

CAVITY ROOSTING, PHILOPATRY, AND COOPERATIVE BREEDING IN THE GREEN WOODHOPOE MAY REFLECT A PHYSIOLOGICAL TRAIT

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ABSTRACT.—Cooperative breeding in birds generally is related to a critical resource. A critical limiting factor for the Green Woodhoopoe (*Phoeniculus purpureus*) is the availability of roost cavities. Although predation at roost holes is the major source of mortality, woodhoopoes invariably roost in cavities or under loose bark. This dependence on cavities appears to be related to the birds' inability to cope physiologically with low nighttime temperatures. This is the first evidence to suggest that a physiological limitation has played a major role in the evolution of philopatry and possibly cooperative breeding in an avian species. Received 2 April 1987, accepted 8 October 1987.

THE prevalent view of the basis of cooperative breeding in birds is that it is related to some kind of resource (e.g. Brown 1974, Koenig and Pitelka 1981, Emlen 1982). In some cases the putative critical resource is territorial space (Woollfenden and Fitzpatrick 1984), while in others it may be costly self-constructed structures such as food storage sites (Stacey and Koenig 1984) or roost cavities excavated into living trees (Ligon 1970). Although the selective basis of the nondispersal element of avian cooperative breeding is unresolved (Stacey and Ligon 1987), the specific factors prohibiting dispersal or, alternatively, favoring group living vary from species to species, and nondispersal of young birds is a necessary precondition for the evolution of cooperative breeding.

We studied the behavior and ecology of the cooperatively breeding Green Woodhoopoe (*Phoeniculus purpureus*) near Lake Naivasha in the Rift Valley of Kenya (0°40'S, 36°23'E) for several years, 1975–1984, and found that for these birds tree cavities suitable for roosting are a critical limiting factor (J. D. Ligon and S. H. Ligon 1978, 1982, 1988). We followed several hundred birds to their roosts, usually to capture them for individual marking (386 woodhoopoes banded). Without exception, the woodhoopoes roosted under cover. They almost always entered a tree cavity and usually roosted in groups; as many as eight birds have been recorded in a single cavity (J. D. Ligon and S. H. Ligon 1982). If, during the day, the roost cavity was occupied by another species, e.g. honeybees (*Apis mellifera*; S. H. Ligon and J. D.

Ligon 1982), the returning woodhoopoes usually flew to a secondary cavity. In the absence of a backup roost hole, the birds crawled under loose bark to spend the night. There is no evidence that they ever roosted in the open. Moreover, because woodhoopoes do not excavate their own cavities and must compete for holes, often unsuccessfully, with numerous other cavity-dwelling animals (J. D. Ligon and S. H. Ligon 1982, 1988), high-quality (i.e. relatively predator-proof) roost sites are scarce. The severe interspecific competition for cavities (honeybees, rodents, other birds) means that safe cavities vary in number both spatially and temporally. Because of the frequent takeover of cavities by other species, a key element of territory quality is the number of potential backup or reserve roost sites.

Although the woodhoopoes thus require cavities in which to roost, this behavior appears to be costly because the holes used often are in weak wood not chosen by other species, and the birds are vulnerable to arboreal nocturnal mammalian predators, such as large-spotted genets (*Genetta tigrina*) and possibly cats (*Felis libyca* and *F. domesticus*; Ligon and Ligon 1978). Driver ants (tribe Dorylini) also capture adult woodhoopoes in their roost holes. Primarily as a result of nocturnal predation at roost sites, Green Woodhoopoes suffer annual mortality rates about twice as high as some other well-studied cooperatively breeding species, about 40% per year for males and 30% per year for females (Ligon 1981, 1983; Ligon and Ligon 1988).

TABLE 1. Metabolic rates and body temperatures of Green Woodhoopoes at different ambient temperatures (T_a).

	Male 1	Male 2	Fe- male
Body mass (g)	71.0	66.1	52.3
Daytime body temperature (°C) at T_a 27°C	42°	42°	40°
Metabolic rate (ml $O_2 \cdot g^{-1} \cdot h^{-1}$)			
At T_a 30.5°C	1.33	1.67	1.14
At T_a 27°C	1.35	1.40	1.09
At T_a 19°C ^a	1.92	2.54	1.31
Body temperature (°C) at T_a 19°C, at 2400	36°	35°	33°

^a Metabolic rates at 19°C were taken as the birds moved about. We were unable to obtain "resting" rates.

