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On No-chickadee Zones in Midwestern North America: Evidence from the Ohio Breeding Bird Atlas and the North American Breeding Bird Survey

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It has been suggested that in midwestern North America (Illinois, Indiana, and Ohio) there are several narrow latitudinal gaps between the breeding ranges of Black-capped (*Parus atricapillus*) and Carolina (*P. carolinensis*) chickadees (Brewer 1963, Merrit 1981). An analogous no-chickadee band of altitude has been reported for the southern Appalachian Mountains (Tanner 1952). Such no-chickadee zones have been thought to exist because they reduce interbreeding of the two species. However, anatomical, behavioral and electrophoretic evidence suggests that the two species freely interbreed in southwestern Missouri (Braun and Robbins 1986, Robbins et al. 1986). Furthermore, these workers suggested that no-chickadee zones in the Midwest could be confined to habitats submarginal for either species. That is, there is a band of formerly prairie habitat where woodlands are too small and scattered, and where potential cavity nest sites are too scarce to support either species. Thus, birds of the two species may not be avoiding each other, but may be independently avoiding inhospitable conditions. Here, we use records from the Ohio Breeding Bird Atlas (Peterjohn and Rice 1991) and the North American Breeding Bird Survey (B. G. Peterjohn pers. comm.) to test this submarginal-habitat hypothesis that no-chickadee zones in the Midwest are a consequence of poor habitat quality.

The Ohio Breeding Bird Atlas resulted from a five-year effort (1983–1987) to document the breeding status and distribution of all bird species in the state. Birds were noted in 764 25-km^2 census blocks assigned statewide in a stratified-random fashion, and in 113 "special areas" of variable extent that were included because they were of particular ornithological interest. For the five-year period within each of these 877 atlas sites, all species were assigned a breeding status of possible, probable, or confirmed. While atlas workers were not provided with specific guidelines for assigning chickadees to either *atricapillus* or *carolinensis* (B. G. Peterjohn and D. L. Rice pers. comm.), song type was apparently the criterion employed most commonly (T. Bartlett pers. comm.).

The North American Breeding Bird Survey (BBS) was initiated in 1966 and consists of routes that are randomly distributed within 1° blocks of latitude and longitude (Robbins and Van Velzen 1967). In the Ohio region, route density is approximately four per 1° block; the 45 routes in Ohio traverse 61 counties. For seven Ohio routes, a replacement route (located near the original) was initiated between 1979 and 1991; in our study, replacement routes were treated as continuations of original routes. Not all routes were run in each year; in Ohio, routes were run an average of 22 of the 26 years between 1966 and 1991. Routes were run at the peak of the breeding season. At each of 50 stops located at 0.8-km intervals along the 40-km route, an observer recorded the number of individuals of each species heard or seen during one 3-min interval.

Using atlas data, BBS data, and records of percent forest cover in each of Ohio's 88 counties (Dennis and Birch 1981), we tested three predictions deduced from the submarginal-habitat hypothesis for no-chickadee zones. First, the proportion of atlas sites in a county occupied by chickadees, regardless of species, was predicted to be positively correlated with percent forest cover. Similarly, the number of individual chickadees reported on a BBS route was predicted to be positively correlated with the average percent forest cover among counties in which the route occurred. Averages were calculated by weighting percent forest

TABLE 1. Ohio Breeding Bird Atlas blocks in which breeding of Black-capped Chickadees (B), Carolina Chickadees (C), or both species of chickadee (Both) was either confirmed or probable. Counties arranged by increasing percent forest cover.

