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Submitted 12 June 1992, accepted 19 August 1993.

The Auk 111(1):197–200, 1994

Composition and Microclimate of Prothonotary Warbler Nests

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During studies of Prothonotary Warblers (*Protonotaria citrea*) nesting in artificial nest boxes, we made two observations suggesting that physical environment affects nesting by this species. First, multivariate analyses of nesting habitat indicate that Prothonotary Warblers prefer nest boxes in shaded sites near water and avoid boxes in open, sunny areas (Blem and Blem 1991). Second, they build distinctive nests consisting of a dry cup (grasses, leaves, and rootlets) on a thick bed of moist, green bryophytes (mosses and liverworts; Bent 1953, Petit 1989, Blem and Blem 1992). In an active nest, the bryophytes are moist to the touch, while the cup is not. We suspect that the composition of these nests affects the environment within the nest cavity (e.g. Mertens 1977a, b). In the present analyses, we examine the composition and microclimate of these nests and ask the following questions: (1) Does their use of moist bryophytes significantly modify the microclimate of the nest cavity? (2) Does ambient temperature affect nest cavity selection by Prothonotary Warblers?

Methods.—We studied Prothonotary Warbler breeding activity in 250 wooden nest boxes in tidal swamps in and near Presquile National Wildlife Refuge on the James River near Hopewell, Virginia (37°20'N, 77°15'W), from 1987 through 1991 (Blem and Blem 1991, 1992). Details of the construction of these boxes and the plant community of this area are presented in Blem and Blem (1991). These swamps have a relatively harsh environment where tree-surface temperatures regularly exceed 45°C and the forest floor periodically is inundated by tidal river waters. Prothonotary Warblers are common in this habitat and, during the study period, our boxes contained at least 689 warbler nests with eggs (Blem and Blem 1992). Warblers have used our boxes so extensively that we have observed few natural nests and have no data from them. Prothonotary Warblers build their nests in this area between mid-April and late June (first nest initiated 28–30 April over five years of study). There are two peaks of nesting activity (Petit 1989). We categorize nests with eggs laid on or before 20 May as early clutches; late (second or replacement) clutches are those laid after that date. During the five years of our study only 3.3% (15/461) of all nests have been initiated between 20 May and 1 June (Blem and Blem 1992).

We simultaneously measured midday (1100–1600 EST) ambient temperature and temperatures within nest boxes with a Bailey BAT telethermometer. Nest temperatures 2 cm above the center of the nest were determined with 10-gauge thermocouples. Measurements were not made if the female was present in the box. In those boxes with nests or eggs, the female was absent for at least 5 min, and we monitored box temperatures until they stabilized before the nest temperature was finally determined. Ambient and nest-box humidities also were measured at the same time and location. We measured relative humidity with a Vaisala meter calibrated every two weeks with sodium-chloride and lithium-chloride solutions.

Over four breeding seasons (1988–1991) we installed max-min thermometers in dummy bird boxes with entrance holes covered by screens. These were placed directly below normal nest boxes by 1 April, or at least two weeks before first warblers arrived on

TABLE 1. Occurrence of mosses and liverworts in Prothonotary Warbler nests in nest boxes along the James River, Virginia.

	Percent occurrence			
Species	Top	Middle	Bottom	Total
Mosses				
Anomodon attenuatus	97.3	96.4	91.4	95.0
Haplocladium microphyllum	20.6	13.4	21.0	18.3
Amblystegium varium	6.7	7.6	1.3	5.2
Plagiomnium cuspidatum	2.7	1.3	3.1	2.4
Thuidium delicatulum	0.4	1.3	0.0	0.6
Liverworts				
Porella platyphylla	21.9	27.3	32.1	27.1
Frullania eboracensis	0.4	0.8	0.8	0.7

the nesting grounds. They were recovered after nesting ended in July, and the maximum nest-box temperatures were recorded. Temperatures of dummy nest boxes ($\bar{x}$ = 28.7 ± SE of 1.8°C, n = 15) did not differ significantly from accompanying nest boxes (28.5 ± 1.9°C). Nest boxes were visited at least every seven days (four to five days when nests were present); thus, we knew when and how warblers had used nest boxes.

At the end of the breeding season, we sampled mosses and liverworts in the upper, middle, and bottom thirds of 14 nests. Thin layers of nest materials were removed from each of these areas and placed on a square 4 × 4 cm clear plastic grid subdivided into 16 1-cm^2 squares. The percentage occurrence of each bryophytic species (Table 1) was calculated as the number of squares within which the species was detected divided by the total number of squares (total = 672 squares = 14 nests × 3 layers × 16 squares/layer). We also measured nest depths (to nearest 0.1 cm) of 28 intact nests. The nests were then collected and air-dried to constant mass. Nest cups and moss bases were separated and weighed separately. To determine effects of size of nest cavity on nest composition, we obtained nests from boxes of two different sizes: 15 × 10 × 10 cm (volume = 1,500 cm^3); and 20 × 10 × 10 cm (2,000 cm^3).

