GREEN WOODHOOPOES (*PHOENICULUS PURPUREUS*) AND OBLIGATE CAVITY ROOSTING PROVIDE A TEST OF THE THERMOREGULATORY INSUFFICIENCY HYPOTHESIS

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ABSTRACT.—In Kenya, Green Woodhoopoes (*Phoeniculus purpureus*) seem constrained to sleep in aboreal cavities in spite of a high risk of capture within these chambers by nocturnal predators. Ligon et al. (1988) proposed that because woodhoopoes are incapable of adequate shivering thermogenesis at low nocturnal ambient temperatures, they are forced to roost in insulated tree cavities to maintain their body temperatures. We tested the thermoregulatory insufficiency hypothesis on 10 wild-caught woodhoopoes. From measurements of oxygen consumption ($\dot{V}O_2$) at ambient temperatures from −10°C to +40°C, we find no support for the hypothesis. Below thermoneutrality, $\dot{V}O_2$ increased linearly as ambient temperature (T_a) decreased. The equation, $\dot{V}O_2$ (ml $O_2 \cdot h^{-1}$) = 525.5 − 5.53 (T_a), described the relationship for males, and $\dot{V}O_2$ (ml $O_2 \cdot h^{-1}$) = 252.8 − 5.65 (T_a) for females. Body temperature (T_b) for the sexes did not differ (mean = 39.3°C). Birds that were in good body condition maintained their T_b even at −10°C for several hours. Within the thermal neutral zone, $\dot{V}O_2$ averaged 124.6 ml $O_2 \cdot h^{-1}$ for males and 115.9 ml $O_2 \cdot h^{-1}$ for females. Body mass averaged 79.70 g for males and 72.19 g for females.

Total evaporative water loss of Green Woodhoopoes showed no relationship to T_a below 25°C. Evaporative water loss averaged 179.6 mg $H_2O \cdot h^{-1}$ in males and 170.9 mg $H_2O \cdot h^{-1}$ in females. Above 25°C, water loss increased exponentially with temperature. At 40°C, woodhoopoes dissipated 55.8% of their metabolic heat production through water evaporation from respiratory passages and skin.

Dry thermal conductance ($\dot{H}_d$) between 0 and 30°C averaged 31.7 mW·°C^{-1} for males and 32.5 mW·°C^{-1} for females. Above 30°C, $\dot{H}_d$ rapidly escalated, reaching nearly 80 mW·°C^{-1} at the highest temperatures. *Received 14 February 1990, accepted 4 October 1990.*

THE GREEN Woodhoopoe (*Phoeniculus purpureus;* a.k.a. Redbilled Woodhoopoe) is distributed across central and southeastern Africa, typically inhabiting open savanna woodland and riverine forest (Ligon and Davidson 1988). These birds live together cooperatively in flocks that comprise a single breeding pair and 2–8 helpers that are often, but not always, offspring of the alpha male and female (Ligon and Ligon 1978). Helpers aid in territorial defense, provide food to the breeding female before egg laying and during incubation, assist in provisioning the young, and participate in detection and harassment of predators. Like most other communal species, woodhoopoes defend a territory, the boundaries of which remain stable over time. These areas provide food resources in the form of bark-dwelling arthropods, and also suitable tree cavities in which the flock spends the night.

Throughout the Green Woodhoopoe range, cavity roosting appears important to their survival. In Kenya, loss of one cavity-containing tree resulted in the disappearance of a flock (Ligon and Ligon 1978). In this same area, when woodhoopoes were supplanted from roost sites by other bird species, the woodhoopoes quickly sought a secondary tree hollow. Apparently they were unwilling to roost in open but protected sites as do other species. In South Africa where roost sites are more plentiful, du Plessis (1990a) blocked entrances to woodhoopoe roost cavities and monitored their subsequent roosting behavior. Flocks always found alternative tree hollows in which to roost within their territory although they used cavities with progressively larger entrances, which escalated the likelihood of predation and perhaps reduced the benefit of the roost as a thermally protected environment.

The proclivity of Green Woodhoopoes for sleeping in arboreal cavities is enigmatic because predation within roost cavities by nocturnal predators, especially genets (*Genetta* spp.), and driver ants (Tribe Dorylini), appears common (Ligon and Ligon 1988). Mean annual mortality rates for this species in Kenya apparently

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exceed those of most other cooperatively breeding birds (Ligon 1983). The avoidance by woodhoopoes of roosting in ostensibly safe open sites, such as thorn-covered branches of acacias, coupled with the high risk of predation at the roost, prompted Ligon and Ligon (1978) to suppose that Green Woodhoopoes were obligated to sleep in tree cavities because of their inability to maintain normothermic body temperatures when exposed to low ambient temperatures.