County	Percent forest cover	Chickadee species	Atlas blocks in which breeding			Total atlas blocks
			B	C	Both	
Madison	3	C	—	5	—	6
Van Wert	4	C	—	3	—	7
Putnam	4	B	4	—	—	9
Wood	4	B	9	—	—	11
Ottawa	4	B	4	—	—	5
Sandusky	4	B	5	—	—	6
Fayette	4	C	—	5	—	9
Allen	5	Both	0	6	1	9
Pickaway	5	C	—	10	—	10
Mercer	6	C	—	5	—	8
Miami	6	C	—	5	—	8
Champaign	6	C	—	10	—	10
Wyandot	6	Both	2	1	2	5
Union	6	C	—	6	—	6
Henry	7	C	3	—	—	8
Auglaize	7	C	—	3	—	6
Clark	7	C	—	7	—	8
Clinton	7	C	—	10	—	11
Franklin	7	C	—	16	—	16
Darke	8	C	—	11	—	12
Hancock	8	Both	8	1	0	12
Seneca	8	B	11	—	—	12
Paulding	9	Both	4	2	0	7
Montgomery	9	C	—	9	—	11
Hardin	9	C	—	7	—	8
Greene	9	C	—	5	—	6
Marion	9	C	—	6	—	8
Logan	10	C	—	10	—	10
Crawford	10	Both	1	1	1	6
Preble	11	C	—	4	—	7
Fulton	11	B	7	—	—	10
Warren	11	C	—	10	—	10
Erie	11	B	6	—	—	7
Butler	12	C	—	9	—	9
Lucas	12	B	13	—	—	15
Huron	12	B	9	—	—	9
Cuyahoga	12	B	12	—	—	12
Shelby	13	C	—	8	—	9
Delaware	14	C	—	11	—	11
Fairfield	15	C	—	9	—	10
Lorain	15	B	13	—	—	13
Morrow	16	C	—	8	—	9
Defiance	17	B	9	—	—	10
Wayne	17	Both	2	7	0	8
Stark	17	Both	3	1	4	10
Williams	19	C	11	—	—	11
Hamilton	19	C	—	13	—	14
Highland	19	C	—	8	—	8
Ashland	19	Both	5	0	3	9
Richland	20	Both	2	2	3	7
Medina	22	B	9	—	—	9
Licking	24	C	—	10	—	12
Summit	24	B	8	—	—	9
Knox	25	C	—	9	—	9
Brown	26	C	—	9	—	9
Mahoning	27	Both	10	0	2	12
Lake	30	C	8	—	—	8

TABLE 1. Continued.

County	Percent forest cover	Chickadee species	Atlas blocks in which breeding			Total atlas blocks
			B	C	Both	
Portage	31	B	13	—	—	14
Holmes	32	C	—	6	—	6
Clermont	33	C	—	10	—	10
Ross	39	C	—	11	—	12
Columbiana	39	Both	1	6	8	14
Trumbull	41	B	10	—	—	11
Ashtabula	43	B	17	—	—	17
Muskingum	45	C	—	—	—	12
Tuscarawas	45	C	—	10	—	11
Carroll	46	C	—	9	—	9
Coshocton	47	C	—	10	—	10
Geuga	50	B	12	—	—	12
Guernsey	50	C	—	11	—	11
Morgan	51	C	—	7	—	7
Jefferson	51	C	—	10	—	10
Adams	53	C	—	12	—	12
Belmont	54	C	—	7	—	8
Washington	56	C	—	11	—	12
Harrison	56	C	—	7	—	7
Gallia	57	C	—	10	—	10
Perry	58	C	—	8	—	8
Athens	60	C	—	6	—	6
Noble	60	C	—	4	—	4
Pike	63	C	—	8	—	8
Hocking	64	C	—	13	—	13
Monroe	64	C	—	10	—	10
Jackson	65	C	—	11	—	11
Meigs	67	C	—	10	—	10
Scioto	69	C	—	11	—	11
Vinton	73	C	—	4	—	6
Lawrence	74	C	—	9	—	9

cover in a county by proportion of route within. The submarginal-habitat hypothesis should apply to both species. Second, the proportion of atlas sites in a county occupied by the congeneric Tufted Titmouse (*P. bicolor*) and the number of individual titmice on a BBS route also were predicted to be positively correlated with percent forest cover. The closely related titmouse is another cavity-nesting permanent resident woodland species whose range in Ohio encompasses those of both chickadees, so the submarginal-habitat hypothesis should apply to that species as well. Third, in each of the counties where both chickadee species were detected, the proportion of atlas sites that contained both species was simply a product of the separate proportions for the two species. If the two species of chickadee in Ohio do not actively avoid each other, but only avoid submarginal habitat, then the chance that both species would be detected in the same atlas site could well be related to the distributions of the two species in a county. In particular, this prediction would be supported if the *Y*-intercept and slope of the regression line of observed on expected co-occurrence (by county) did not differ from 0 and 1, respectively. Because "two-species" counties contained only four BBS routes and few chickadees were recorded per route ($\bar{x}$ = 1.8), there were too few BBS data for an analogous test.

For each county, we assigned atlas sites to the following categories: (1) no chickadees; (2) Black-capped Chickadees only; (3) Carolina Chickadees only; or (4) both species present. Similar records were tallied for the titmouse.

For statistical analysis, we used linear regression on arcsine-transformed values where the assumptions of the model were met (Cohen and Cohen 1983). Otherwise, we employed Spearman's rank correlation. We considered all comparisons to be one-tailed, unless stated otherwise, and accepted significance at the 0.05 level. We performed three versions of most analyses involving atlas data, one using only confirmed records of breeding, a second using the combined categories of confirmed and probable breeding, and a third including any indication of breeding (confirmed, probable, or possible).