In order to test for significant effects of nest-box contents on internal temperature and humidity, we performed analyses of covariance (ANCOVAs) in which temperature or humidity inside of the nest box was the covariate, and nest contents the classification variable. The nest-content categories were (1) empty, (2) partial nest, and (3) nest with eggs.

Results.—Prothonotary Warbler nests at our site are mostly composed of mosses/liverworts (74.7–80.2% of total dry mass of nest, depending upon size of nest box). Small nest boxes (1,500 cm^3; n = 19) had nests with less moss (9.6 g) and were smaller in total mass than nests from the larger boxes (2,000 cm^3; n = 9; 16.9 g). Nest depth was less in small boxes (6.8 ± 0.35 cm) than in large boxes (8.6 ± 0.20; $t = 4.5$; $P < 0.05$). Five species of mosses and two liverworts were recorded in Prothonotary Warbler nests (Table 1). One species, *Anomodon attenuatus*, greatly outnumbered all others and was found in nearly all sample cells. There was no significant difference in occurrence of species between layers when variation among layers and boxes was considered simultaneously (all F values for variation among layers <1.7 for all moss species). There was significant variation among boxes for three species (*Porella platyphylla*, $F = 12.8$; *Amblystegium varium*, $F = 4.5$; and *Haplocladium microphyllum*, $F = 3.9$).

An ANCOVA indicated that temperatures varied significantly ($F = 4.16$, $P < 0.05$, df = 45) among boxes categorized by content (empty, partial nests, and nests with eggs; Fig. 1A). Relative humidity also varied significantly among these categories (Fig. 1B; $F = 10.8$, $P < 0.001$, df = 45). Even when nests with eggs were removed from the analyses, there was still a significant difference in humidity between empty boxes and boxes with partial nests ($F = 4.9$, $P < 0.05$, df = 21).

Maximum temperatures differed by about 9°C among nest boxes (Table 2). To test for effect of temperature on use of individual boxes, we divided this range at the midpoint and categorized nest boxes as low-temperature boxes (maximum temperature 30–34°C) and high-temperature boxes (35–39°C). Eggs were laid in similar numbers of boxes in each category (13 vs. 15), even though there were fewer low-temperature boxes (20 vs. 28). None of the high-temperature boxes but eight low-temperature boxes were used for late clutches. Furthermore, partial nests were placed in nine high-temperature boxes, but in only three low-temperature boxes. A chi-square test of the 2 × 2 contingency table for time of clutches and box temperatures is significant ($X^2 = 13.0$, $P < 0.01$, df = 1). It appears that warblers select high-temperature boxes for early clutches and avoid high-temperature boxes for later clutches.

Discussion.—The Prothonotary Warbler is one of only two species of wood warblers regularly nesting in tree cavities (Bent 1953, Morse 1989). Use of artificial boxes by these warblers has been well documented (Fleming and Petit 1986, Petit et al. 1987, Blem and Blem 1991). The selection of bryophytes (mosses and liverworts) for nest materials is not unusual as these are common constituents of avian nests. For example, Breil and Moyle (1976) listed 60 species of mosses and five species of liverworts found in nests of birds of the eastern deciduous forest in western Virginia. Most instances of use of bryophytes by cavity nesters involve at least small amounts of green materials (Clark and Mason 1985); however, the large quantity of bryophytes and the high degree of moistness of Prothonotary Warbler nests makes them unique among cavity-nesting species (see Chapman 1917, Bent 1953).

Why do Prothonotary Warblers use moist moss in their nests? Construction of a distinctly different nest

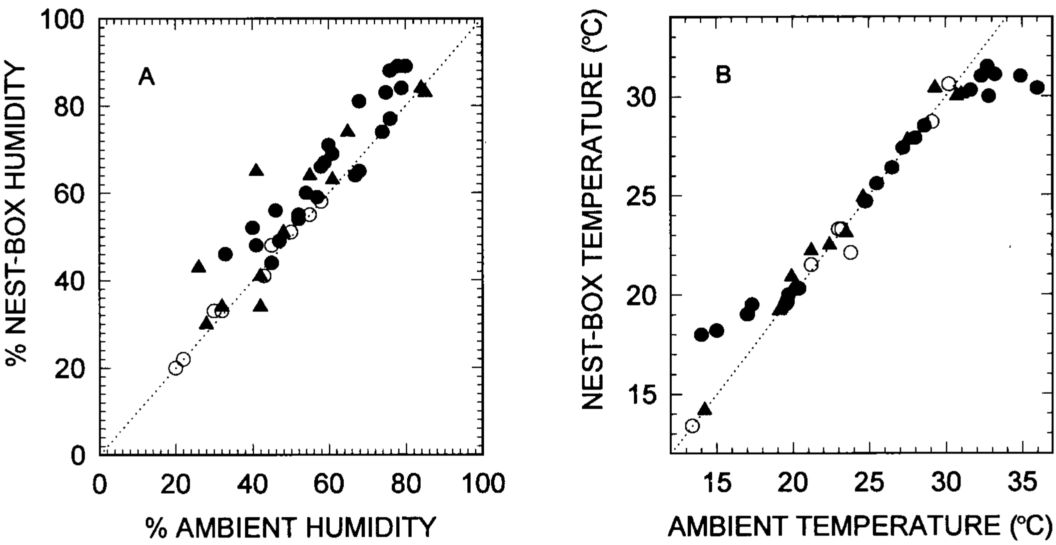

Fig. 1. (A) Temperatures and (B) relative humidities of nest boxes. Solid circles represent nests with eggs, hollow circles empty nest boxes, and solid triangles partial nests.

