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NEST-BOX SELECTION BY PROTHONOTARY WARBLERS

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Abstract.—Prothonotary Warblers (*Protonotaria citrea*) laid eggs in 27.2% (37/141) and 34.1% (73/214) of wooden nest boxes placed in tidal swamp in the coastal plain of Virginia in 1987 and 1988, respectively. Only 15.2% of the boxes housed warblers both years. Stepwise discriminant function analyses were used to identify three significant environmental factors that seem to be important determinants of the attractiveness of boxes to warblers: proximity to open water, average basal area of the nearest four trees and percent of the day during which the nest box is exposed to direct sunlight. Warblers preferred sites near water surrounded by relatively large trees. Preferred sites were shaded most of the day. Directions of the entrance holes of nest boxes used by warblers did not deviate significantly from those of all boxes, nor did they deviate from a random direction. Paper wasps (Vespidae) and mud-daubers (Sphecidae) occupied 41.8% (1987) and 28.5% (1988) of the boxes and appeared to exclude warblers. Those boxes containing wasps and no nests were directed to the southeast. During 2 yr of study, only three boxes contained both wasps and successful nests. Canonical correlation analyses, however, indicated that wasps select boxes that generally were not acceptable to warblers and that warblers and wasps were in contention for only a few boxes in an intermediate set of conditions.

SELECCIÓN DE CAJAS PARA ANIDAR POR PARTE DE *PROTONOTARIA CITREA*

Sinopsis.—Individuos de *Protonotaria citrea* anidaron en cajas de madera que se colocaron en un anegado inundadizo de la planicie costanera de Virginia. El 27.2% (37/141) y el 34.1% (73/214) de las cajas fueron utilizadas por los pájaros en el 1987 y 1988, respectivamente. Sólo el 15.2% de las cajas albergaron aves durante los dos años. Un análisis discriminante de funciones fue utilizado para identificar entre tres factores ambientales que parecen ser importantes en lo atractivo de las cajas a las aves. A saber: proximidad al agua, área basal promedio de los cuatro árboles más cercanos y lapso de tiempo, durante el día, en que la caja esta directamente expuesta al sol. Las aves prefieren localidades cerca del agua rodeadas por árboles. Estos lugares preferidos están cubiertos de sombra la mayor parte del día. La dirección de la entrada de la caja utilizada por las aves, no se desvió significativamente de aquéllas de las demás cajas, ni se desviaron de una dirección al azar. Avispas de las familias Vespidad y Sphecidae, ocuparon el 41.8% (1987) y el 28.5% (1988) de las cajas lo que pareció excluir de estas a las aves. Las cajas conteniendo avispas estaban en dirección al sureste. Tan sólo en tres cajas coexistieron avispas y aves en donde las últimas anidaran exitosamente. Sin embargo, un análisis de correlación indicó que las avispas seleccionaban las cajas que no eran aceptables para las aves, y que ambos grupos estaban tan sólo en contención de algunas cajas con un conjunto de condiciones intermedias.

Only two of the 110 species of Parulinae (wood-warblers) regularly nest in tree cavities: Lucy's Warbler (*Vermivora luciae*) and the Prothonotary Warbler (*Protonotaria citrea*) (Bent 1953, Terres 1980). As there is intensive competition for nest cavities among conspecifics, other bird species, and even mammals (Guillory 1987, Petit and Petit 1988), the shelter provided by tree holes must provide substantial benefits. The present study is intended to identify those factors that determine use of nest boxes by Prothonotary Warblers. We assume that the factors affecting choice of nest boxes should be similar to those affecting selection of natural cavities.

METHODS

In March 1987, we placed 141 nest boxes in or near Presquile National Wildlife Refuge, near Hopewell, Virginia (37°20′N, 77°15′W). All boxes were placed within swamps along tidal creeks. The swamp forest was dominated by red maple (*Acer rubrum*), black gum (*Nyssa sylvatica*) and ash (*Fraxinus* spp.). Boxes were constructed of salt-treated pine (28 L × 9 W × 6 D cm) with an entrance hole 3.8 cm in diameter. An additional 80 boxes were placed in the field in March 1988. The habitat of the study area was a mosaic of tidal swamp, tidal marsh and riverine forest. Boxes were attached to the sides of trees at heights and distances from the water that depended upon availability of suitable attachment sites. The distance from the ground or water to the center of the entrance hole was measured to the nearest cm. The facing direction of the entrance hole was determined with a compass. Directions were chosen by lottery so as to place equal numbers of boxes within each 30° angle of the compass. Boxes were placed at 100-m intervals along the banks of the tidal creeks.

