The Auk 109(4):812-818, 1992

CHARACTERISTICS AND CONSEQUENCES OF NEST-SITE FIDELITY IN WOOD DUCKS

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ABSTRACT.—We used nine years of nesting data from a population of Wood Ducks (*Aix sponsa*) using nest boxes to test predictions regarding proximate controls of nest-site fidelity and the consequences of returning to the same nest site. Overall, 41.9% of females returned to the same nest box in year $t + 1$, 37.5% nested in a different box on the same wetland, and 20.5% of females moved to a different wetland to nest. There were no yearly differences in the degree of nest-site fidelity, and females using different wetlands between years travelled a median of two wetlands and moved an average distance of 1.3 km. Females nesting successfully used the same nest box to a greater extent in year $t + 1$ than females that were not successful. The positive association between nest success and nest-site fidelity also occurred within breeding seasons. Degree of nest-site fidelity exhibited by females was similar within and between breeding seasons. After controlling for variation in nest success, nest-site fidelity of yearlings did not differ from that of adults. Proportion of females returning to the same box in year $t + 1$ was not correlated with estimated population size of breeding females in that year. Females returning to the same box nested earlier than females using different boxes, but clutch size did not differ. Overall, females nesting in the same box did not have greater nest success in year $t + 1$, were not more likely to have nests parasitized, and did not survive better to year $t + 2$ than females nesting in different boxes. However, females that nested unsuccessfully tended to improve nest success by moving to a different nest box. *Received 1 August 1991, accepted 18 February 1992.*

MANY SPECIES of migratory birds show a high degree of fidelity to previous breeding sites both within and between seasons (Greenwood and Harvey 1982). Males of most species have greater breeding-site fidelity than do females (Greenwood 1980). In waterfowl, however, female-biased natal philopatry and nest-site fidelity is the rule (Rohwer and Anderson 1988). Pair bonds are formed on winter areas or during spring migration, and the pair returns to the female's natal area or previous nesting location (Dow and Fredga 1983, Hepp et al. 1989, Gauthier 1990).

Widespread occurrence of breeding-site fidelity in birds suggests that the behavior is beneficial. Familiarity with an area may increase foraging efficiency, predator avoidance, dominance status, and the likelihood of pairing with a familiar partner, all of which may enhance reproductive success (Greenwood and Harvey 1982). Common Goldeneyes (*Bucephala clangula*), for example, that changed nest boxes nested later, produced smaller clutches, and had lower nesting success than females that did not change nest sites (Dow and Fredga 1983). Female Willow Ptarmigans (*Lagopus lagopus*) pairing with previous mates nested earlier and produced heavier chicks than females that switched partners (Schieck and Hannon 1989).

The decision to return to a previous breeding site may involve several factors. Competition for nest sites may influence whether individuals return and may be especially important in cavity-nesting species (Dow and Fredga 1983). Previous experience is another factor influencing nest-site fidelity in birds. Individuals nesting successfully are more likely to return to the same nest site than individuals that are not successful (Gavin and Bollinger 1988, Gauthier 1990, Beletsky and Orians 1991; but see Haig and Oring 1988). Site quality may interact with nest success to influence subsequent nesting decisions (Weatherhead and Boak 1986, Bollinger and Gavin 1989). Nest-site fidelity also may be influenced by age, with yearlings having a greater probability of changing nest sites than adults (Newton and Marquiss 1982). Causes for age-specific differences in fidelity are unclear (Greenwood and Harvey 1982). It is possible that young individuals use poor-quality sites during initial nest attempts and move to better-quality sites when these sites become available.

Nesting data from a population of Wood Ducks (*Aix sponsa*) using nest boxes were collected during nine breeding seasons. This information was used to test the following predictions regarding the proximate control of nest-site fidelity and the consequences of returning to the same nest site. First, if nest sites can be used to help predict nest success, then females of failed nests should use different nest sites more frequently than females of successful nests. This relationship should occur within breeding seasons as well as between seasons. Second, we predicted that nest-site fidelity would be age-specific. Because yearling Wood Ducks generally nest later than adults (Haramis 1990), they may have to use low-quality sites for first nests and, therefore, be more likely to change nest sites regardless of nest success. Third, fidelity to nest sites should decline as size of the breeding population increases and competition for nest sites intensifies (D. Grice and J. P. Rogers unpubl. report). This may result from females being excluded from previous nest sites, or moving to new sites to avoid being parasitized by other females (Dow and Fredga 1983). Finally, if our first prediction is confirmed, then we would expect females of unsuccessful nests that change nest sites to improve their nest success.

