ENERGETIC BENEFITS OF COMMUNAL ROOSTING BY ACORN WOODPECKERS DURING THE NONBREEDING SEASON[1]

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Abstract. We examined the thermal consequences, energy benefits and patterns of night-time communal roosting in Acorn Woodpeckers (*Melanerpes formicivorus*) during the non-breeding season, the period when they are most reliant on nutrient-poor acorn stores. Because the oak limbs (*Quercus*) in which Acorn Woodpeckers excavate roost cavities cool more slowly than the surrounding air, the nighttime temperature inside unoccupied woodpecker roost cavities averaged 4.3°C higher than the outside ambient temperature, when the latter was approximately 0°C. The temperature of occupied roosts was further augmented in proportion to the number of birds sharing the roost. A single woodpecker increased the cavity temperature an additional 1.2°C, whereas four birds increased it an additional 6.0°C. Acorn Woodpeckers did not huddle together at low air temperatures when placed in a simulated roost-cavity metabolism chamber. Consequently their nighttime, fasted oxygen consumption was independent of group size (one, two, or four birds) and was described by the relation: ml O_2/(g hr) = 3.33–0.055 T_a. From this relation and our cavity temperature measurements, we estimate that at an outside temperature of 0°C a single cavity-roosting woodpecker would reduce its heat loss by at least 9%, whereas four birds would reduce their heat loss by at least 17%, and even more in the presence of wind. This energy savings may contribute to the higher winter survival noted for male Acorn Woodpeckers that live in larger groups.

Key words: Melanerpes formicivorus; communal roosting; energy metabolism; survivorship; microclimate.

INTRODUCTION

For many temperate zone birds, winter is a period of potential energy stress due to low temperatures combined with limited food supplies and foraging time. Winter may be an especially challenging time for Acorn Woodpeckers (*Melanerpes formicivorus*), because at that time of year they feed extensively on stored acorns (their diet consisting of 94% acorns in November, Beal 1911) which may contain appreciable amounts of tannins (Koenig and Heck 1988). Koenig (1991) demonstrated that high tannin levels reduce protein availability to woodpeckers and thus diminish the nutritive value of their primary

winter food. Nevertheless, acorn stores appear to be critically important to overwinter survival and reproductive success in this species throughout its range (Stacey and Koenig 1984, Koenig and Mumme 1987), and are postulated to be an important constraint leading to the evolution of its cooperative breeding behavior. The coincidence of this species' subsistence on a largely nutrient-poor diet with inclement winter conditions sets the stage for adaptations enabling Acorn Woodpeckers to maintain a positive energy balance.

Acorn Woodpeckers are cooperative breeders that live in family groups of up to 15 adults, all of which collaborate in rearing young at a single nest (Koenig and Mumme 1987). On most nights of the year, two or more individuals roost communally in the same cavity (mean ± SD roosting

group size = 2.8 ± 1.7, n = 216 groups; Koenig, unpubl. observ.). Cavity roosting provides a thermal benefit by shielding birds from wind and by exposing them to higher temperatures than they would encounter outside the cavity. Communal roosting could further enhance the benefit of cavity use by warming individuals directly through contact with conspecifics and by enhanced warming of the cavity space (Walsberg 1990). Green Woodhoopoes (*Phoeniculus purpureus*) reduce their energy expenditure by almost 31% at 5°C by sharing a communal roost with four conspecifics, and this advantage translates into increased overwinter survival of adults in larger groups (du Plessis and Williams 1994). In this study, we examine the thermal consequences and energy benefits of communal roosting in Acorn Woodpeckers and provide data on how these relate to adult survivorship and group size.

METHODS

We captured a group of five Acorn Woodpeckers (four males, one female) near Hastings Natural History Reservation (a 900-ha reserve in upper Carmel Valley, Monterey County, California) during June 1990 and maintained them in a 5 × 4 × 2.5 m outdoor flight aviary on an *ad libitum* diet of kibble-type dog food and water until we began collecting cavity-roosting data in March 1991. The birds were part of a color-marked population that has been under continuous investigation since 1971 at Hastings Reservation (MacRoberts and MacRoberts 1976, Koenig and Mumme 1987). For a description of the reserve, its plant communities and climate, see Koenig and Mumme (1987).