The above hypothesis has recently gained support. Ligon et al. (1988) found that rates of oxygen consumption were relatively constant in the thermal neutral zone, but woodhoopoes became hypothermic when exposed to 19°C, even though they increased their oxygen consumption. These data supported the idea that woodhoopoes slept in cavities despite the high risk of mortality due to their inability to thermoregulate (see Ward et al. 1989 for an alternative interpretation of these data).

A theory concerning the evolution of cooperative breeding in Green Woodhoopoes has now developed, the cornerstone of which is the birds' thermoregulatory inadequacy (Ligon and Ligon 1978, Stacey and Ligon 1987, Ligon and Ligon 1988). The theory posits that (1) the thermoregulatory insufficiency of Green Woodhoopoes has led to the evolution of cavity roosting; (2) their dependence on tree hollows, which are often in short supply, mandated extreme philopatry; and (3) offspring retention within the parental territory led to the evolution of various forms of cooperation, such as helping to rear young and territorial defense.

We tested the thermoregulatory insufficiency hypothesis on wild-caught Green Woodhoopoes and found that birds in good body condition increased their oxygen consumption in response to decreasing temperatures and, at the same time, maintained their normal body temperature. Our data do not support the hypothesis. We provide an alternative wherein energy considerations may have been influential in the evolution of group living in woodhoopoes.

METHODS

Study animals.—During mid-September 1989, we captured two flocks of Green Woodhoopoes containing 5 and 6 birds, near Kidd's Beach, South Africa (32°02'S, 27°40'E), and we transported them to the University of Cape Town. There, each flock was housed separately in large outdoor flight aviaries. Flock 1 comprised 3 females and 2 males. All birds were 3 yr old or older except for one 2-yr-old female. Flock 2 comprised 3 males and 3 females. Two males were >3 yr old, and one was a yearling; two females were >2 yr old, and one was a yearling. We used size and coloration of the bill (du Plessis 1990b) to determine gender and age of birds. During habituation to aviary conditions, one male (>3 yr old) of Flock 2 died of apparent starvation. Birds were provided with roost boxes, and a variety of foods including a mixture of scrambled eggs, dog food, Pro Nutro cereal, and minced beef, along with various arthropods such as mealworms, grasshoppers, and isopods. Water was provided *ad libitum*.

Measurement of oxygen consumption and evaporative water loss.—Rates of oxygen consumption ($\dot{V}O_2$) and total evaporative water loss (EWL) were determined for postabsorptive birds, during their nocturnal phase (2000-2400), by standard flow through respirometry and hygrometry methods (Gessaman 1987). We constructed metabolism chambers from 10-l metal paint cans with blackened inner surfaces. Inside each chamber, we placed a wire mesh platform and a wooden dowel on which birds perched during experiments. For some trials we added a layer of light-gauge oil to the bottom of chambers to trap voided feces and urine to measure evaporative water loss (EWL). During each experimental period, chambers containing woodhoopoes were placed in a temperature-controlled environmental cabinet that held temperature constant to ±0.1°C. Air was drawn under negative pressure through columns of silica gel, soda lime, and silica gel to remove H_2O and CO_2 from the air stream, then through the chamber. Exiting air was passed through a Hanna Thermohygrometer (model HI 8564) to measure relative humidity, then through more scrubbing columns before a subsample was routed through an Applied Electrochemistry oxygen analyzer to determine the fractional concentration of oxygen in dry, CO_2-free air. The O_2 analyzer was zeroed with pure nitrogen and calibrated with dry, CO_2-free air. Flow rates were monitored continuously with rotameters to assure constancy but were measured several times during each hour-long trial with a 500-ml glass bubble meter (Levy 1964).

Air was metered through the chambers at a rate of ca. 1,300 ml/min (STPD) for temperatures below 35°C and increased to 3,000 ml/min at higher temperatures. Above 35°C, birds often became active, whereupon we immediately terminated the experiment. Hence our data are few for these temperatures.

We calibrated our hygrometer each week over LiCl and NaCl standards. Air temperature within the chamber was monitored with a 28-gauge copper constantan thermocouple and a Wescor digital thermometer (model TH-65). Both were calibrated against a Fluke digital thermometer (model 2180A) that had a recent calibration certificate from the South Africa bureau of standards (CSIR). Because downstream air-

TABLE 1. Mean (±SD) values for mass and basal metabolism of Green Woodhoopoes.

