

A MICROCLIMATE ANALYSIS OF NEST-SITE SELECTION BY MOUNTAIN CHICKADEES

DOUGLAS G. WACHOB

Wyoming Cooperative Fish & Wildlife Research Unit
Department of Zoology & Physiology
University of Wyoming
Laramie, Wyoming 82071 USA

Abstract.—The relationships between the thermal microclimate of nest sites and reproductive success were examined in a free-ranging population of Mountain Chickadees (*Parus gambeli*). I measured temperatures and wind speeds at nest boxes and natural cavities in high-elevation forests of south-central Wyoming during 1991 and 1992. Solar radiation was estimated with hemispherical photographs. Compared with unused boxes, successful Mountain Chickadee nests had higher air and vegetation temperatures, higher daily solar radiation, more open canopies in the southeast quadrant, and more closed canopies in the northwest quadrant. Unsuccessful nests (mostly due to nest abandonment) did not differ from unused boxes for any measured variables.

UN ANALISIS MICROCLIMATICO DE LA SELECCION DE NIDOS EN *PARUS GAMBELI*

Sinopsis.—Se examinaron las relaciones entre el microclima termal de la localidad de los nidos y el éxito reproductivo en una población de *Parus gambeli* de movimientos libres. Yo medí las temperaturas y velocidad del viento en cajas de nidos y en cavidades naturales en bosques de alta elevación en el centro y sur de Wyoming entre 1991 y 1992. Se estimó la radiación solar con fotografías hemisféricas. Comparados con cajas no usadas, nidos exitosos de *Parus gambeli* tenían mayores temperaturas de aire y vegetación, mayor radiación solar diaria, más doseles abiertos en el cuadrante sureste, y más doseles cerrados en el cuadrante noroeste. Nidos no exitosos (principalmente debido al abandono del nido) no difirieron de cajones no utilizados en ninguna variable medida.

Nest placement resulting in thermal advantage has been described for several avian species (e.g., Calder 1973, Petersen and Best 1985). Birds have been found to place their nests on a specific side of a tree (Balda and Bateman 1973) or within a particular arrangement of leaf canopy (Walsberg 1981). Nest placement can provide thermal benefits to developing nestlings (Webb and King 1983) or incubating females (Austin 1974, Walsberg and King 1978).

Research on the thermal environment and nest selection in cavity-nesting birds has centered on detailed analyses of brood and incubation heat fluxes (Mertens 1977, 1980) or entrance orientation (Balgooyen 1990, Conner 1975, Inouye 1976, Inouye et al. 1981). A warmer site has been shown to reduce interruptions in egg laying (Yom-Tov and Wright 1993), decrease the energetic costs of incubation (Haftorn and Reinertsen 1985), and allow the incubating female longer off-nest foraging bouts (Haftorn 1988). Few studies have specifically addressed variation in the thermal environment around cavity nest-sites (e.g., McComb and Noble 1981) and its effect on nest-site selection and reproductive success. The thermal environment of the nest-site should be important to cavity-nesting birds in systems where thermal stress influences reproductive success.

I investigated selection of nest boxes and nest success by Mountain Chickadees (*Parus gambeli*) in south-central Wyoming to test if cavity-nesting birds actively select warmer nest sites in a cold environment and to determine if any reproductive benefits exist at warmer nest sites. Specifically, I predicted that Mountain Chickadees would select nest sites with higher air and substrate temperatures, lower wind speeds, and higher solar radiation levels than unused sites. Among active nests, I predicted that successful sites would have higher air and substrate temperatures, lower wind speeds, and higher solar radiation levels than unused sites, whereas, unsuccessful sites would not differ from unused sites.