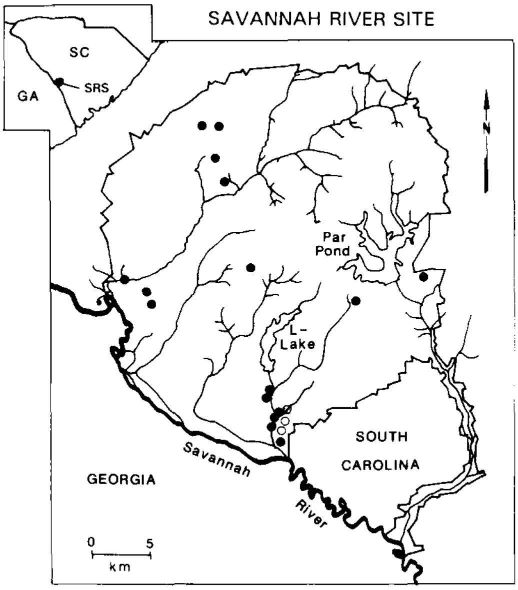

Fig. 1. Distribution of nest box locations on Savannah River Site. Locations (n = 16) designated by closed circles were available 1982–1990; additional locations (n = 3) designated by open circles were available 1984–1990.

Methods

The study was conducted from 1982 to 1990 on the Department of Energy's Savannah River Site in west-central South Carolina (33.1°N, 81.3°W; Fig. 1). In 1982–83, 120 nest boxes were available at 16 sites; nest boxes were added to two existing sites and three new sites before the 1984 breeding season (Fig. 1). There were approximately 150 nest boxes available to Wood Ducks from 1984 to 1990. All nest boxes were made of wood and were of similar size.

Nesting data.—Each year we checked nest boxes weekly during the breeding season (January–July) to obtain information on nesting activity. Checking nest boxes this frequently allowed us to find nests before they were completed (i.e. during egg laying). We estimated date of nest initiation by subtracting the number of eggs in the nest when it was first found from the Julian date that the nest box was checked. A laying rate of one egg per day was assumed (Bellrose 1980). Female Wood Ducks frequently engage in intraspecific nest parasitism, where more than one female deposits eggs in a nest (Clawson et al. 1979, Semel and Sherman 1986). Identification of parasitic (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 greater than 16 eggs (Morse and Wight 1969). Nest-initiation dates were estimated similarly for parasitic and nonparasitic nests. Dump nests occasionally contained more eggs than the elapsed time (days) between nest-box checks. These nests were estimated to have been initiated one day after the previous check of the nest box. Successful nests were considered those in which at least one duckling hatched and exited the box; unsuccessful nests hatched no eggs.

Capture of nesting females.—Females were captured during incubation. Unmarked females were banded with U.S. Fish and Wildlife Service leg bands, and band numbers of previously banded females were recorded. Females were aged as yearlings or adults using three methods: (1) individuals captured and banded in previous years as nesting females were classified as adult; (2) females web-tagged (Haramis and Nice 1980) as day-old ducklings in the previous breeding season were classified as yearlings; and (3) from 1987 to 1990, unmarked females were assigned to age classes using methods of Harvey et al. (1989a). After recording data, females were released back into the nest box.

Population size (N_t) and capture probability (p_t) were estimated for female Wood Ducks using the Jolly-Seber (J-S) capture–recapture model for open populations (Jolly 1965, Seber 1965), where N_t is defined

TABLE 1. Annual frequencies of female Wood Ducks that nested in the same box, in a different box on the same wetland, and in a different box and wetland.