Ambient temperatures during the breeding season were high. Mean daily maximum temperatures from the NOAA station at Hopewell, Virginia, are 26.0 C (May), 30.1 C (June) and 31.5 C (July). We visited each box 5–7 times each year from 20 April–5 July and recorded the contents of each nest. Prothonotary Warblers appear to produce two clutches each year (see Petit 1989). Earliest eggs were found on 27 April and last eggs probably were laid on about 25 June. We defined early clutches as nests with eggs from 27 April–20 May and late clutches as nests with eggs after 20 May. Nest materials and wasp nests were removed from all boxes in March of both years.

In order to evaluate the importance of the position of the nest box and the surrounding vegetation, we made measurements at 55 boxes randomly selected by lottery. These measurements (acronyms in parentheses) included: (1) distance from the nest tree to the nearest tree (D1), (2) distance and diameter at breast height (dbh) of nearest trees in each quadrant around the nest tree, (3) the dbh of the tree on which the box was placed, (4) distance from the nest box to the nearest open water (WATER), (5) height of the nest tree in m, (6) direction the box faced (DIR) and (7) distance from the center of the entrance hole to the ground or to the water surface at high tide in cm (HEIGHT). In addition, the percent of time the box was exposed to direct sunlight was estimated from the portion of canopy coverage in line with the overhead passage of the sun during the breeding season (PEX). Percent cover of the herbaceous understory within 1 m of the nest tree was categorized visually as either 0, 25, 50, 75 or 100% (COVER). Several variables were computed from the above measurements, including: (1) tree density from the point-quarter method (DENSITY; see Brower et al. 1990), (2) mean distance from the nest to the nearest trees in the four quadrants (MEAND), (3) mean dominance

TABLE 1. Direction of entrance hole of nest boxes.

Occupancy	1987		1988	
	N	Direction[a]	N	Direction[a]
Wasps only[b]	54	107.5 ± 32.2	41	100.9 ± 22.1
No nest; no wasps	17	21.8 ± 11.2	46	11.0 ± 23.0
Partial nest; wasps	5	22.5 ± 20.1	17	38.6 ± 19.8
Partial nest; no wasps	27	40.2 ± 12.2	31	41.9 ± 24.3
Nest with young; wasps	0	—	3	25.7 ± 22.2
Nest with young; no wasps	37	353.8 ± 15.5	73	3.1 ± 33.2
Total boxes	141	15.6 ± 24.0	214	18.4 ± 24.0

[a] Compass direction in degrees (mean ± SD) of the nest-box opening.
[b] Direction is significantly different from nest with young; no wasps in both years.

(average of tree basal areas; AVEDOM) of the trees in the four quadrants and (4) mean dbh (MDBH) of the nearest four trees.

We analyzed the nest box location and surrounding vegetation by means of stepwise discriminant analyses (SAS Institute 1985, STEPDISC; see Clark et al. 1983). Canonical correlation analyses were used to examine the relationship of these variables for boxes that contained nests, wasps, or nothing (SAS Institute 1985, CANDISC). The 0.05 significance level was used in all statistical tests.

RESULTS

Warblers visited most nest boxes, placing at least small amounts of moss in >90% of them each year. Partial nests were common, but complete nests always consisted of 4–10 cm of green moss with terminal nest cups composed of grasses and other dry materials derived mostly from vascular plants (see Petit 1989, Petit and Petit 1988). Nesting activities were categorized as: (1) no nest, which includes boxes containing 2 cm or less of material; (2) partial nests (2–8 cm of moss base, no final cup); and (3) complete nests (terminal nest cup present, usually with eggs or young). Boxes with no nests often contained wasps of several species, including paper wasps (Vespidae) and mud-daubers (Sphecidae). Wasps occupied 41.8% (59/141) and 28.5% (61/214) of all boxes in 1987 and 1988, respectively.

Trees along the margins of tidal creeks along the lower James River tend to slump as their root masses wash free from the soil and some trees eventually fall into the water. This has been a significant cause of loss of nest boxes, and accounts for the occasional difference between sample sizes (Table 1) and the total number of boxes placed in the field.

The mean direction of the openings of all boxes was 3.3°. The openings distributed evenly around the points of the compass in both 1987 and 1988, respectively (divided into 12 quadrants; $\chi^2 = 6.8$ and 6.1, $P < 0.05$; Zar 1984). The direction of boxes containing compete nests with eggs did not deviate from normality either year ($\chi^2 = 6.3$ and 7.7, 1987 and 1988, respectively), and did not differ from the mean direction of all boxes (Fig.