METHODS

Study area.—The study was conducted in the Medicine Bow National Forest in the Sierra Madre Mountains of south-central Wyoming (41°N, 107°W). The study area encompassed the Upper East Fork of the Encampment River (912 ha) and Coon Creek (1615 ha) watersheds, at an elevation of 2650–3100 m. Lodgepole pine (*Pinus contorta*) stands dominated the study area (58% by area) with Engelmann spruce (*Picea engelmannii*) and Subalpine fir (*Abies lasiocarpa*) stands predominating on north-facing slopes (38% by area). Meadows and rock outcrops covered the remaining 4%. During the peak nesting period of Mountain Chickadees in May and June, the overall mean, mean maximum, and mean minimum temperatures were 6.2 C, 22.8 C, and –8.9 C, respectively (U.S. Forest Service weather station data, 1984–1992).

Nest boxes.—The U.S. Forest Service placed 380 nest boxes in the study area during 1985, 73 of which were permanently removed from areas to be clearcut before the 1990 breeding season. The cement and sawdust nest boxes (25 cm × 15 cm, 25-mm entrance hole, removable front, Schwegler and Sons, Munich, Germany) were placed 2-m high on tree trunks. Boxes were placed in ten grids of 20 boxes each (50 m between boxes) and two grids of 90 boxes each (200 m between boxes, on transects separated by 400 m).

Microclimate sampling.—Microclimate data were collected from 12 Jun.–15 Jul. 1991 and 18 May–10 Jul. 1992. These dates corresponded to first egg laying and latest fledging for each year. I sampled 13 active nest boxes (100% of 1991 box use) and two natural cavities in 1991, and 47 active nest boxes (75% of 1992 box use) and six natural cavities in 1992. Chickadees were using the active sites at the time of sampling.

I quantified nest-site temperatures and wind speeds using a paired design, sampling at an active site and an unused site simultaneously over the same 24-h period. Instrumentation was moved to a different nest pair for the next 24-h period. Temperature and wind speed data were collected with 2–4 electronic dataloggers (Model CR10, Campbell Scientific, Inc., Logan, Utah). Measurements were made every second and averaged every 10 min. Nest pair categories were: active versus unused nest boxes ($n = 60$) and natural-cavity nests versus unused nest boxes ($n = 8$). At the conclusion of the breeding season, I subdivided the active group into

unsuccessful nests (no young fledged during the sampling year, $n = 18$) and successful nests (at least one young fledged during the sampling year, $n = 42$) to examine reproductive outcome. The reproductive outcome was typically not known at the time of sampling. The natural-cavity groups were not divided by reproductive outcome due to small sample size. Unused boxes were assumed to be available to the breeding pair. The breeding territory size of chickadees is highly variable (Smith 1991), but M. G. Raphael (pers. comm.) estimated an average breeding territory of 3 ha at the study area. Therefore, several nest boxes at the 50 m spacing and two nest boxes at the 200 m spacing could lie within a circular breeding territory.

Temperatures were measured with 24-gauge copper constantan thermocouples. Exterior air temperatures (T_{air}) were sampled from the shaded area 5 cm below the nest box. Substrate temperatures (T_{sub}) were collected during 1992 (total $n = 38$, successful $n = 27$, unsuccessful $n = 11$) at the surface of the tree bark at the nest box-tree interface.

Wind speeds were measured using Thornthwaite sensitive cup anemometers (Model 901, C. W. Thornthwaite Associates, Elmer, New Jersey) and heated bead thermistor anemometers (Bergen 1971). Anemometers were placed 1 m directly below the nest entrance to avoid disturbing the birds. Wind speeds within nest boxes were measured with a commercial heated bead thermistor anemometer (Model 1440, Kurz Instruments Inc., Monterey, California). The minimum sensitivity of all anemometers was $\leq 0.05 \text{ m sec}^{-1}$ and all were calibrated in a wind tunnel with a pitot tube.