Analyses using only confirmed breeding records were always very similar to those employing con-

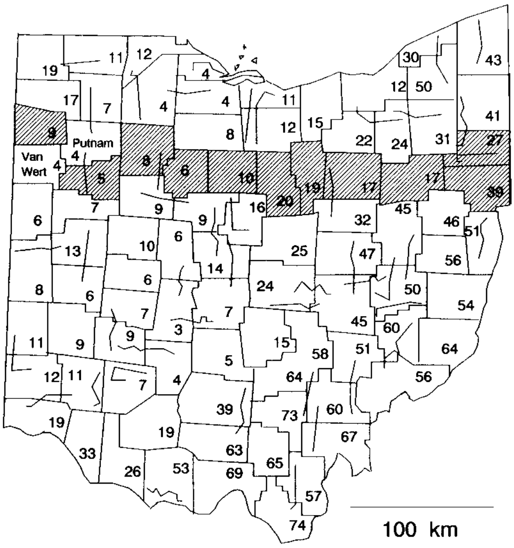

Fig. 1. Distributions of breeding Black-capped and Carolina chickadees in Ohio counties based on records of confirmed and/or probable breeding in Ohio Breeding Bird Atlas. Both species bred in cross-hatched counties, with Black-capped and Carolina chickadees, respectively, breeding north and south of cross-hatched area. In northwestern part of state, Black-capped Chickadees were reported breeding in Putnam County and Carolina Chickadees in Van Wert County. Numerical values indicate percent forest cover in each county. Lines depict routes of North American Breeding Bird Survey.

firmed and probable records combined. Furthermore, it appears very likely that, in these permanent-resident species, the probable records were valid indicators of breeding. For example, in Morrow County, Carolina Chickadees were listed as confirmed breeders at only one atlas site and probable at seven sites; yet, after 20 years of fieldwork in that county, T.C.G. is quite confident that any woodlot greater than 5 ha in size contains breeding chickadees, and every atlas site in Morrow County had such woodlands.

Tufted Titmice were recorded on atlas sites in all of Ohio's 88 counties and were detected on all of Ohio's 45 BBS routes. Regardless of whether atlas records of possible breeding were included, 21 counties contained breeding Black-capped Chickadees only, 56 counties contained breeding Carolina Chickadees only, and 11 counties contained breeding chickadees of both species (Table 1). The two-species counties comprised an east-west band across the state about one-fourth of the way south from the northern boundary (Fig. 1). "Black-capped-only" counties encompassed 12 BBS routes ($\bar{x}$ individuals/route = 2.2). "Carolina-only" counties included 29 routes ($\bar{x}$ individuals/route = 2.4), and two-species counties included 4 routes ($\bar{x}$ Black-capped Chickadees/route = 1.2; $\bar{x}$ Carolina Chickadees/route = 0.6).

Considering the state as a whole, the wooded proportion of a county diminished progressively from the south and east (e.g. Lawrence County, 74%; Monroe County, 64%) to the north and west (e.g. Wood, Putnam, and Van Wert counties, 4%). However, in the far northwestern corner, forest cover again increased (e.g. Defiance County, 17%; Williams County, 19%), a trend continuing on into Michigan (Table 1, Fig. 1).

Whether we considered either set of one-species counties, the set of both-species counties only, or all counties combined, and whether we included possible records in the analysis, there was always a significant correlation between proportion of atlas sites containing breeding chickadees and proportion of a county covered by woodland (Table 2, Fig. 2A). In every case, the correlation became greater once the possible records had been removed. The correlations in Table 2 were very similar for single-species and both-species counties. This occurrence was particularly striking for the confirmed-plus-probable records in Black-capped-only counties (r_s = 0.68) and both-species counties (r_s = 0.69), both of which extended

TABLE 2. Rank correlations (r_s) between forested proportion of Ohio counties and proportion of counties' atlas sites in which Black-capped Chickadees, Carolina Chickadees and Tufted Titmice detected. All correlations $P < 0.001$.

	Breeding status[b]	
Species recorded (n)[a]	Confirmed or probable	Confirmed, probable or possible
Black-capped Chickadee only (21)	0.68	0.58
Carolina Chickadee only (56)	0.51	0.45
Both species of chickadee (11)	0.69	0.51
Either or both species of chickadee (88)	0.57	0.36
Tufted Titmouse (88)	0.45	0.39

[a] Number of counties.
[b] One-tailed tests.