	Males	Females	*t*-value	*P*
Mean mass (g)	79.70 ± 5.8	72.19 ± 4.6	3.71	<0.001
Body temperature (°C)	39.6 ± 1.2	39.7 ± 0.7	0.14	NS
BMR (ml $O_2 \cdot h^{-1}$)	124.6 ± 10.9	115.9 ± 10.9	2.18	<0.04
BMR (ml $O_2 \cdot g^{-1} \cdot h^{-1}$)	1.53 ± 0.13	1.61 ± 0.11	1.53	NS
BMR (kJ$\cdot$day^{-1})	60.0 ± 4.8	55.9 ± 5.2	2.18	<0.04
Allometric prediction (kJ$\cdot$day^{-1})[a]	48.2	44.8		
Percent difference[b]	+24.5	+24.8		
N/*n*[c]	13/4	15/6		

[a] Aschoff and Pohl (1970) prediction for nonpasserine birds in their rest phase.

[b] Percent difference was calculated as (Actual minus Predicted) divided by Predicted.

[c] *N* = number of 1-h trials; *n* = number of birds.

flow rates were measured before removal of CO_2, we used equation 4b of Withers (1977) to calculate $\dot{V}O_2$. Rates of EWL were calculated from airflow rates and measured values for relative humidity of the excurrent air stream. We continuously monitored $\dot{V}O_2$ during each run with the aid of a BBC Acorn computer and commercially available data acquisition software (Lighton 1985). After birds remained at a given temperature for 1 h, we recorded the fractional oxygen concentration of the air stream when the trace on the computer screen was constant. In practice, birds were remarkably quiescent during experiments except for some at temperatures above 35°C. We used 20.08 J$\cdot$ml O_2^{-1} to convert oxygen consumption into energy expenditure (Schmidt-Nielsen 1983) and 2.427 J$\cdot$mg H_2O^{-1} to convert EWL into dissipated heat (Calder and King 1974). Metabolism trials began on 13 October and lasted 1 month.

Body temperature.—At the end of each hour-long trial, we measured deep-core body temperature (T_b) by a 36-gauge teflon coated thermocouple, inserted into the proventriculus. The thermocouple was lubricated with vaseline before introduction into the esophagus. We recorded T_b when readings had stabilized and removal of the thermocouple by 2-3 mm brought about no change in measured T_b. During several of our first measurements of $\dot{V}O_2$, three birds that had not regained their field body mass registered T_b values below 39°C even at moderate ambient temperatures. We report data for oxygen consumption and T_b for these few individuals separately rather than include them in our general analysis (see below).

Statistics.—Data were analyzed by means of a SPSS statistical package (Norusis 1984). Differences between two regression lines were evaluated following Zar (1974). We used analysis of covariance to compare three or more lines. Means are presented ±1 SD.

RESULTS

From 97 measurements of $\dot{V}O_2$ at various ambient temperatures, metabolic rates of 10 Green Woodhoopoes responded to temperature like those of a wide array of other avian species (Calder and King 1974; Fig. 1). Between 22 and 35°C, $\dot{V}O_2$ appeared constant. Males averaged 124.6 and females 115.9 ml $O_2 \cdot h^{-1}$ (Table 1). These values are ca. 25% higher than those obtained with the appropriate Aschoff and Pohl (1970) equation. Body temperature within the zone of thermoneutrality averaged 39.6°C for males and 39.7°C for females. Body mass for males averaged 79.70 ± 5.8 g and for females 72.19 ± 4.54 g.

For measurements of $\dot{V}O_2$ at temperatures below thermoneutrality, we calculated regressions for each individual and tested for differences among individuals by analysis of covariance (Snedecor and Cochran 1980). We found no differences between slopes or elevations for regressions for birds within either group, and pooled our data within groups. As ambient temperature decreased, $\dot{V}O_2$ steadily increased. The equation, $\dot{V}O_2$ (ml $O_2 \cdot h^{-1}$) = 252.5 − 5.53 (T_a) ($N = 4$ birds, $n = 34$ measurements, $r^2 = 0.81$, $F = 140.4$, $P < 0.0001$), described the relationship for males, and $\dot{V}O_2$ (ml $O_2 \cdot h^{-1}$) = 252.8 − 5.65 (T_a) ($N = 6$ birds, $n = 32$ measurements, $r^2 = 0.85$, $F = 134.8$, $P < 0.0001$) for females. At zero metabolism, these equations intersect the abscissa at 45.7°C for males and 44.7°C for females. Slopes and intercepts of these equations do not differ significantly ($t_{\text{slope}} = 0.71$, $P > 0.40$; $t_{\text{elevation}} = 0.11$, $P > 0.5$). The intersection method of Kendeigh et al. (1977) indicated that the lower critical temperature (T_{lc}) was 23.1°C for males and 24.2°C for females. Body mass used in these measurements averaged 79.6 ± 3.0 g for males and 71.2 ± 3.0 g for females.