Solar radiation was estimated at the nest boxes using hemispherical photographs. Nest boxes were temporarily removed (after the nesting season) and the lens oriented vertically at the precise location of the box with the top of the frame aligned to true north. The photographs were digitized and analyzed with the computer program Solarcalc (Chazdon and Field 1987). Solarcalc produced estimates for each nest-site photograph of percent canopy openness by quadrant (centered on compass bearings 45° , 135° , 225° , and 315°), total daily solar radiation, and total min d^{-1} of direct solar radiation. Radiation estimates were calculated from the solar track for 29 May (median Mountain Chickadee nest selection date) and the latitude and longitude of the study area. Solarcalc also produced estimates of instantaneous solar radiation for each 2-min period from sunrise to sunset.

Data analyses.—Data sets that deviated from a normal distribution (D'Agostino's normality test, $\alpha = 0.05$, Zar 1984) were tested with appropriate nonparametric tests (e.g. Wilcoxon paired-sample tests). Power values were calculated for each variable. Hypothetical differences in means (between active and unused boxes) with potential biological significance were used for power calculations rather than actual mean differences from the data. Standard deviations in the range of actual data were used to estimate power.

The temporal variability of temperature and wind speed was much greater between 24-h sampling periods than the variability between a sin-

TABLE 1. Summary means (and SD) of T_{air} , wind speed, and solar radiation from 60 Mountain Chickadee nests and T_{sub} from 38 nests. Data were tested with paired t -tests in successful versus unused box pairs ($n = 42$; $T_{\text{sub}} n = 27$), unsuccessful versus unused box pairs ($n = 18$, $T_{\text{sub}} n = 11$), and active natural cavity versus unused box pairs ($n = 8$; $T_{\text{sub}} n = 6$).

	Successful boxes	Unused boxes	Unsuc- cessful boxes	Unused boxes	Active cavities	Unused boxes
T_{air} (°C)	7.63*** (4.37)	7.13 (3.91)	5.86 (3.70)	6.02 (3.89)	9.05* (3.24)	8.42 (3.12)
T_{sub} (°C)	7.48* (3.70)	7.18 (3.35)	6.29 (3.15)	6.02 (3.85)	8.42 (2.71)	7.71 (2.63)
Wind speed (m s ⁻¹)	0.28 (0.15)	0.25 (0.11)	0.31 (0.16)	0.28 (0.12)	0.28 (0.15)	0.30 (0.16)
Total daily radiation (W m ⁻²)	91.5* (26.6)	78.0 (21.2)	92.3 (31.1)	81.9 (24.2)	122.3 (56.9)	85.7 (65.9)
Total minuses direct radiation (min d ⁻¹)	297* (86.2)	252 (82.2)	292 (95.3)	248 (65.9)	355 (138.8)	284 (49.1)

a * = $P < 0.05$, ** = $P < 0.005$.

gle nest pair within one 24-h sampling period. All 24-h data sets from one member of a nest pair were highly correlated to the same variable at the other member of a nest pair during the same 24 hours (correlation coefficients > 0.90). Therefore, I tested temperature and wind speed data with paired t -tests. A single pair consisted of a mean from an entire 24-h sample at an active site versus the mean from the same 24-h sample at its unused site.

Individual 24-h temperature and wind speed data sets (one data point = 10-min mean) were tested pairwise to determine if a few nest pairs disproportionately influenced the above analyses (Wilcoxon paired-sample tests, successful vs. unused pairs $\alpha = 0.05/42 = 0.001$, unsuccessful vs. unused pairs $\alpha = 0.05/18 = 0.003$, overall $\alpha = 0.05$).

Solar radiation and canopy openness data were tested with two-sample t -tests rather than paired t -tests because the variables measured were not highly correlated (correlation coefficients < 0.30) between nest pairs and did not vary temporally in the manner of wind speed and temperature.

RESULTS

Temperature and wind speed.—Successful boxes had higher mean T_{air} than their paired unused boxes ($n = 42$, $t = 3.11$, $P = 0.003$; Table 1). Mean T_{sub} was also higher at successful sites ($n = 27$, $t = 2.71$, $P = 0.013$; Table 1). Wind speed did not differ between successful and unused boxes ($P = 0.149$; Table 1). Unsuccessful boxes showed no significant differences from unused boxes for T_{air} , T_{sub} , and wind speed ($P = 0.361$, $P = 0.466$, $P = 0.506$, respectively; Table 1). The number of nests with higher T_{air} , T_{sub} , and wind speed (Table 2) indicates the above analyses are influenced by a large number of nests, rather than a disproportionate few.