Degree of nest-site fidelity	Year $t + 1$								Total
	1983	1984	1985	1986	1987	1988	1989	1990	
Same nest box	8	7	9	6	15	17	19	25	106
Different nest box, same wetland	5	7	10	13	21	14	13	12	95
Different nest box and wetland	6	7	3	5	6	13	8	4	52
Total	19	21	22	24	42	44	40	41	253

as the population size of females using nest boxes at the midpoint of the banding period in year t, and p_t is the probability that a female alive and in the population in year t will be captured. From 1982 to 1989, $\hat{p}_t$ averaged 0.88, which indicates that most surviving females returned to nest boxes and were captured (see Hepp et al. 1987, 1989). We also used the J-S model to estimate annual survival of females on the Savannah River Site (Hepp et al. 1987). Capture-recapture estimates reflect the proportion of individuals surviving from one year to the next and returning to the general area sampled. We compared J-S survival estimates with those computed with band-recovery models (Brownie et al. 1978) for Wood Ducks in the southeastern United States and found no difference (Hepp et al. 1987). Because estimates of survival using band recovery models reflect only survival, this is further evidence that most surviving hens returned to the same breeding area and were captured.

Data analysis.—Nest fidelity of females between years was measured from the location of the final nest attempt in year t to the first nest in year $t + 1$. Distance (km) moved by females using different wetlands was measured with the aid of aerial photographs as the straight-line distance from the center of one wetland to the center of the other. Nest initiation dates were expressed as number of days elapsed since initiation of the first nest each year to reduce annual differences in time of nesting. We refer to adjusted nest dates as the relative date of nest initiation.

Likelihood-ratio tests with Williams correction (G_{adj}) were used for contingency table analyses (Sokal and Rohlf 1981). Cochran-Mantel-Haenszel statistics allowed the control of one variable (e.g. nest success) while testing for associations between other variables (SAS Institute 1988). A two-way analysis of variance (ANOVA) was used to test whether the degree of nest-site fidelity influenced date of nest initiation and clutch size. The Statistical Analysis System (SAS; SAS Institute 1988) was used for all data summaries and tests.

RESULTS

Nest-site fidelity.—During nine breeding seasons, 41.9% ($n = 106$) of returning female Wood Ducks nested in the same box in year $t + 1$ that they last used in year t, 37.5% ($n = 95$) nested in a different box on the same wetland, and 20.5% ($n = 52$) of females moved to a different wetland to nest (Table 1). There were no year-specific differences ($G_{adj} = 19.70$, df = 14, $P > 0.12$) in the degree of nest-site fidelity. Females that nested in boxes on different wetlands moved a median of two wetlands from their previous nest site. Distance between nest sites averaged 1.31 ± SE of 0.10 km ($n = 52$, range 0.33–2.56 km).

Factors influencing nest-site fidelity.—Nest success in year t influenced whether females returned to the same nest box in year $t + 1$ or changed locations ($G_{adj} = 19.78$, df = 2, $P < 0.001$; Table 2). Females that nested successfully used the same nest box to a greater extent (47.2%, $n = 216$) in the next breeding season than females that were unsuccessful (10.8%, $n = 37$). A positive association between nest success and nest-site fidelity also occurred within breeding seasons ($G_{adj} = 16.7$, df = 2, $P < 0.001$; Table 3). Females that had successful first nests used the same box more frequently (39.0%, $n = 40$) for second nests than females whose first nests were unsuccessful (5.4%, $n = 37$). After controlling for variation in nest success, degree of nest-site fidelity was the same (Cochran-Mantel-Haenszel [CMH] statistic = 1.5, df = 2, $P = 0.46$) within and between breeding seasons. Comparison of distances travelled by females that moved to different wetland areas also revealed no differences ($t = -0.20$, df = 72, $P = 0.84$) within ($\bar{x} = 1.35 \pm 0.16$ km, $n = 22$) and between (1.31 km) breeding seasons.

In an analysis controlling for nest success, there was no association between age class (yearling or adult) in year t and nest-site fidelity in year $t + 1$ (CMH statistic = 0.22, df = 2, $P = 0.89$; Fig. 2). There also was no relationship be-

TABLE 2. Association between nest success of female Wood Ducks in year t and nest-site fidelity in year $t + 1$. Percentages indicated for columns.