Our data above the thermoneutral zone are few and should be viewed with caution. The

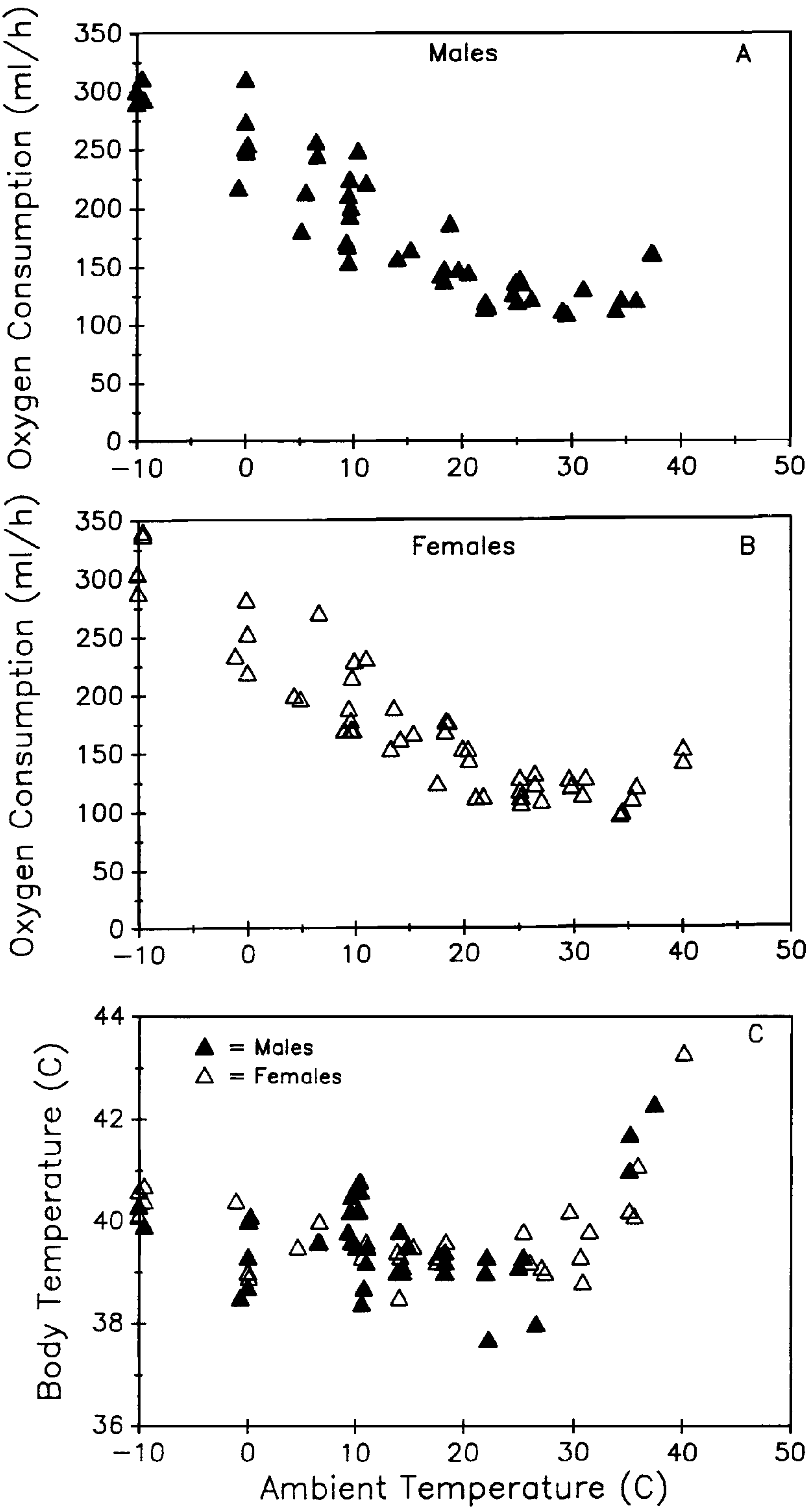
Males
A
Oxygen Consumption (ml/h)
350
300
250
200
150
100
50
0
−10
0
10
20
30
40
50
Females
B
Oxygen Consumption (ml/h)
350
300
250
200
150
100
50
0
−10
0
10
20
30
40
50
C
▲ = Males
△ = Females
Body Temperature (C)
44
42
40
38
36
−10
0
10
20
30
40
50
Ambient Temperature (C)