TABLE 2. Frequency of individual nest sites with statistically higher T_{air} , T_{sub} , or wind speed means. Twenty-four hour data sets of each variable were tested (Wilcoxon paired-sample tests, overall $\alpha = 0.05$, individual $\alpha = 0.05/n$) in successful versus unused box pairs ($n = 42$; $T_{\text{sub}} n = 27$), unsuccessful versus unused box pairs ($n = 18$; $T_{\text{sub}} n = 11$), and active natural cavity versus unused box pairs ($n = 8$; $T_{\text{sub}} n = 6$).

	T_{air}	T_{sub}	Wind speed
Successful boxes	31	17	13
Unused boxes	6	6	19
Equal	5	4	20
Unsuccessful boxes	7	5	2
Unused boxes	6	3	9
Equal	5	3	7
Active cavities	6	4	3
Unused boxes	1	1	2
Equal	1	3	3

The power ($1 - \beta$) to detect a 0.5 C difference between successful and unused boxes was 0.16 for T_{air} and 0.13 for T_{sub} , and between unsuccessful and unused boxes was 0.11 for T_{air} and 0.09 for T_{sub} . The power to detect a 0.10 m s⁻¹ difference in wind speed was 0.91 between successful and unused boxes and 0.62 between unsuccessful and unused boxes.

Canopy density.—The canopies above successful nest boxes were more open in the southeast quadrant ($t = 2.23$, $P = 0.029$) and less open in the northwest quadrant ($t = 2.07$, $P = 0.043$) than those above unused boxes (Table 3). Canopy openness did not differ between unsuccessful and unused boxes in any of the quadrants ($P > 0.05$, Table 3). The power to detect a 10% difference in canopy density was 0.91 between successful and unused boxes and 0.62 between unsuccessful and unused boxes.

Solar radiation.—Successful nest boxes had higher daily total solar radiation ($t = 2.30$, $P = 0.025$) and a greater number of min d⁻¹ of direct

TABLE 3. Mean (and SD) percent canopy openness by quadrant. Data were tested with t -tests in successful versus unused box pairs ($n = 42$), unsuccessful versus unused nest box pairs ($n = 18$), and active natural cavity versus unused box pairs ($n = 8$).

Quadrant	Successful boxes	Unused boxes	Unsuccessful boxes	Unused boxes	Active cavities	Unused boxes
NW	29.2 (14.5)	37.1* ^a (15.4)	30.8 (13.6)	35.7 (17.7)	26.6 (18.3)	29.4 (12.9)
SW	29.1 (13.0)	23.6 (9.7)	31.0 (11.5)	28.1 (9.4)	39.4 (17.0)	26.6 (15.8)
SE	30.3* (17.2)	21.1 (13.7)	27.3 (18.6)	19.8 (15.6)	41.2 (22.2)	21.5 (14.2)
NE	32.1 (18.0)	31.4 (18.5)	34.2 (16.8)	29.7 (21.0)	36.6 (15.3)	30.1 (18.9)

^a * = $P < 0.05$.

radiation ($t = 2.08$, $P = 0.042$) than unused boxes (Table 1). Neither radiation variable differed between unsuccessful and unused boxes ($P > 0.05$, Table 1). The hourly mean of instantaneous solar radiation was higher at successful nests ($\bar{x} = 435.3 \text{ W m}^{-2}$, $\text{SD} = 323.3$) than their unused pairs ($\bar{x} = 261.9 \text{ W m}^{-2}$, $\text{SD} = 264.6$) only during 0800–0859 h ($t = 2.24$, $P = 0.029$). Hourly means from all other hours (0600–1800) did not differ between successful and unused boxes ($P > 0.05$). No hourly means differed between unsuccessful and unused boxes ($P > 0.05$). The power to detect a 15 W m^{-2} difference in total solar radiation was 0.86 between successful and unused boxes and 0.55 between unsuccessful and unused boxes. The power to detect a 50 min d^{-1} difference in direct solar radiation was 0.81 between successful and unused boxes and 0.50 between unsuccessful and unused boxes.