In view of the high risk of mortality associated with roosting in cavities, the obvious question is why woodhoopoes do not roost among the thorny branches and twigs of the acacia trees (*Acacia xanthophloea*) on the study site, as do most other small birds, including some other group-living species of similar mass such as two species of *Turdoides* babblers (pers. obs.) and the Grey-backed Fiscal Shrike (*Lanius excubitorius*; Zack 1986). The low, 7–10°C, nighttime temperatures characteristic of the study site at 1,860 m above sea level, together with the extreme agitation shown by woodhoopoes when denied access to their roosts at dusk, suggested they might be physiologically incapable of coping successfully with low nocturnal ambient temperatures (Ligon and Ligon 1978). To address this possibility, we investigated thermoregulatory responses of three captive Green Woodhoopoes to low nocturnal ambient temperatures.

METHODS

We borrowed 2 adult male Green Woodhoopoes from the Denver Zoo and 1 young female from the Rio Grande Zoo in Albuquerque, New Mexico. One of the males and the female had been hatched in captivity; the other male was captured from the wild.

Measurement of oxygen consumption ($\dot{V}O_2$) was conducted using 3.8-l metabolic chambers with blackened inner surfaces. Air temperatures within the chamber were measured with a copper-constantan thermocouple connected to a Soltex millivolt recorder. The birds were placed individually in the chambers at 1600. The chambers were then placed in a constant-temperature box, and the birds were allowed to adjust to conditions in the chamber at 30.5°C for 4

h. During this period dried air flowed continuously through the chamber at approximately 725 ml/min.

Measurement of $\dot{V}O_2$ was conducted in a manner similar to that described by Dawson and Carey (1976). Dry air was channeled through flow meters, into the metabolic chambers, through tubes containing Ascarite and Drierite for removal of CO_2 and water vapor, respectively, and then into a Beckman model 755 paramagnetic oxygen analyzer for analysis. The air from each chamber was sampled sequentially for 5 min, and room air was sampled once an hour. After steady values were obtained at the chamber air temperature of 30.5°C, the temperature of the constant-temperature box was lowered to 27°C, and finally to 19°C. The birds were exposed to 27°C and 19°C for at least 1 h after the temperature in the chamber had stabilized before measurements of $\dot{V}O_2$ were made. Two or three measurements were taken at 30.5°C and 27°C and averaged to represent the value for that individual at those temperatures.

Body temperatures were taken cloacally with a YSI telethermometer used in conjunction with a YSI small-animal probe.

RESULTS

Average oxygen consumption of the three birds at 30.5°C fell within 5% of the value predicted by the equation of Aschoff and Pohl (1970) for nonpasserine birds measured in the inactive phase of their daily cycle (Table 1). Although we did not measure $\dot{V}O_2$ at a wide enough variety of temperatures to describe a thermoneutral zone, the similarity between the predicted and measured values and information about typical lower critical temperatures in birds of similar body mass (Calder and King 1974) suggest that these birds were in what would be termed a thermally neutral condition. The $\dot{V}O_2$ of these birds remained relatively stable as ambient temperature was lowered to 27°C, but increased sharply when air temperature dropped to 19°C. Although the birds were totally inactive at 30.5° and 27°C, the elevated rates at 19°C were coincident with frantic hopping and fluttering movements of the bird against the sides and roof of the metabolic chambers. These movements became progressively more frequent the longer the birds remained at 19°C. To avoid damage to the woodhoopoes, we terminated the experiment at 2400 and immediately removed them from the environmental chamber. The body temperature of each woodhoopoe, measured as it was taken from the chamber, indicated that despite the increased activity, the birds were becoming hypothermic (Table 1). The

hypothermia was not an adaptive response to low ambient temperatures; rather, it occurred despite the metabolic heat production associated with intense locomotor activity.

DISCUSSION

Compared with the Temperate Zone avian species that have been studied (mostly passerines), these tropical coraciiform birds demonstrated a very different and apparently inappropriate pattern of response to cold air temperatures. In general, birds maintain normothermia during exposure to cold by elevating heat production through shivering thermogenesis and by minimizing activity, which would otherwise disrupt the insulative qualities of the feathers (Dawson and Carey 1976). In contrast, although the woodhoopoes remained quiet at 30.5°C and 27°C, they became extremely active when air temperatures were lowered to 19°C. We cannot prove that these birds did not employ shivering thermogenesis, but if they did so, it was ineffective at preventing hypothermia at what appears to be a moderate ambient temperature. The intense activity we observed at 19°C may be the sole means these birds have of generating extra metabolic heat. In short, in the absence of insulated roost cavities, or other birds with which to cluster, the woodhoopoes showed little ability, physiological or behavioral, to cope appropriately with low nighttime ambient temperatures.