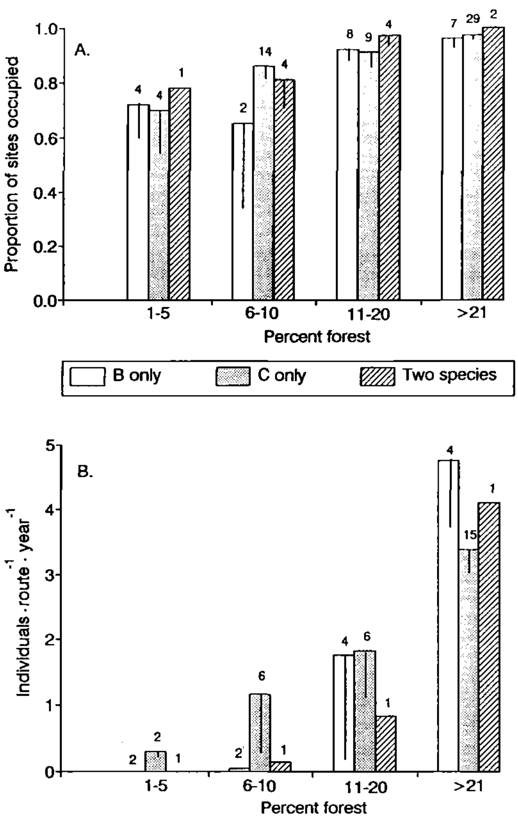

Fig. 2. Relationship between: (A) percent forest cover in an Ohio county and mean percent of atlas sites where chickadee breeding was categorized as confirmed or probable; and (B) mean percent forest cover among counties in which a BBS route occurred and number of individuals/year recorded on route. Standard errors shown in bars and sample sizes (number of counties or BBS routes) above or in bars. B and C refer to Black-capped and Carolina chickadees, respectively.

out into the lightly wooded northwestern part of the state more than did the Carolina-only counties. The proportion of atlas sites in a county where Tufted Titmice were detected breeding was also positively correlated with proportion of forest cover (Table 2). Also, the various positive correlations of breeding status with forest cover for both chickadees and the titmice meant that the proportion of atlas sites in a county occupied by any form of chickadee was strongly correlated with the proportion of atlas sites housing the titmouse (confirmed-plus-probable records, $r_s = 0.52$, $P < 0.001$, $n = 88$; all records combined, $r_s = 0.54$, $P < 0.001$, $n = 88$).

Similarly, analyses using BBS data (1966–1991) showed strong, positive correlations between numbers of chickadees or titmice and forest cover (Table 3, Fig. 2B). Percent forest cover was correlated with number of chickadees/route in Black-capped-only counties, Carolina-only counties, both-species counties, and all counties combined. Likewise, percent forest cover was strongly correlated with the number of Tufted Titmice/route. Analyses using only 1983–1987 BBS data (i.e. data gathered concurrently with atlas data) revealed similar significant correlations between number of individuals and forest cover (Table 3).

Finally, in the 11 counties where both species of chickadee occurred, the observed percent of census sites with both species was significantly positively related to the expected percent:

$$O = 0.82E - 0.019, \quad (1)$$

where O is the observed percent and E is the expected percent ($r^2 = 0.823$, $F_{1,9} = 41.77$, $P < 0.0001$, $n = 11$; Fig. 3). The 95% confidence intervals for the slope and Y-intercept contained the values of 1 and 0, respectively (Fig. 3B).

Our analysis using the Ohio Breeding Bird Atlas and the North American Breeding Bird Survey indicated that, regardless of species, the distribution and abundance of chickadees in Ohio were positive functions of woodland cover, and so were the distri-

Table 3. Rank correlations between number of individuals·BBS route^{-1}·year^{-1} and average percent forest cover among counties in which the route occurred.

Subset of Ohio counties (n, n)[a]	1966–1991[b]	1983–1987[b]
Black-capped Chickadee only (12, 11)	0.75**	0.82***
Carolina Chickadee only (29, 26)	0.65***	0.46**
Both chickadee species (4, 3)	1.00*	—[c]
Either or both chickadee species (45, 40)	0.71***	0.61***
Tufted Titmouse (45, 40)	0.65***	0.51***

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

[a] Subsets defined as those counties in which Black-capped-only, Carolina-only, or both species of chickadee observed on atlas sites. All counties had either or both chickadees and Tufted Titmice. Sample sizes indicate number of BBS routes for 1966–1991 and 1983–1987, respectively.

[b] One-tailed probability values.