Natural cavity nests.—Mean T_{air} was higher at active cavities ($n = 8$, $t = 2.57$, $P = 0.037$) than at unused boxes (Table 1). No significant differences were detected in T_{sub} and wind speed means between active cavity nests and unused boxes ($P > 0.05$, Table 1). The number of nest sites with higher T_{air} , T_{sub} , and wind speed means from individual active cavity and unused box pairs was similar to unused and used nest box frequencies (Table 2). No difference was detected between natural cavities and unused boxes for total daily radiation, daily minutes of direct radiation, or canopy openness by quadrant ($P > 0.05$, Tables 1 and 3). The power to detect differences between cavities and unused boxes of 0.5 C in T_{air} and T_{sub} , 0.10 m s^{-1} in wind speed, 10% in canopy density, 15 W m^{-2} in total solar radiation, and 50 min d^{-1} were 0.08, 0.07, 0.59, 0.17, 0.30, and 0.27, respectively.

DISCUSSION

Mountain Chickadees were more successful at nest boxes within a warmer environment. T_{air} reflects the cumulative effects of many thermal influences, such as weather events; short-wave solar radiation; long-wave radiation from sky, vegetation, and ground; evaporation; and convective heat transfer. T_{sub} is related to the long-wave radiative environment surrounding nest boxes. Greater daily solar radiation at successful sites was presumably the driving force behind higher T_{air} and T_{sub} .

Amelioration of convective cooling has been found to be an important benefit of nest-site selection in open cup nesting species (Webb and King 1983). It appears, however, that wind is not important to Mountain Chickadee nest success. Wind direction under the canopy was highly variable; it may have been difficult to select a nest box that would consistently provide shelter from any wind direction. Wind speeds inside the boxes (sampled during the same period as exterior thermal parameters) never exceeded 0.05 m s^{-1} , the minimum instrument sensitivity (unpubl. data). Similarly, Mayer et al. (1982) found no forced convection in Carolina Chickadee roost cavities. Therefore, convection would have its greatest effect by altering the surface temperature of the cavity, rather than directly exchanging heat from the interior.

Solar radiation analyses suggest that Mountain Chickadees select nests for specific thermal benefits. Increased solar radiation may be a major benefit of the open sites (Dahlsten et al. 1992) and sparse canopy (Brennan 1989) that characterize Mountain Chickadee nests. Early morning is a critical time period for nesting Mountain Chickadees because parents and young have fasted for several hours and T_{air} is near its daily minimum. Brennan (pers. comm.) found that Mountain Chickadees in the Sierra Nevada left the nest at first light to forage and bring food to nestlings. Selecting nest sites to maximize direct solar radiation at 0800 h would quickly warm the nest without risks that may be associated with greater day-long canopy openness. The greater canopy openness in the southeast quadrant at successful boxes presumably resulted in higher early morning solar radiation. The reduced canopy openness in the northwest quadrant may have provided some protection from rain and snow storms, which were typically accompanied by west to northwest winds (pers. obs.). Chickadees may select sites with some vegetation cover for protection from precipitation, predation, or nocturnal heat loss.

Brennan (1989) found that Mountain Chickadees seldom used west-facing boxes. However, I detected no differences in entrance orientation for either selection or success of the nest box (unpubl. data). The thermal quality of a nest box would not necessarily be correlated to the entrance orientation. The relationship of the canopy over the nest site to the thermal environment should be more important to nest success than entrance orientation alone. If nest boxes are to be placed to improve nesting success for Mountain Chickadees, care should be taken to place them in suitable thermal environments, which may include sufficient early morning solar radiation. Clearing obstructions, for example, that would shade the box from early morning sun should result in greater nesting success than simply orienting the entrance to a particular compass bearing.