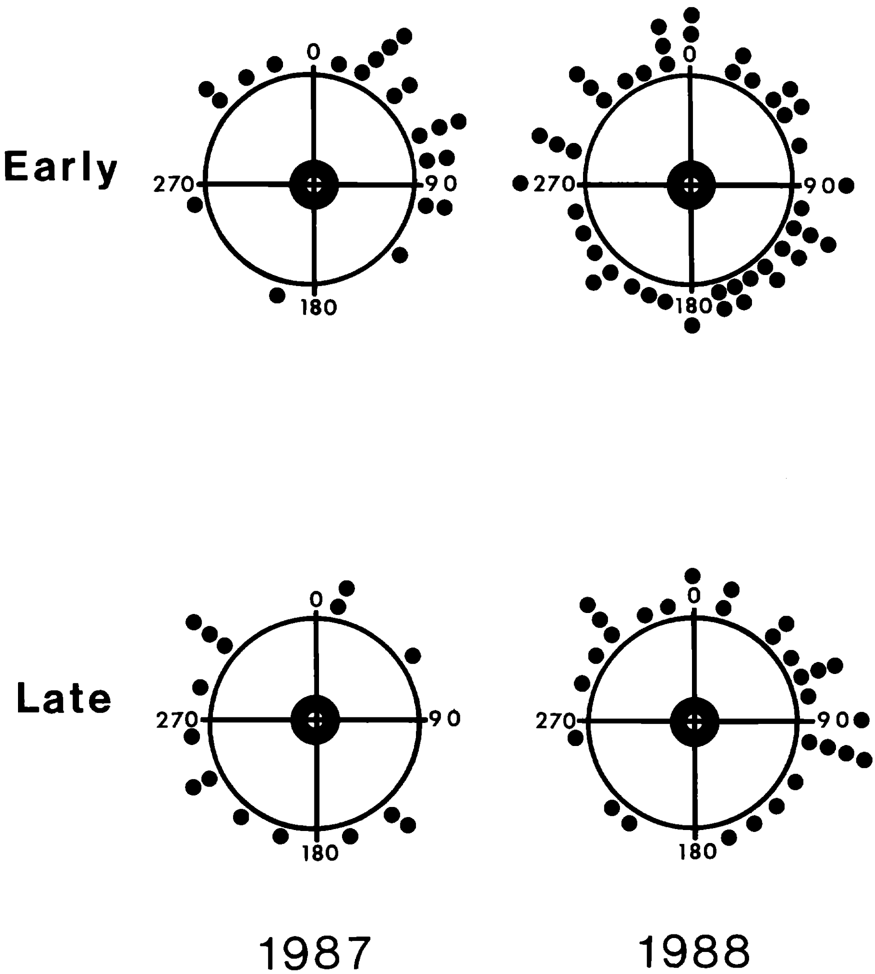

FIGURE 1. Distributions of compass directions of Prothonotary Warbler nests with eggs, 1987 and 1988.

1). In 1987 the mean direction of entrance holes of boxes having late ("second") clutches differed significantly from that of boxes having first clutches (Fig. 1; $F = 24.3$, df = 1, 34), but this trend was not evident in 1988 (Watson-Williams test, Zar 1984). Over both years, the direction of the entrance holes of boxes containing wasps only differed significantly from those having nests with eggs or young (Watson-Williams test, $F = 6.9$, df = 1, 203; Table 1).

The mean height of all boxes ($N = 221$) was 154.4 ± 5.4 (SE) cm (range 20–280 cm). Boxes with complete warbler nests ranged in height from 20 to 280 cm above the ground or highest tides. Distance of boxes

TABLE 2. Statistics of nest site characteristics. See methods for acronyms. Values are means ± SE.

Variable	Occupants of the nest box: Nest with young (N = 29)	No nest (N = 17)	Wasps (N = 9)
D1 (M)	1.9 ± 0.2	1.9 ± 0.3	1.4 ± 0.5
AVEDOM (cm^2)	737.4 ± 195.4	462.5 ± 63.2	539.9 ± 107.1
HEIGHT (cm)	148.2 ± 6.4	152.5 ± 7.8	147.8 ± 16.6
COVER (%)	51.1 ± 6.3	55.9 ± 7.0	86.1 ± 7.4*
MEAND (M)	2.7 ± 0.2	2.8 ± 0.4	3.0 ± 0.7
DENSITY (N/Ha)	2603 ± 436	3812 ± 1288	2892 ± 1233
WATER (M)	1.2 ± 0.3	2.2 ± 0.3	4.2 ± 0.3*
PEX (%)	31.9 ± 4.5	26.5 ± 4.8	53.3 ± 8.3*
DIR (°)[a]	36.6 ± 22.3	44.6 ± 24.9	100.0 ± 12.2*

* Significantly different from other occupancy categories as determined by analysis of variance and Duncan's multiple range test.