Degree of nest-site fidelity	Nest success	
	Successful (%)	Failed (%)
Same nest box	102 (47)	4 (11)
Different nest box, same wetland	72 (33)	23 (62)
Different nest box and wetland	42 (19)	10 (27)

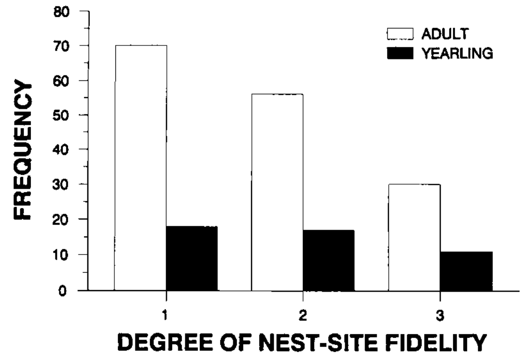

Fig. 2. Age class of female Wood Ducks in year t and its relationship to the degree of nest-site fidelity in year $t + 1$. Degree of nest-site fidelity: (1) same nest box; (2) different nest box, but same wetland; and (3) different nest box and wetland.

tween estimates of female population size in year $t + 1$ and the percentage of females that nested in the same box in year $t + 1$ (Spearman rank correlation: $r_s = -0.14$, $n = 7$, $P = 0.76$).

Consequences of nest-site fidelity.—There was a strong relationship ($F = 13.99$, df = 2, 229; $P < 0.0001$) between the degree of nest-site fidelity and the relative initiation date of nests in year $t + 1$ (Table 4). Females nesting in the same box began laying eggs approximately 13 days earlier than females that nested on the same wetland but changed boxes, and 19 days earlier than females that nested on different wetlands. Females nesting in different boxes on the same wetland initiated nests six days earlier than females that moved to different wetlands, but differences, while suggestive, were not statistically significant ($P = 0.10$; Table 4). For females that nested on different wetlands in year $t + 1$, distance moved to new nest sites was not correlated ($r_s = 0.01$, $n = 52$, $P = 0.96$) with relative dates of nest initiation in year $t + 1$. Clutch size of nonparasitized nests did not differ ($P > 0.10$) with the degree of nest-site fidelity (Table 4).

Females returning to the same nest box in year $t + 1$ did not nest more successfully than females that did not use the same box ($G_{adj} = 3.02$, df = 2, $P > 0.10$; Fig. 3A). Proportion of females having their nests parasitized in year $t + 1$ also was not associated with degree of nest-site fidelity ($G_{adj} = 0.49$, df = 2, $P > 0.25$; Fig. 3B). Finally, there was no association between fidelity to nest sites in year $t + 1$ and survival of females from year $t + 1$ to $t + 2$ ($G_{adj} = 3.36$, df = 2, $P > 0.10$; Fig. 3C).

Females that nested unsuccessfully in year t and used different nest boxes in year $t + 1$ tended to nest more successfully (70%) than unsuccessful females that returned to the same nest site (25%); differences were not significant ($G_{adj} = 2.98$, df = 2, $P > 0.25$), but sample sizes were small (Table 5). Within breeding seasons, most (95%) females that had unsuccessful first nests moved to different boxes for renesting (Table 3). Success of second nests was the same ($G_{adj} = 0.24$, df = 1, $P > 0.50$) for females that nested successfully (34 of 40, 85.0%) or unsuccessfully (30 of 37, 81.1%) the first time.

TABLE 3. Association between the success of first nests of female Wood Ducks and the degree of nest-site fidelity of second nests within the same breeding season. Percentages indicated for columns.

Degree of nest-site fidelity for second nests	Success of first nests	
	Successful (%)	Failed (%)
Same nest box	16 (40)	2 (5)
Different nest box, same wetland	18 (45)	19 (51)
Different nest box and wetland	6 (15)	16 (43)

DISCUSSION

Nest-site fidelity.—Return of female Wood Ducks to previous breeding sites on the Savannah River Site was high; approximately 79% of females returned to the same wetland area and 42% used the same nest box in successive years. These results are similar to studies of Wood Ducks in Massachusetts, where on one site 83% (135 of 163) of surviving females nested in the immediate vicinity of their original nest sites (D. Grice and J. P. Rogers, unpubl. report). Other cavity-nesting species of waterfowl have similar degrees of nest-site fidelity as Wood Ducks.