The similar microclimates of unsuccessful and unused boxes further indicates that warm nest sites may be important to reproductive success. Pre-nesting investigations of nest-site suitability by breeding pairs would not be expected to be absolutely accurate (i.e., birds sometimes make poor nest selections which result in decreased nest success). Sixteen of 18 unsuccessful boxes were abandoned (1 nest predation and 1 nest lost to wind throw of the box tree), suggesting that Mountain Chickadees may abandon nests that do not prove to be thermally suitable. The precise causes of nest abandonments were not usually known, however, because only the presence of dead nestlings or unhatched eggs indicated abandonment. Factors other than the thermal environment (e.g., adult death, poor food availability, etc.) could also have been responsible for abandonments.

T_{air} analysis of natural cavities versus unused boxes provides marginal evidence that the thermal microclimates and the patterns of nest selection (relative to the thermal environment) are similar between natural cavities and nest boxes.

The relationship between warmer nest sites and nest success in this

population of Mountain Chickadees may be the result of several mechanisms. Warmer nest environments may decrease incubation costs to the female (Haftorn and Reinertsen 1985). Reduced incubation costs may exist but are not large. Haftorn and Reinertsen's (1985) incubation energy cost equation predicts only a 3% energy savings at successful versus unused boxes. A more important influence of a warm site may be to allow the female longer foraging bouts off the nest without severely reducing egg temperatures (Haftorn 1988) or increasing heat loss from nestlings. Female Black-capped Chickadees (*Parus atricapillus*) brood extensively until about 12 d post-hatching; males do most of the feeding of the young and the females during this time. Females gradually increase their feeding of the young as brooding time decreases (Odum 1941). Similar patterns were reported for Carolina Chickadees (*Parus carolinensis*, Brewer 1961). Female Mountain Chickadees often brooded young nestlings during the day at the study area. Warmer nest sites should allow the female to spend more time feeding, rather than brooding, young. Higher prey delivery rates should increase nestling survival (Hussel and Quinney 1987).

Selection of thermally favorable nest sites has potential importance to Mountain Chickadee distribution. The birds may be able to enhance reproductive success at the upper altitudinal and latitudinal fringes of their range by selecting warm nest sites, enabling use of a breeding habitat that might be otherwise unproductive. Warmer nest sites could allow successful breeding by taking advantage of earlier nesting seasons, protecting against inclement weather events, and reducing nest failures due to thermal stress on developing nestlings. Together with other energy conservation strategies such as the selection of thermally favorable foraging or roosting sites, nest selection based on thermal parameters may be an important component influencing the distribution and abundance of Mountain Chickadees.

ACKNOWLEDGMENTS

This research was funded by the George E. Menkins Memorial Scholarship, was conducted as a part of a graduate program in the Department of Zoology & Physiology at the University of Wyoming. I thank L. Ruggiero of the U.S. Forest Service Rocky Mountain Forest and Range Experiment Station for logistical support and access to the nest box study area. I thank D. R. Webb for the concept of the study, technical advice, and equipment. I gratefully acknowledge G. Brown, R. Frakes, J. Harvey, W. Hastings, S. Henry, E. Kainer, D. LaVilla, and M. Miller for assistance with field work, and J. Zuver for assistance with hemispherical photograph analyses. I appreciate the critique of early drafts of this manuscript by S. Anderson, K. Parker, J. Loworn, H. Harlow, W. Smith, D. R. Webb, and L. Ruggiero.

LITERATURE CITED

- AUSTIN, G. T. 1974. Nesting success of the Cactus Wren in relation to nest orientation. *Condor* 76:216-217.
- BALDA, R. P., AND G. BATEMAN. 1973. The breeding biology of the Pinon Jay. *Living Bird* 11:5-42.
- BALGOOYEN, T. G. 1990. Orientation of American Kestrel nest cavities revisited. *J. Raptor Res.* 24:27-28.