[a] Mean ± SD (see Zar 1984).

from the ground or water apparently did not affect nest-box selection, at least within the restricted range of heights available, as there was no statistical difference between the mean heights of boxes with complete nests and those unoccupied by warblers (Table 2).

Comparison of nest site characteristics among boxes with nests, no nests, and no nests with wasps (Table 2) indicated that several variables play a role in use of boxes by warblers compared with use by wasps. Warblers preferred boxes on trees near the water which were surrounded by relatively large trees. Increases in distance from the nest to the water, percent of the ground cover under the box, percent of the day during which the box was exposed to direct sunlight, and direction of the nest entrance all seemed to increase the probability of wasps' colonizing the nest box. Boxes with nests and boxes with neither wasps nor birds, however, tended to be at similar sites. Stepwise discriminant analysis (Table 3) indicated that distance to water, average dominance (dbh) of trees in the four quadrants around the nest tree and percent exposure of the nest box were all significant factors determining the occupants of the box.

TABLE 3. Summary of stepwise discriminant function analyses for comparison of nest boxes used by Prothonotary Warblers vs. those not occupied by warblers.

Step	Variable[a]	Wilk's λ	P	Coefficient[b]
1	Distance to nearest open water	0.555	0.0001	0.385
2	Average basal area	0.470	0.038	0.435
3	Exposure to sunlight	0.421	0.042	0.466

[a] See methods for descriptions of these variables.

[b] Standardized canonical discriminant function coefficient.

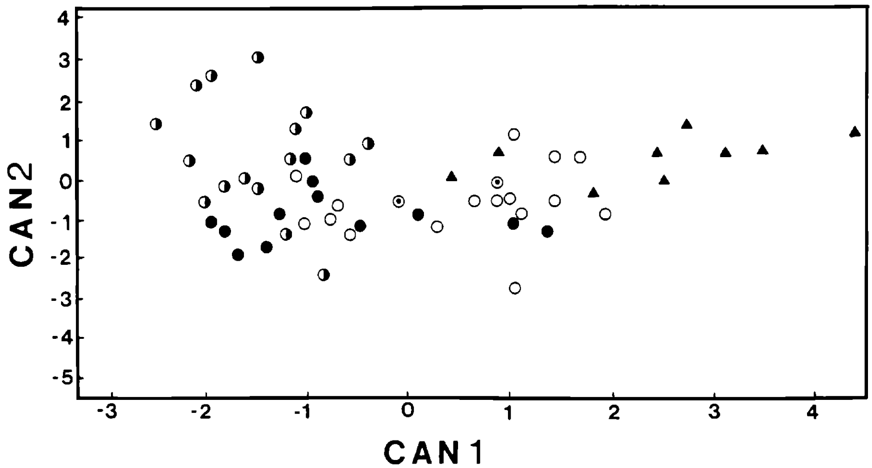

FIGURE 2. Canonical correlation analysis of occupancy of nest boxes. Solid circles represent boxes containing nests with eggs in both years, half-solid circles nests with eggs in only one year, hollow circles were empty both years, and triangles represent boxes that had wasps both years. Circles with dots in them represent boxes that housed wasps one year and warblers the other.

Canonical discriminant analyses (Fig. 2) indicated that boxes occupied by warblers were distinctive. Only a few intermediate boxes were not correctly identified by the analyses and 87.3% of the boxes were identified correctly as occupied by warblers or not occupied. It may be noteworthy that boxes used by wasps but not by warblers were widely separated in multivariate space from boxes used by warblers both years. Notice also that the two boxes that had wasps one year and warblers the other were in an intermediate zone.

DISCUSSION

Major factors affecting selection of nest boxes by Prothonotary Warblers potentially include predation, competition for available cavities and the environment in and around the nest box. In the present study it appears that environmental factors are of greatest impact.