Assessment of roost-cavity temperature. To ascertain how roost-cavity temperature varies with the number of woodpeckers sharing the cavity, we provided the aviary-housed birds with three identical logs which they excavated. We placed two 0.8 mm diameter copper-constantan thermocouples in each cavity; one near the top, the other near the bottom. The thermocouples were centered in 1 cm diameter plastic mesh tubes which prevented them from touching the birds, and insured accurate measurements of cavity temperature. Two additional thermocouples were placed outside two of the cavities to monitor ambient temperature. Thermocouple temperatures were monitored at 10-sec intervals with a

Campbell Scientific datalogger (model 21X) and averaged at 5-min intervals throughout 24 one-day periods during March and April, two of the coldest months at Hastings Reservation. The duplicate temperature readings inside and outside the cavity were averaged to provide a single temperature for the two sites.

We determined the degree to which roosting birds warmed their cavity by comparing the temperature of an unoccupied roost cavity (control) with that of occupied cavities, after taking differences in the cavities' thermal properties into account. The three cavities that the woodpeckers created in the aviary logs were similar, but their *in situ* temperatures when no birds were present were not identical. At outside air temperatures between about 0 and 7°C, temperatures within the two most similar cavities, when unoccupied, differed by an average (±SD) of −0.15 ± 0.22°C (n = 363) (range, −0.46 to 0.31°C). This difference, although small, is statistically highly significant (paired t = −13.4, P < 0.001). To compensate for the three cavities' differing thermal characteristics, we designated one cavity the control (always unoccupied) and derived empirical relations that related its temperature and that of the two experimental cavities. Coefficients of determination (least squares regression) for experimental cavity temperature versus control cavity temperature exceeded 0.99 for data from four nights during which all three cavities were unoccupied (n = 363 simultaneous measurements of each cavity). Thus by monitoring the temperature of the unoccupied (control) roost cavity, we were able to distinguish delayed cooling of the occupied cavities (due to the wood's thermal inertia) from heating attributable to the roosting birds' metabolism.

We manipulated the number of birds roosting in the same cavity by moving them after dark to a pre-selected cavity. A 1-cm mesh screen was placed firmly over the cavity entrance to prevent the birds from escaping. The birds soon settled down after these transferals as evidenced by both the lack of sounds coming from the cavities and by inspection of the cavity-temperature data. Roost-group sizes were set at either one or four birds.

Oxygen consumption measurements. All metabolic determinations were made at the University of California, Davis, where four of the above birds were housed in two 1.5-m³ welded-wire cages on an artificial 12-hr daylight cycle (06:00–

18:00 hr). Between metabolic determinations, the birds were exposed to a mean T_a of 22.3°C (range, 22.1–22.3°C), a mean relative humidity of 50.6% (range, 48.7–51.5%) and were fed a combination of dog food pellets and meal worms. Metabolic measurements began only after the birds had lived under these conditions for four days, by which time all birds' masses remained nearly constant. Rates of oxygen consumption ($\dot{V}O_2$) were determined for post-absorptive birds at night (22:00–05:00 hr) by standard flow-through respirometry methods. In brief, dry CO_2-free air passed through a rotometer (calibrated with a bubble meter, Levy 1964) and then into the metabolism chamber. Flow rate was maintained at about 0.5 liter/min for single birds, 0.8 liter/min for pairs, and 1.8 liter/min for groups of four. The fractional concentration of O_2 in inlet and outlet chamber air (both dry and CO_2-free) was determined with an Applied Electrochemistry S3-A oxygen analyzer and $\dot{V}O_2$ was calculated by Eq. (2) of Hill (1974). We monitored metabolism chamber temperature with a shielded 0.8 mm diameter copper-constantan thermocouple connected to a Bailey/Sensortek model BAT-12 thermocouple thermometer. Thermocouple calibration was against a mercury thermometer traceable to the National Bureau of Standards. We corrected $\dot{V}O_2$ to STPD and calculated rates of metabolic heat production assuming 20.1 kJ of heat were produced per liter of O_2 consumed by the fasted birds. The oxygen analyzer was calibrated to within 0.005% O_2 using certified gas standards (±10 ppm). The analyzer response was linear over the range 0–21% O_2. The measurement error in $\dot{V}O_2$ was <5%, based on imprecisions in flow measurement and fractional concentration of O_2.

The metabolic chambers were fabricated from ca. 4-liter metal paint cans that were lined with a layer of 0.8-cm cardboard into which numerous holes had been punched and onto which the birds could (and did) cling vertically. Inner dimensions of metabolic chambers were designed to simulate the dimensions of cavities used under natural conditions (10.5 cm, $n = 18$ cavities; du Plessis, unpubl. data). Metabolism chamber temperature was controlled (±0.2°C) during $\dot{V}O_2$ measurements by placing the chamber within a temperature-controlled cabinet. Metabolism measurements lasted from 2–4 hr.