TABLE 2. Measurements of body temperature (T_b) at various ambient temperatures (T_a) for 3 Green Woodhoopoes.

Bird ID	Sex	Mass (g)	Wing length (mm)	T_a (°C)	$\dot{V}O_2$ (ml $O_2 \cdot h^{-1}$)	T_b (°C)	Date (1989)
005	M	73.44	140.0	26.6	93.1	38.0	13 Oct
005	M	70.53	140.0	10.8	99.9	38.7	18 Oct
005	M	79.34	140.0	6.5	256.6	39.6	6 Nov
012	M	75.99	137.0	−0.7	217.7	38.5	13 Oct
012	M	73.04	137.0	22.3	107.1	37.7	16 Oct
012	M	80.69	137.0	0.0	310.6	39.3	25 Oct
011	F	62.50	129.0	14.1	103.7	38.5	7 Oct
011	F	65.20	129.0	14.2	161.2	39.8	12 Oct

equation which describes the relationship between $\dot{V}O_2$ and temperature in this region is $\dot{V}O_2$ (ml $O_2 \cdot h^{-1}$) = $-879.2 + 27.9$ (T_a) ($n = 3$, $r^2 = 0.99$, F and 151.0, $P < 0.05$) for males, and $\dot{V}O_2$ (ml $O_2 \cdot h^{-1}$) = $-143.3 + 7.24$ (T_a) ($n = 4$, $r^2 = 0.99$, $F = 151.0$, $P < 0.04$) for females. Accordingly, the upper critical temperatures were 36.0°C for males and 35.8°C for females.

Below 30°C, body temperature for the sexes did not differ ($t = 0.4$, $P > 0.7$), and they averaged 39.3°C ($n = 46$, SD = 0.52; Fig. 1). Above 30°C with data for both sexes combined, body temperature rose as T_a increased; $T_b = 29.66 + 0.32$ (T_a) ($n = 10$, $r^2 = 0.71$, $F = 19.6$, $P < 0.002$).

During our first few metabolism experiments, we noted some birds with body temperatures slightly below 39°C even at fairly moderate ambient temperatures (Fig. 1). Compared with other avian species (King and Farner 1961), these values seemed low, which suggested the possibility that some woodhoopoes either regulated their T_b below values for other species or that these individuals were unable to maintain normothermic body temperatures. As experiments progressed, we found that maintenance of T_b below 39°C was related to body condition (Table 2). For example, Male 012 had a T_b of 38.5°C at 0°C when he weighed 76.0 g, but 12 days later with a mass gain of 4.7 g, he maintained a T_b of 39.3°C at 0°C.

Body temperatures below 39°C occurred in woodhoopoes that weighed less than other flock members, which prompted us to examine the relationship between body condition of laboratory birds relative to free-living woodhoopoes. We plotted wing lengths against body masses of 118 field-caught woodhoopoes that were nonmolting adults (Fig. 2). For males ($n = 60$), wing length averaged 139.9 ± 2.84 mm and body mass averaged 84.0 + 4.28 g. For females wing length was 132.2 ± 3.37 mm and body mass 71.6 ± 3.7 g ($n = 58$). Intersexual differences were significantly different. We suggest that birds with a body mass ca. 2 SD below the mean body mass of field-caught birds were in a depressed body condition. We do not intend to imply that this body condition boundary is a fixed line, but rather that it is a representation of the region where birds are in a weakened state. Masses of laboratory birds with low T_b typically fell below these limits for field-caught birds, which implies that body condition may have influenced thermogenesis.