Prothonotary Warbler nests often are low (Walkinshaw 1953), frequently less than 1 m from the water or ground. Such low nests could be subject to predation and a variety of predators are known to exploit Prothonotary Warbler nests. In the present study the mean height of boxes used for nesting did not differ from that of all available boxes, but vertebrate predators, particularly raccoons (*Procyon lotor*) destroyed at least 10% of the nests over both years. Additionally, cotton mice (*Peromyscus gossypinus*) occupied five boxes in 1988 and six boxes in 1989. We suspect that both *P. gossypinus* and the white-footed mouse (*P. leucopus,* found in two boxes both years) have depredated Prothonotary Warbler nests in our study. Partly eaten young warblers were found in one box that subsequently housed cotton mice. Petit (1989), also studying nest boxes, found high predation rates (>20%) on Prothonotary Warbler nests and attributed this to raccoons and snakes. We saw no indication of snakes depredating warblers, but black rat snakes (*Elaphe obsoleta*) were plentiful in the area, and removal of young by snakes is difficult to detect. No insect predators such as mosquitos (Culicidae) or botflies (Cuterebridae) were seen in or near any nest. Brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) was very rare; we only saw two instances over both years of the study.

Competition for nest cavities may limit the population density of secondary cavity-nesters (Holroyd 1975, Munro and Rounds 1985, Swallow et al. 1986, Rendell and Robertson 1989). Not all cavities are used, however, possibly because of a variety of factors including variation in location of the cavity, and dimensions of the cavity and its entrance hole. Studies of nest-box utilization allow researchers to examine the first effect while holding the second factors constant. The nest boxes used in our study appear to be acceptable by Prothonotary Warblers because they began to build nests in some boxes within 1–2 d after arriving on the breeding site, occupied many for both years and appeared to ignore some natural cavities. Avian competitors rarely excluded warblers. Avian competitors (and the number of times they nested in our boxes in 1987–1988) include: Eastern Bluebird (*Sialia sialis,* 2), Carolina Chickadee (*Parus carolinensis,* 1), Tufted Titmouse (*P. bicolor,* 1), Carolina Wren (*Thryothorus ludovicianus,* 0). All of these species begin nesting before Prothonotary Warblers and presumably had first chance at nest sites. As so few other species nested in nest boxes, we conclude that other avian species have little affinity for our nest boxes relative to that of Prothonotary Warblers, and thus probably had little effect on warbler choice of boxes.

Superficially, it appears that the major competitors for box space were wasps. We found only three boxes (1988) with both wasps and young warblers. The wasp nests (Vespidae) in all three cases were relatively small, but contained active adult wasps. Furthermore, we only found three boxes that shifted from "wasp" boxes to successful warbler boxes or vice versa. Our canonical correlation analyses indicate, however, that wasps choose boxes that are exposed to sunlight for longer periods of the day and at sites with relatively smaller trees than do warblers. The canopy is open and the herbaceous covering of the ground around the nest tree is relatively high. Wasps also preferred boxes directed more to the south. In general, wasps are choosing boxes with different physical characteristics than those favored by warblers. Observations that further support this hypothesis are: boxes seldom housed wasps one year and warblers the other, and those few boxes that did have wasps one year and warblers another were in an intermediate zone in the canonical correlation analyses. We have no evidence of warblers removing wasp nests or killing wasps.

Nest cavities could protect eggs and young from extreme weather conditions. Prothonotary Warblers begin nesting relatively early in the season when many other small passerines also use cavities (chickadees, titmice, nuthatches, wrens, bluebirds). Nest cavities could protect offspring from low temperatures and heavy spring rains. Likewise, Prothonotary Warblers appear to choose boxes that are less vulnerable to heat. Walkinshaw (1953), studying natural Prothonotary Warbler nests, noted that warblers built nests in cavities that were shaded most of the day. He also observed mortality of young apparently caused by excessive heat. Our discriminant function analyses lead us to believe that Prothonotary Warblers choose shaded nest cavities for protection from the sun. We suggest that the warblers' use of fresh green moss is a further attempt to modify the microclimate around eggs, because the moss increases the relative humidity in the box (C. R. Blem and L. B. Blem, unpubl. data). It is possible that positioning the nest in a low cavity near the water facilitates collecting large quantities of nearby moss.

Our results indicate that warbler utilization rates of nest boxes can be increased by placing boxes on trees near or in the water, on trees others with relatively large dbh's and at sites that are not frequently exposed to direct sunlight. It also may be best to direct nest box openings toward the north. We conclude that such boxes have little attraction for other small passerines, possibly because they are so low.

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