Body temperature. We measured deep core temperature (T_b) of all individuals immediately after removing them from the metabolic cham-

bers with a 0.2 mm diameter, teflon-coated thermocouple inserted into the cloaca. The thermocouple was lubricated with petroleum jelly prior to insertion. We recorded T_b when readings had stabilized and when removal of the thermocouple by 2–3 mm produced no change in measured T_b.

RESULTS

Temperatures of roost cavities. The nightly decline in air temperature within unoccupied cavities lagged behind the fall in outside T_a owing to the cavity's thermal inertia. As a consequence, nighttime temperature inside unoccupied cavities averaged between 2.7 and 5.6°C higher than the mean outside ambient temperature when the latter was between −2.0 and 7.1°C. There was an insignificant tendency for the temperature differential inside unoccupied cavities to increase as ambient temperature decreased ($n = 17$ nights; $r^2 = 0.012$). The temperature of cavities containing four roosting birds was significantly higher than that of cavities containing only one bird (Wilcoxon signed-rank test: $Z = 2.52$; $n = 8$ pairs; $P < 0.05$). Birds roosting singly raised their cavity temperatures on average by 1.2°C at mean control temperatures ranging from 1.0 to 5.0°C. Over the same range of ambient temperatures, four communally-roosting birds raised cavity temperature on average by 6.0°C over control levels.

Oxygen consumption versus group size. Between −2.5 and 26°C, $\dot{V}O_2$ was a linear function of ambient temperature for single birds and for groups of either two or four birds. Least squares regression equations of $\dot{V}O_2$ versus T_a for individual woodpeckers and groups of either two or four woodpeckers were compared by analysis of covariance (SAS Institute 1985, Snedecor and Cochran 1980). Finding no differences between slopes or elevations for any of the regressions, we pooled data and calculated the common regression equation (Fig. 1) as

$$\dot{V}O_2 \text{ (ml } O_2/\text{g hr)} = 3.33 - 0.055T_a \quad (1)$$
$$(r^2 = 0.701, s_{yx} = 0.323, s_b = 0.007, n = 29)$$

Body temperature. Body temperature of roosting individuals at a variety of ambient temperatures varied between 38.0 and 41.0°C, irrespective of the number of birds roosting together.
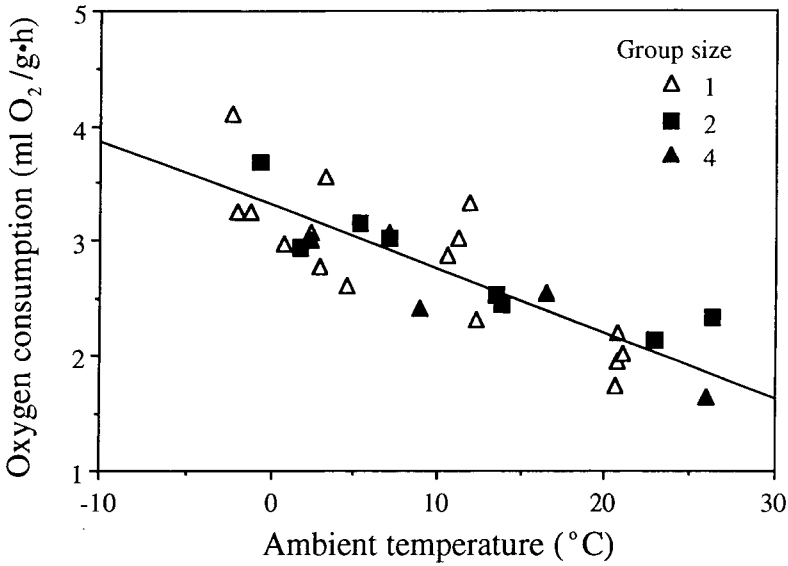
FIGURE 1. Relationship between the temperature inside a simulated roost-cavity metabolism chamber and the oxygen consumption of individuals roosting on their own, in pairs and in groups of four.

DISCUSSION

Many vertebrates seek more favorable micro-environments when exposed to adverse environmental circumstances (Kelty and Lustick 1977), and nighttime communal cavity roosting, one version of microhabitat selection, has been described in many bird and mammal species (e.g., White et al. 1978; Pitts 1976; see also Walsberg 1985, 1990). Communal roosting can potentially ameliorate the thermal environment in three ways: (1) by warming the roosting cavity, (2) by providing shelter from wind, and (3) by physical contact between individuals (i.e., huddling). Although the last two factors are difficult to separate and have usually been considered as operating jointly (see du Plessis and Williams 1994), our data allow us to evaluate the significance of each of these factors separately for the Acorn Woodpecker.

