 1972. Survival of Wood Duck broods from dump nests. J. Wildl. Manage. 36: 620–624.

HEUSMANN, H. W., R. H. BELLVILLE, AND R. G. BURRELL. 1980. Further observations on dump nesting by Wood Ducks. J. Wildl. Manage. 44: 908–915.

JONES, R. E., AND A. S. LEOPOLD. 1967. Nesting interference in a dense population of Wood Ducks. J. Wildl. Manage. 31:221–228.

KERAN, D. C. 1978. Site selection for Wood Duck nest boxes. Loon 50:191–194.

LACKI, M. J., S. P. GEORGE, AND P. J. VISCOSI. 1987. Evaluation of site variables affecting nest box use by Wood Ducks. Wildl. Soc. Bull. 15:196–200.

LEE, J. A. 1954. Wood Duck research investigations. New Hampshire Fish and Game Dept. Fed. Aid Proj. W7-R.

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

MCCABE, R. A. 1947. The homing of transplanted young Wood Ducks. Wilson Bull. 59:104–109.

MCCAMANT, R. E., AND E. G. BOLEN. 1979. A 12-

year study of nest box utilization by Black-bellied Whistling Ducks. J. Wildl. Manage. 43:936–943.

McGilvrey, F. B. 1968. A guide to Wood Duck production habitat requirements. Bur. of Sport Fish. and Wildl., Resour. Publ. 60.

McLaughlin, C. L., and D. Grice. 1952. The effectiveness of large-scale erection of Wood Duck boxes as a management procedure. Trans. N. Am. Wildl. Conf. 17:242–259.

Moore, W. P. 1981. Utilization of colonial structures and other artificial nest cavities by Wood Ducks. M.Sc.thesis. Louisiana State Univ., Baton Rouge.

Morse, T. E., and H. M. Wight. 1969. Dump nesting and its effect on production in Wood Ducks. J. Wildl. Manage. 33:284–293.

Muldal, A., H. L. Gibbs, and R. J. Robertson. 1985. Preferred nest spacing of an obligate cavity-nesting bird, the Tree Swallow. Condor 87:356–363.

Norusis, M. J. 1986. SPSS/PC+: SPSS for the IBM/PC/XT/AT. SPSS, Chicago, IL.

Payne, R. B. 1977. The ecology of brood parasitism in birds. Annu. Rev. Ecol. Syst. 8:1–28.

Prince, H. H. 1965. The breeding ecology of Wood Duck (*Aix sponsa* L.) and Common Goldeneye (*Bucephala clangula* L.) in central New Brunswick. M.Sc.thesis. Univ. of New Brunswick, Fredericton.

Prince, H. H. 1968. Nest sites used by Wood Ducks and Common Goldeneyes in New Brunswick. J. Wildl. Manage. 32:489–500.

Quinney, T. E. 1983. Tree Swallows cross a polygyny threshold. Auk 100:750–754.

Robb, J. R. 1986. The importance of nesting cavities and brood habitat to Wood Duck production. M.Sc.thesis. Ohio State Univ., Columbus.

Robinson, R. H. 1958. Use of nest boxes by Wood Ducks in the San Joaquin Valley, California. Condor 60:256–257.

Semel, B., and P. W. Sherman. 1986. Dynamics of nest parasitism in Wood Ducks. Auk 103:813–816.

Semel, B., P. W. Sherman, and S. M. Byers. In press. Nest boxes and brood parasitism in Wood Ducks: a management dilemma. *In* L. H. Fredrickson and G. V. Burger [eds.], North American Wood Duck Symposium. St. Louis, MO.

Sheppard, C. D. 1977. Breeding in the Tree Swallow, *Iridoprocne bicolor,* and its implications for the evolution of coloniality. Ph.D.diss. Cornell Univ., Ithaca, NY.

Soulliere, G. J. 1988. Density of suitable Wood Duck nest cavities in a northern hardwood forest. J. Wildl. Manage. 52:86–89.

Sousa, P. J., and A. H. Farmer. 1983. Habitat suitability index models: Wood Duck. U.S. Dept. Inter., Fish and Wildl. Serv. FWS/OBS-82/10.43.

Stouffer, P. C., L. C. Romagnano, M. P. Lombardo, A. S. Hoffenberg, and H. W. Power. 1988. A case of communal nesting in the European Starling. Condor 90:241–245.

Strange, T. H., E. R. Cunningham, and J. W. Goertz. 1971. Use of nest boxes by Wood Ducks in Mississippi. J. Wildl. Manage. 35:786–793.

Texas Instruments. 1977. Applied statistics. Texas Instruments, Dallas, TX.

United States Fish and Wildlife Service. 1976. Nest boxes for Wood Ducks. U.S. Dept. of Inter. Washington, DC. WL #510.

United States Fish and Wildlife Service. 1987a. Annual Report, Union Slough NWR Titonka, IA. IA.

United States Fish and Wildlife Service. 1987b. Annual Report, Yazoo NWR. Hollandale, MS.

United States Fish and Wildlife Service. 1987c. Great Swamp NWR Wood Duck program progress report. Basking Ridge, NJ.

Webster, C. G., and F. M. Uhler. 1964. Improved nest structures for Wood Ducks. U.S. Bur. Sport Fish. Wildl., Wildl. Leafl. 458.

Weier, R. W. 1966. A survey of Wood Duck nest sites on Mingo National Wildlife Refuge in southeast Missouri, p. 91–112. *In* J. B. Trefethen [ed.], Wood Duck management and research: a symposium. Wildlife Management Institute, Washington, DC.

Weller, M. W. 1959. Parasitic egg laying in the Redhead (*Aythya americana*) and other North American Anatidae. Ecol. Monogr. 29:333–365.

Yoakum, J., W. P. Dasmann, H. R. Sanderson, C. M. Nixon, and H. S. Crawford. 1980. Habitat improvement techniques, p. 329–403. *In* S. D. Schemnitz [ed.], Wildlife management techniques manual. The Wildlife Society, Washington, DC.

Yom-Tov, Y. 1980. Intraspecific nest parasitism in birds. Biol. Rev. 55:93–108.

Zipko, S. J. 1979. Effects of dump nests and habitat on reproductive ecology of Wood Ducks, *Aix sponsa* (Linnaeus). Ph.D.diss. Rutgers Univ., Newark, NJ.