- BERGEN, J. D. 1971. An inexpensive heated thermistor anemometer. *Agr. Meteorol.* 8:395-405.
- BRENNAN, L. A. 1989. Comparative use of forest resources by chestnut-backed and mountain chickadees in the western Sierra Nevada. Ph.D. thesis. Univ. California, Berkeley, California.
- BREWER, R. 1961. Comparative notes on the life history of the Carolina Chickadee. *Wilson Bull.* 77:388-395.
- CALDER, W. 1973. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. *Ecology* 54:127-134.
- CHAZDON, R. L., AND C. B. FIELD. 1987. Photographic estimation of photosynthetically active radiation: evaluation of a computerized technique. *Oecologia* 73:525-532.
- CONNOR, R. N. 1975. Orientation of entrances to woodpecker nest cavities. *Auk* 92:381-374.
- DAHLSTEN, D. L., W. A. COPPER, D. L. ROWNEY, AND P. K. KLEINTJES. 1992. Population dynamics of the mountain chickadee in northern California. Pp. 502-511, in D. R. McCullough and R. H. Barrett, eds. *Wildlife 2001: Populations*. Elsevier Applied Science, New York, New York.
- HAFTORN, S. 1988. Incubating female passerines do not let the egg temperature fall below the physiological zero temperature during their absences from the nest. *Ornis Scand.* 19:97-110.
- , AND R. E. REINERTSEN. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living Blue Tit (*Parus caeruleus*). *Auk* 102:470-478.
- HUSSEL, D. J., AND T. E. QUINNEY. 1987. Food abundance and clutch size of Tree Swallows (*Tachycineta bicolor*). *Ibis* 129:243-258.
- INOUE, D. W. 1976. Nonrandom orientation of entrance holes to woodpecker nests in aspen trees. *Condor* 78:101-102.
- INOUE, R. S., N. J. HUNTLEY, AND D. W. INOUE. 1981. Non-random orientation of Gila Woodpecker nest entrances in saguaro cacti. *Condor* 83:88-89.
- MAYER, L., S. LUSTICK, AND B. BATTERSBY. 1982. The importance of cavity roosting and hypothermia to the energy balance of the winter acclimatized carolina chickadees. *Int. Biometeor.* 26:231-238.
- MCCOMB, W. C., AND R. E. NOBLE. 1981. Microclimates of nest boxes and natural cavities in bottomland hardwoods. *J. Wildl. Manage.* 45:93-101.
- MERTENS, J. A. 1977. Thermal conditions for successful breeding in great tits. II. Thermal properties of nests and nest boxes and their implications for the range of temperature tolerance of great tit broods. *Oecologia* 28:31-56.
- . 1980. The energy requirements for incubation in Great Tits and other bird species. *Ardea* 68:185-192.
- ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee. *Auk* 58:518-534.
- PETERSEN, P. L., AND L. B. BEST. 1985. Nest-site selection by Sage Sparrows. *Condor* 87:217-221.
- SMITH, S. M. 1991. The black-capped chickadee: behavioral ecology and natural history. Cornell University Press, Ithaca, New York. 362 pp.
- WALSBERG, G. E. 1981. Nest-site selection and the radiative environment of the Warbling Vireo. *Condor* 83:86-88.
- , AND J. R. KING. 1978. The heat budget of incubating mountain white-crowned sparrows. *Physiol. Zool.* 51:147-153.
- WEBB, D. R., AND J. KING. 1983. An analysis of the heat budgets of the eggs and nest of the white-crowned sparrow in relation to parental attentiveness. *Physiol. Zool.* 56:493-505.
- YOM-TOV, Y., AND J. WRIGHT. 1993. Effect of heating nest boxes on egg laying in the Blue Tit (*Parus caeruleus*). *Auk* 110:95-99.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey. 718 pp.

Received 9 Oct. 1995; accepted 1 Dec. 1995.