Temperature effects. Woodpeckers that roost in cavities at night encounter higher air temperatures than those existing outside the cavity for two reasons. First, the cavity's thermal inertia insures that the cavity cools more slowly than the outside air, and second, the woodpecker's body heat raises the cavity temperature. Although both factors are important, the number of woodpeckers sharing the cavity determines which is pre-

dominant. The temperature inside unoccupied woodpecker cavities averaged 4.3°C higher than outside ambient temperature when the latter was 0°C (Table 1). The temperature of cavities containing a single woodpecker averaged 5.5°C whereas that of cavities with four woodpeckers averaged 10.3°C. Subtracting the temperature of the unoccupied (control) cavity from these values reveals that a single bird increased the cavity temperature by 1.2°C, whereas four birds produced a 6.0°C increase in temperature (Table 1).

The energy saving attributable to the above increases in cavity temperature can be calculated from Eq. (1). The 4.3°C increase in temperature attributable to thermal inertia would result in a 7.1% reduction in energy expenditure. A similar savings was reported for Green Woodhoopoes using roost cavities in South Africa (du Plessis and Williams 1994). Because the thermal properties of cavities vary widely (du Plessis and Williams 1994; P. N. Hooge and M. T. Stanback, unpubl. data), the attendant energy savings to other cavity-roosting birds may be higher or lower than those observed in woodpeckers and woodhoopoes.

Calculating the net energy savings attributable to the cumulative effect of body heat and thermal inertia reveals that individuals that roosted with

three conspecifics saved nearly twice as much energy as birds that roosted alone (Table 1), at least under the conditions prevailing during our study.

Wind effects. Cavity roosting also provides a thermal benefit by reducing convective heat loss. The magnitude of the benefit depends upon the wind speed and temperature prevailing outside the cavity. We can illustrate the potential savings by calculating the standard operative temperature (T_{es}) that woodpeckers would experience outside cavities at various wind speeds and calculate their associated heat production by substituting T_{es} for T_a in Eq. (1). We estimate T_{es} from Bakken's (1990) equation: $T_{es} = T_b - (1 + 0.26\ u^{0.5})(T_b - T_e)$, where u is wind speed in m/sec. For our estimations we assume $T_b = 39°C$ and that nighttime operative temperature (T_e) equals T_a.

At an ambient temperature of 0°C, woodpeckers perched in the open would experience a T_{es} of -3.2 and $-7.2°C$, respectively, at wind speeds of 0.1 and 0.5 m/sec. From Eq. (1), an 80-g woodpecker roosting at 0°C and zero wind speed would have a resting energy expenditure of 5.35 kJ/hr. Thus *very modest* breezes of 0.1 and 0.5 m/sec would increase a woodpecker's rate of energy expenditure by 5.6% and 12.0%, respectively, to 5.64 kJ/hr and 5.99 kJ/hr. Stronger winds would result in even higher rates of heat loss and hence greater benefits from cavity roosting. For example, a 5 m/sec wind would increase heat loss by 38% to 7.36 kJ/hr. Thus by shielding birds from forced convection, cavities provide a substantial energy savings that is supplementary to, and may exceed, the savings attributable to cavity warming per se. The combined thermal benefit of convective shielding and higher temperatures would be even greater. For example, if air temperature and wind speed outside the cavity were 0°C and 5 m/sec, a woodpecker perched in the open would have a rate of energy expenditure 66% higher than one roosting in a cavity with three conspecifics (T_{es} outside cavity $= -22.8°C$, that inside $= 10.3°C$).

Huddling. Roosting Green Woodhoopoes that huddle together in groups of three or more birds expend less energy per unit body mass than do single birds (du Plessis and Williams 1994). In contrast, Acorn Woodpeckers, unlike many cooperative breeders, are not a 'contact' species and apparently do not huddle, as there was no significant difference between the oxygen con-

TABLE 1. Contribution of cavity thermal inertia versus bird's body heat to the temperature elevation (dT) within roost cavities and the estimated metabolic heat production and energy savings from the temperature elevation accruing to single woodpeckers vs. groups of four woodpeckers.