The metabolic data can account for the apparent paradox that woodhoopoes roost in cavities despite the fact that the associated risk of mortality is high. Interpreting the basis for this situation is more difficult, however (Gould and Lewontin 1979; see also Murray 1986). In the case considered here several plausible interpretations exist. These fall into one of two broad categories, "adaptationist" or "phylogenetic history." We briefly present these alternative perspectives and interpretations without attempting to marshal arguments for either.

Adaptationist interpretations.—The key distinction between an adaptive interpretation and an interpretation based on phylogenetic history is that in the former, low standard metabolic rates (SMR) are presumed to be adaptive. For example, low metabolic demands reduce foraging requirements, or lower growth rates of young birds reduce their risk of starvation. A second possibility is that cavity roosting decreases noc-

turnal metabolic costs. Early selection for cavity roosting could have led to an eventual loss of thermoregulatory abilities at low ambient temperatures.

If cavity roosting is adaptive, low metabolic rates make for more efficient use of cavities, in that O₂ uptake and CO₂ production in the cavities is less than if the birds had higher rates. This could be an important consideration in an environment where cavities are in limited supply and where several birds sometimes roost together. Nondispersal of young as a result of their dependence on scarce cavities could have set the stage for the eventual development of cooperative breeding.

Phylogenetic history interpretation.—The metabolic rates of Green Woodhoopoes probably are characteristic of the woodhoopoe family Phoeniculidae. All eight members of this distinctive group are confined to sub-Saharan Africa, and most occur in warm, equatorial lowlands (Davidson and Ligon in press). Thus, an ability to maintain normothermia through shivering thermogenesis may never have been present in this lineage. This could have promoted cavity-roosting behavior early in the group's history, because heat produced by even a single bird in a protected cavity can raise air temperature sufficiently so that an increase in metabolic heat production is unnecessary (Kendeigh 1961). Limited data on a few other coraciiforms also either suggest low metabolic rates (Kendeigh et al. 1977, Oniki 1975) or indicate use of cavities to ameliorate ambient temperatures (White et al. 1978, Hamas 1981).

Only two members of the woodhoopoe family, the Green Woodhoopoe (plus fellow superspecies members *P. somaliensis* and *P. damarensis*) and the White-headed Woodhoopoe (*P. bollei*), occur commonly at high elevations (Davidson and Ligon in press). These also are the largest species, 2.5–3.0 times the size of the others, and are the only ones that exhibit cooperative breeding. Large body size may increase resistance to low ambient temperatures, but it also reduces the number of cavities the birds potentially could use for roosting, thus favoring long-term retention of young birds in their natal territories, where known roost sites are available. Retention of young birds is a necessary precursor of cooperative breeding.

The high mortality rate of Green Woodhoopoes as compared with other well-studied cooperative breeders makes their metabolic pat-

tern appear to be a constraint: The birds apparently must roost in cavities, and our evidence suggests that most mortality results from nocturnal predation on roosting birds. It is impossible to determine, however, whether the dependence on cavities is primarily a constraint or an adaptation. Knowledge of roost habits of other species of phoeniculids and of Green Woodhoopoes in areas where nighttime temperatures are warm, together with knowledge of standard metabolic rates of the other species, would provide valuable insights; even such information, however, would not lead to unequivocal falsification of either alternative. Moreover, elements of each interpretation probably are correct, and they most likely influence each other. Thus, at present, about all that can be concluded is that contemporary Green Woodhoopoes require access to roost cavities, and that this requirement may have had a profound effect on the social behavior of these birds. First, most woodhoopoes move only 1–2 territories when they disperse, occupying territories where they probably know the location and quality of cavities (Ligon and Ligon 1988). Second, the scarcity of safe cavities could have promoted the development of extended or permanent tolerance of young birds by their parents (Ligon 1981), which in turn may have set the stage for the eventual evolution of the suite of behaviors that characterize cooperative breeding.

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