cup suggests that the warblers are not just randomly collecting available materials. If this were so, they would construct a cup in the moss. Since the materials that comprise the cup are widely available in the swamp, it appears that the birds are selectively making a nest of two distinctly different groups of plants. Alternatively, mosses or liverworts may possess insecticidal properties and use of them could control invasions by parasites or pathogens (Wimberger 1984, Clark and Mason 1985). We have no empirical evidence on this point other than to note that we have observed a wide diversity of spiders and insects in these boxes. Ant colonies (unidentified species) are commonplace on the side of active nests. Use of green bryophytes significantly raises humidity in the nest cavity, which may prevent desiccation of eggs, thus enhancing hatching success (see Clark and Mason 1985).

Warblers undoubtedly abandon nests for reasons other than physical environment. For example, predation can be a severe problem in Prothonotary Warbler habitat (Petit 1989, Blem and Blem 1992), and encounters with predators could cause nest abandonment. Competitors for nest sites also could interfere with use of cavities. However, in 1,342 box-years (box-year = one box available for one breeding season), Prothonotary Warbler eggs were deposited in 689 boxes and partial warbler nests were built in 286 boxes, but other species produced only 38 nests (2.8% of all box-years). Other species using these boxes included Eastern Bluebirds (*Sialia sialis*, 17), Carolina Wrens (*Thryothorus ludovicianus*, 13), Carolina Chickadees (*Parus carolinensis*, 6), and Tufted Titmice (*P. bicolor*, 2).

Our observations indicate that Prothonotary Warblers early in the breeding season work on nests in more than one cavity at a time, but eventually only select one nest to complete. Partial nests have been considered to be "dummy" nests (Bent 1953), constructed perhaps for the purpose of confusing predators. It also is possible that the birds detect differences in temperature between boxes in the process of selecting a cavity. In early stages of the season boxes with higher internal temperatures are preferred. In late nests, boxes with greater exposure to heat are abandoned after partial nests are constructed,

TABLE 2. Maximum temperatures and contents of Prothonotary Warbler nest boxes.

Maximum temperature of nest box[a] (°C)	Contents of nest box				Total
	Empty box	Partial nest	Early clutch[b]	Late clutch[b]	
30–34°	4	3	5	8	20
35–39°	4	9	15	0	28
Total	8	12	20	8	48

[a] Maximum summer temperature within dummy boxes below box occupied by birds.
[b] Early clutches are those in which first eggs were laid on or before 20 May, with late clutches being initiated after that date.

and only those sites in shade and with low maximum temperatures ultimately are used to incubate eggs.

Acknowledgments.—We thank Barry Brady, refuge manager, Presquile National Wildlife Refuge, for permission to study warblers there. Hill Carter kindly gave us access to the study area from historic Shirley Plantation. Harold Robinson, U.S. National Museum of Natural History, helped L.B.B. identify bryophytes. Susan Moyle Studlar and Larry Clark kindly shared their knowledge of mosses and bird nests with us. We also thank Larry Clark, Richard N. Conner, and Douglass H. Morse for reviewing drafts of this manuscript. Members of several Virginia Commonwealth University ornithology classes helped with maintenance of nest boxes.

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Received 5 October 1992, accepted 11 April 1993.

The Auk 111(1):200–204, 1994

The Gray-necked Wood-Rail: Habits, Food, Nesting, and Voice

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The large, elegant Gray-necked Wood-Rail (*Aramides cajanea*) ranges widely over all except the more arid regions of continental America, from eastern Mexico to Uruguay and northern Argentina. For many years, one or more pairs have inhabited light second-growth woods and high, dense thickets on stony land, separated by a creek from our garden and house at Los Cusingos, near Quizarrá in the valley of El General on the Pacific slope of southern Costa Rica (9°20'N, 83°38'W, altitude 740 m). About 20 years ago, a pair of these wood-rails began more frequently to approach our house, where they could be watched from windows or a porch. They have continued to remain shy, ready to run swiftly over the lawn to the nearest sheltering shrubbery when they become aware of being watched, although occasionally they appear more confident. I have never seen them in the mature rain forest that adjoins the garden, possibly because this is mostly on a ridge, and Gray-necked Wood-Rails prefer the vicinity of water.

Throughout the year, these wood-rails live as a pair, with varying degrees of intimacy. Much of the time, one member holds its partner with threats at a distance of a few meters while eating the corn or rice that we give them. However, at certain seasons, probably when they are preparing to nest, they eat close together, or one picks up a grain in the tip of its bill, runs to the other, who may be as much as 10 m away, and passes it directly to the recipient, or lays it at this bird's feet. Probably the male feeds his consort; but the sexes are indistinguishable except by voice, and at these times they are silent.

Food.—Over the years, I have seen these rails eat a wide diversity of foods. They join White-tipped Doves