TABLE 4. Least squares means ± SE of relative date of nest initiation and clutch size of first nests of female Wood Ducks by degree of nest-site fidelity. Sample sizes in parentheses.

Degree of nest-site fidelity	Relative date of nest initiation[a]	Clutch size[b]
Same nest box	23.3 ± 2.3 (106) A[c]	12.3 ± 0.4 (33) A
Different nest box, same wetland	35.9 ± 2.3 (95) B	11.2 ± 0.4 (31) A
Different nest box and wetland	42.4 ± 3.2 (52) B	12.0 ± 0.5 (20) A

[a] Initiation date of nests expressed as number of days elapsed since initiation of first nest each year.
[b] Nonparasitized nests.
[c] Means in columns followed by different uppercase letters are significantly different ($P < 0.05$).

In Sweden, 42% of female Common Goldeneyes returned to the same nest box, and those that changed boxes moved a median distance of 0.75 km (Dow and Fredga 1983). Buffleheads (*Bucephala albeola*) showed greater fidelity to nest sites (68%) than either Common Goldeneyes or Wood Ducks (Gauthier 1990). Breeding-site fidelity of ground-nesting ducks is similar to that of cavity-nesting species (Sowls 1955). Doty and Lee (1974) reported that approximately 73% of female Mallards (*Anas platyrhynchos*) using nest baskets returned to the same North Dakota marsh in successive years.

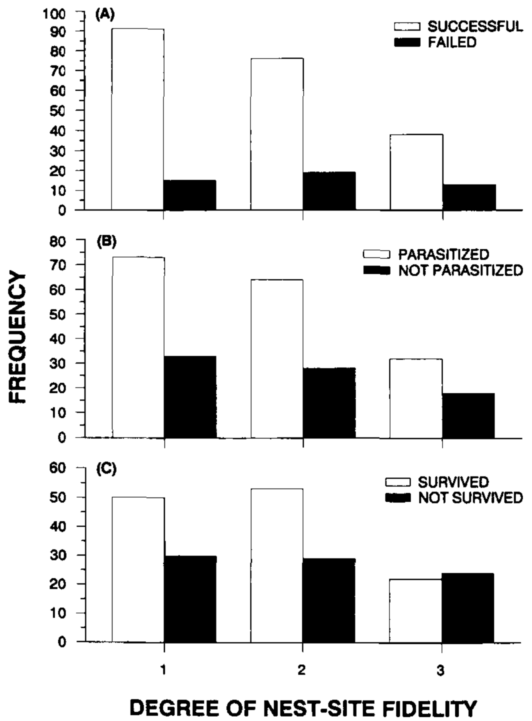

Fig. 3. Degree of nest-site fidelity of female Wood Ducks in year $t + 1$ and its relationship to: (A) nest success in year $t + 1$; (B) intraspecific nest parasitism in year $t + 1$; and (C) survival of females to year $t + 2$. Degree of nest-site fidelity: (1) same nest box; (2) different next box, but same wetland; and (3) different nest box and wetland.

Factors influencing nest-site fidelity.—Breeding experience is one factor that affects probability of individuals returning to previous nesting locations. In many bird species, individuals nesting successfully are more likely to return to previous nest sites than birds of failed nests (Dow and Fredga 1983, Shields 1984, Gavin and Bollinger 1988, Gauthier 1990, Beletsky and Orians 1991). Females nesting successfully on the Savannah River Site were four times more likely to return to the same nest box in successive years as females of failed nests. An even stronger relationship between nest success and fidelity to nest sites existed within breeding seasons. These results are consistent with other studies and support our initial prediction.

Yearling Wood Ducks nested less successfully than adults and tended to exhibit less nest-site fidelity. After controlling for variation in nesting success, however, we found no age-specific

TABLE 5. Association between nest success and nest-site fidelity in year $t + 1$ of female Wood Ducks that nested unsuccessfully in year t. Percentages indicated for rows.