No. of birds	dT due to:		Effective T_c (°C)	Energy expenditure (kJ/h)[a]	Energy savings (%)[b]
	Inertia	Birds			
1	4.3	1.2	5.5	4.87	9.0
4	4.3	6.0	10.3	4.44	17.0

[a] Predicted for an 80-g woodpecker based on Eq. (1).
[b] As compared with an energy expenditure of 5.35 kJ/hr at 0°C.

sumption of birds roosting on their own as opposed to multiple birds roosting together, after accounting for the effects of cavity warming. Absence of huddling was confirmed by inspection through a Plexiglas window in the lid of one of the metabolic chambers.

The pattern of communal roosting and its fitness consequences. We examined two predictions that follow from the hypothesis that communal roosting entails significant energy savings leading to increased fitness. The first is that roosting aggregations of Acorn Woodpeckers should be larger in the winter than during other seasons, both because temperature is lower then and because woodpeckers rely heavily on a relatively low-quality diet at that time. The second is that woodpeckers living in larger groups should experience lower winter mortality than those living in smaller groups, as has been demonstrated in Green Woodhoopoes (du Plessis and Williams 1994).

We tested the first prediction by examining the absolute size of communal roosts and the proportion of a given group that roosted together using data from 216 roost observations collected between 1974 and 1992. The number of free-living Acorn Woodpeckers roosting in the same cavity did not vary seasonally (ANOVA $F_{3,209} = 1.31, P = 0.27$), even though winter roost-group sizes were fractionally, yet insignificantly, bigger than for other seasons combined (winter mean $\pm$ SD = 3.2 $\pm$ 2.1, $n = 48$; mean other seasons 2.6 $\pm$ 1.6, $n = 168$: Mann Whitney $U = 1.21, P = 0.23$). Additionally, neither the total number of birds, nor the proportion of the family group that roosted together, were correlated with minimum nighttime temperature (all $P > 0.2$). This suggests that woodpeckers do not alter their tendency to roost with conspecifics in anticipation
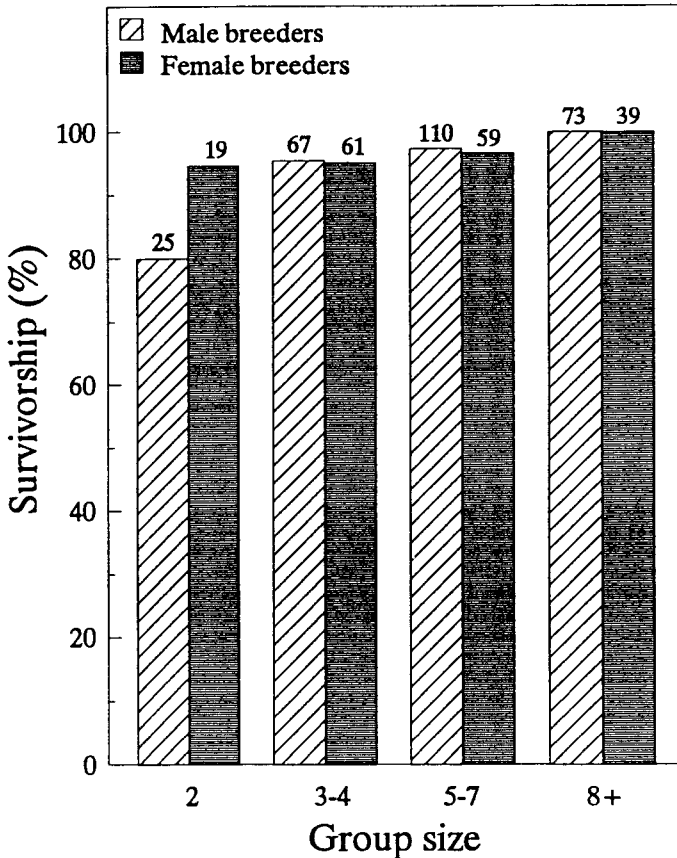
FIGURE 2.   Winter survival (Dec–Feb) of Acorn Woodpecker breeding males and females living in different-sized groups; sample sizes are indicated above each bar.

of cold nights, but rather that they respond to seasonally low nocturnal temperatures. However, we cannot rule out a direct thermal effect on nightly group size because we lack information on wind speed outside roosts over the 18-year period. As illustrated above, wind is as important as temperature in determining the heat loss from small birds.