[c] Sample size of 3 is too small to detect significance in a Spearman's rank correlation (i.e. even if ranking were perfect, P-value would be >0.05).

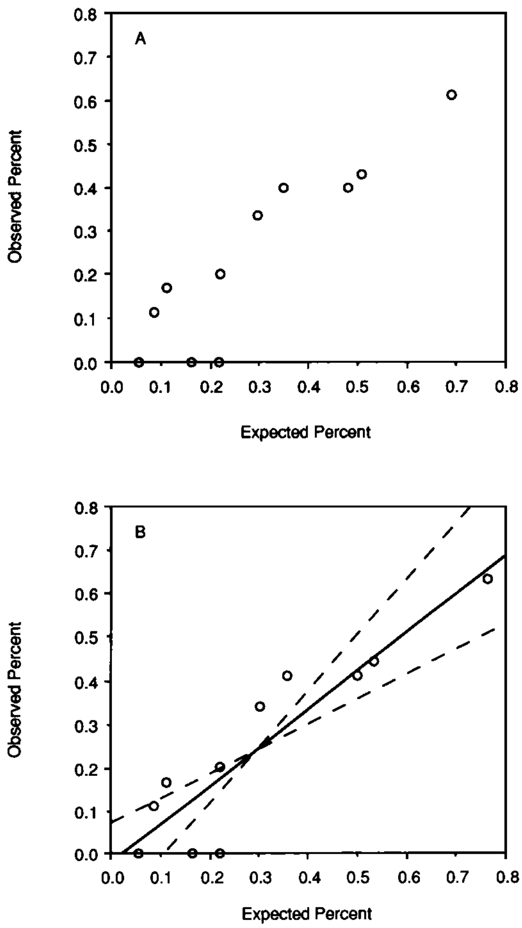

Fig. 3. (A) Expected and observed proportions of atlas sites containing both Black-capped and Carolina chickadees for 11 Ohio counties where both species were reported. (B) Regression of arcsine-transformed values of two proportions. For each county, expected proportion of sites containing both species calculated as product of proportions of sites containing each species separately. In B, solid line denotes regression line, while dashed lines bound the 95% confidence intervals for regression coefficient (0.573 to 1.19) and Y-intercept (−0.132 to 0.094).

bution and abundance of the congeneric titmouse. Correlations involving atlas data became stronger when we restricted analysis to confirmed and probable breeders. Other studies of parids during the breeding season have revealed some birds to be living in habitat submarginal for breeding (e.g. Krebs 1971). Perhaps relaxed habitat selection was responsible for the presence in some atlas sites of certain possible breeders that were not actually breeding.

The 95% confidence intervals for the regression of observed on expected overlap in atlas sites contained the values for the Y-intercept and slope predicted by the null hypothesis of no avoidance. Thus, it appears that explanations of no-chickadee zones based on unilateral or mutual avoidance are not required to explain the Ohio distributions of the two chickadees.

A potential criticism of our analysis concerns the possibility that sampling effort might have been correlated with proportion of forest cover. If this were true, the low number of atlas sites containing chickadees and the low number of chickadees per BBS route in low-woodland counties could have been a sampling artifact. While it remains possible that effort per atlas site or BBS route varied positively with percent woodland cover, there was no significant correlation between the percent forest cover and the number of atlas sites in a county ($r_s = 0.21$; two-tailed $P > 0.05$; $n = 88$) or presence of a BBS route in the county ($r_s = 0.005$; two-tailed $P = 0.96$; $n = 88$).

In conclusion, our findings support the hypothesis that any gaps between the ranges of Black-capped and Carolina chickadees in the former prairie regions of Illinois, Indiana and Ohio are caused by habitat that is submarginal for both species and are not the result of avoidance of heterospecifics. The present results shed no light on whether or how gene flow between the two species is prevented in the mountainous East or in areas of the Midwest where the two species are in contact.

Acknowledgments.—We thank the hundreds of Ohio bird enthusiasts who contributed an aggregate of 30,000+ person-hours toward production of the Ohio Breeding Birds Atlas. Bruce G. Peterjohn and Daniel L. Rice provided valuable interpretation and discussion of atlas records. We also thank the volunteers who run the BBS routes each year, and Bruce G. Peterjohn for providing the BBS records. The comments of Jonathan Bart, Michael J. Braun, Sandra L. L. Gaunt, Kathleen K. Harris, Peter G. Merritt, Vladimir V. Pravosudov, Mark B. Robbins, Sally Waterhouse, and particularly Thomas A. Waite improved earlier drafts.

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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