Degree of nest-site fidelity	Nest success	
	Successful (%)	Failed (%)
Same nest box	1 (25)	3 (75)
Different nest box, same wetland	14 (70)	6 (30)
Different nest box and wetland	7 (70)	3 (30)

differences in nest-site fidelity. Breeding experience, and not age, was the more important factor influencing nest-site fidelity in female Wood Ducks. Young females that nested successfully were just as likely to return to the same nest box (43%) as were adults (48%). Results do not confirm our second prediction that female age influenced nest-site fidelity.

Quality of breeding sites can interact with nest success to influence fidelity. In a study of breeding-site fidelity at high- and low-quality breeding areas, Bollinger and Gavin (1989) showed that nest success of Bobolinks (*Dolichonyx oryzivorus*) only influenced breeding-site fidelity at low-quality sites. At high-quality sites, nesters that were successful or failed had the same probability of returning. Bollinger and Gavin (1989) suggested that in addition to nest success Bobolinks used an assessment of site quality in deciding whether or not to return. Although we do not have information regarding breeding-site quality for Wood Ducks, it is apparent that many females did not return to the same box or wetland after nesting successfully. Other factors obviously are important in determining nest-site fidelity. Quality of breeding sites may be one of them. Wetland conditions often change in response to, among other things, variation in amount of precipitation. Drought reduces availability of seasonal wetlands that provide important foraging areas for breeding ducks (Krapu et al. 1983). Harvey et al. (1989b) showed that low rainfall affected availability of wetland habitats on the Savannah River Site, which in turn may have influenced loss of body mass by incubating female Wood Ducks. Besides an assessment of past breeding-site quality (cf. Bollinger and Gavin 1989), it seems likely that current quality of wetland habitats may also influence fidelity to nest sites, independent of previous nest success.

D. Grice and J. P. Rogers (unpubl. report) speculated that competition for nest boxes was the most important factor causing Wood Ducks not to return to the same box in successive years. If competition is important, then we expected an inverse relationship between the estimated population size of breeding females using nest boxes on the Savannah River Site and the percentage of females returning to the same box. We found no evidence that the proportion of females returning to previous nest sites was related to population size of females. The probability of nests being parasitized by other females also was not influenced by nest-site fidelity of females. If hens moved to new sites in part to avoid nest parasitism (see Dow and Fredga 1983:693), this behavior was ineffective.

Consequences of nest-site fidelity.—Return of birds to the same breeding site may increase reproductive success because of advantages associated with site familiarity (Greenwood and Harvey 1982). Gauthier (1990) reported that female Buffleheads using the same cavity nested earlier and had larger clutches than females that changed nest sites. Female Common Goldeneyes returning to the same nest site in successive years initiated nests earlier, produced larger clutches and had greater hatching success compared to females that changed nest sites (Dow and Fredga 1983). In their analysis of clutch-size differences, however, Dow and Fredga (1983) did not exclude nests in which more than one female had laid eggs. This is important to interpretation of their results, because parasitized nests occurred more frequently early in the nesting period (Dow and Fredga 1983:687). Females that returned to the same box, nesting early, would be more likely to be parasitized. Differences in clutch size that were attributed to variation in nest-site fidelity may simply have been a consequence of increased frequency of intraspecific nest parasitism.

In our study, females returning to the same box nested earlier than females that changed boxes. Nesting early may improve reproductive success by giving females a greater chance of renesting or producing two broods. Production of two broods in a single season by females on the Savannah River Site occurred most frequently in years when nesting began relatively early (Kennamer and Hepp 1987). Overall, there was no association between degree of nest-site fidelity and either clutch size or nest success, but female Wood Ducks nesting unsuccessfully appeared to improve nest success by changing nest sites.

Acknowledgments

We thank Bill Harvey, Rich Hoppe, Larry Vangilder, Terry Walton, and Howard Zippler for helping with field work. Troy Best, Craig Guyer, Nick Holler, and Dennis Jorde provided helpful reviews of the manuscript. Research was supported by U.S. Department of Energy contract DE-AC09-76SROO-810 with the University of Georgia's Savannah River Ecology Laboratory. G.R.H. was supported in part by the Alabama Agricultural Experiment Station during preparation of the manuscript (AAES Journal No. 15-913075).

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