We tested the prediction that birds living in larger groups should experience lower mortality by comparing the winter survivorship of breeding pairs with that of breeders living in larger groups. Winter survival of breeder males living in pairs was significantly lower than that of males living in larger groups (log-likelihood ratio $\chi^2 = 15.32$, 3 df, $P = 0.002$), but this was not the case for female breeders ($P = 0.35$) (Fig. 2). Although other factors are certainly important, this supports the hypothesis that the thermal benefits of

group living may contribute to higher survivorship, at least in males.

Overall, Acorn Woodpeckers mitigate the effects of subsisting on a nutrient-limited diet during the nonbreeding season both behaviorally and physiologically. First, large numbers of acorns are stored during fall specifically for use during periods when other food sources are either scarce or unavailable (MacRoberts and MacRoberts 1976). Second, adult field metabolic rates are 30% lower than predicted from adult mass (Weathers et al. 1990). Third, roosting in cavities provides an improved thermal environment, the benefits of which vary with weather conditions and cavity features. Fourth, roosting with conspecifics additionally ameliorates the effects of low temperatures when multiple bodies warm the cavity micro-environment. An 80-g woodpecker roosting in a cavity with three conspecifics

when T_a outside the cavity was 0°C would potentially expend 4.44 kJ/hr, compared to 5.35 kJ/hr if it slept alone outside a cavity—a cumulative energy saving of 17%. The savings would be even greater if there were any wind or if more individuals shared the cavity (up to 10 woodpeckers have been observed roosting together; W. D. Koenig, unpubl. data).

ACKNOWLEDGMENTS

LITERATURE CITED

BAKKEN, G. S. 1990. Estimating the effect of wind on avian metabolic rate with standard operative temperature. Auk 107:587–594.

BEAL, F.E.L. 1911. Food of the woodpeckers of the United States. U.S. Dept. Agric., Biol. Surv. Bull. No. 37.

DU PLESSIS, M. A., AND J. B. WILLIAMS. 1994. Communal cavity-roosting in cooperatively-breeding Green Woodhoopoes: consequences for energy expenditure and the seasonal pattern of mortality. Auk 111(2):292–299.

HILL, R. W. 1974. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. J. Appl. Physiol. 33:261–263.

KELTY, M. P., AND S. I. LUSTICK. 1977. Energetics of the Starling (Sturnus vulgaris) in a pine woods. Ecology 58:1181–1185.

KOENIG, W. D. 1991. The effects of tannins and lipids on digestion of acorns by Acorn Woodpeckers. Auk 108:79–88.

KOENIG, W. D., AND M. K. HECK. 1988. Ability of two species of oak woodland birds to subsist on acorns. Condor 90:705–708.

KOENIG, W. D., AND R. L. MUMME. 1987. Population ecology of the cooperatively-breeding Acorn Woodpecker. Princeton Univ. Press, Princeton, NJ.

LEVY, A. 1964. The accuracy of the bubble meter method for gas flow measurements. J. Sci. Instrumentation 41:449–453.

LIGON, J. D., AND S. H. LIGON. 1978. The communal social system of the Green Woodhoopoe in Kenya. Living Bird 17:159–197.

MACROBERTS, M. H., AND B. R. MACROBERTS. 1976. Social organization and behaviour of the Acorn Woodpecker in central coastal California. Ornithol. Monogr. 21. American Ornithologists' Union, Washington, DC.

PITTS, T. D. 1976. Fall and winter roosting habits of Carolina Chickadees. Wilson Bull. 88:603–610.

SAS INSTITUTE. 1985. SAS user's guide: statistics, version 5th ed. SAS Institute, Cary, NC.

SNEDECOR, G. W., AND W. G. COCHRAN. 1980. Statistical methods, 7th ed. Iowa State Univ. Press, Ames, IA.

STACEY, P. B., AND W. D. KOENIG. 1984. Cooperative breeding in the Acorn Woodpecker. Sci. Am. 251: 114–121.

WALSBERG, G. E. 1985. Physiological consequences of microhabitat selection, p. 389–413. In M. L. Cody [ed.], Habitat selection in birds. Academic Press, New York.

WALSBERG, G. E. 1990. Communal roosting in a very small bird: consequences for the thermal and respiratory gas environments. Condor 92:795–798.

WEATHERS, W. W., W. D. KOENIG, AND M. T. STANBACK. 1990. Breeding energetics and thermal ecology of the Acorn Woodpecker in central coastal California. Condor 92:341–359.

WHITE, F. N., G. A. BARTHOLOMEW, AND J. L. KINNEY. 1978. Physiological and ecological correlates of tunnel nesting in the European Bee-eater Merops apiaster. Physiol. Zool. 51:140–154.