Total EWL of Green Woodhoopoes showed no relationship to T_a below 25°C (Fig. 3: $n = 19$, $r^2 = 0.17$, $F = 3.01$, $P > 0.10$ males; $n = 23$, $r^2 = 0.09$, $F = 1.7$, $P > 0.20$ females). Evaporative water loss averaged 179.6 ± 44.2 mg $H_2O \cdot h^{-1}$ in males and 170.9 ± 42.0 mg $H_2O \cdot h^{-1}$ in females, values which are indistinguishable ($t = 0.65$, $P > 0.5$). Above 25°C, EWL rose with increasing T_a; for males EWL (mg $H_2O \cdot h^{-1}$) = $3.8e^{0.073(T_a)}$ ($n = 6$, $r^2 = 0.74$, $F = 10.9$, $P = 0.03$), for females EWL (mg $H_2O \cdot h^{-1}$) = $29.1e^{0.08\,(T_a)}$ ($n = 8$, $r^2 = 0.64$, $F = 14.4$, $P < 0.005$). Total evaporative water loss deviated from the equation of Crawford and Lasiewski (1968) by −15.5% in males and −12.9% in females. The thermal sig-

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Fig. 1. Oxygen consumption as a function of ambient temperature for (A) male Green Woodhoopoes, and (B) female Green Woodhoopoes; and (C) body temperature as a function of ambient temperature for Green Woodhoopoes.

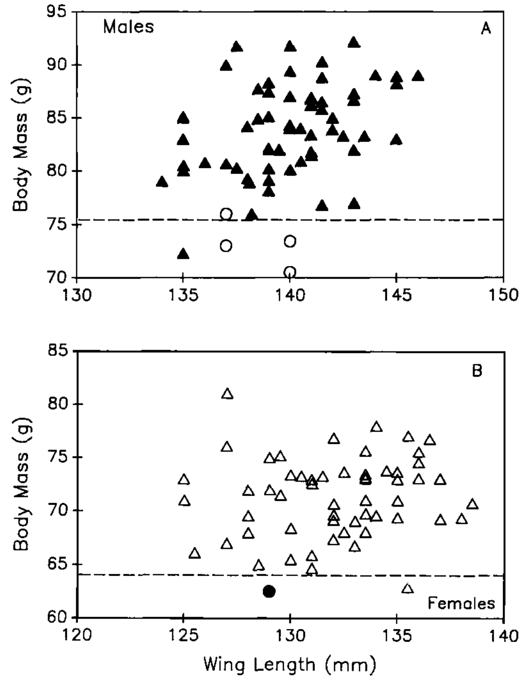

Fig. 2. (A) Body mass as a function of wing length for (A) male Green Woodhoopoes and (B) females. Triangles represent values for field-caught nonmolting adults. Open circles represent males in the laboratory with body temperatures below 39°C. Filled circle represents a female in the laboratory with a body temperature below 39°C. Dashed line on each graph indicates the value 2 SD below the mean.

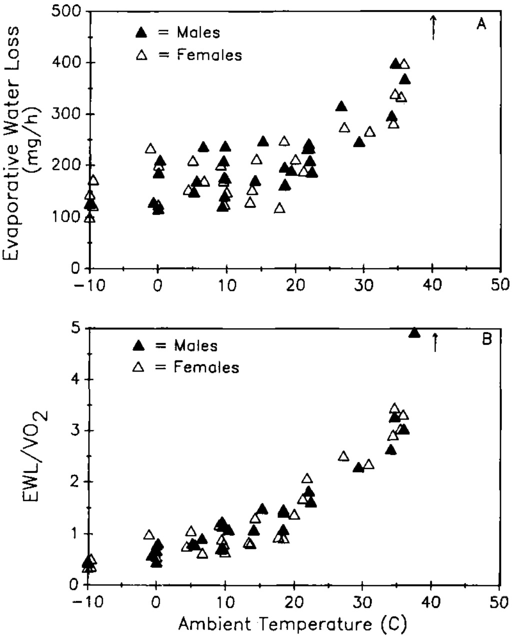

Fig. 3. (A) Evaporative water loss of Green Woodhoopoes as a function of ambient temperature. (B) The ratio EWL to $\dot{V}O_2$ as a function of ambient temperature. The arrow on each graph represents data at 40°C that exceeded limits of graph.

nificance of EWL is often expressed as the ratio of the heat dissipated by evaporation ($\dot{H}_e$) divided by the heat of metabolism ($\dot{H}_m$). Independent of body size, this ratio can be approximated by the equation $\dot{H}_e/\dot{H}_m = 5 + 1.48e^{0.087(T_a)}$ (Calder and King 1974). Combining data for both sexes, woodhoopoes dissipated 55.8% of their metabolic heat production by evaporating water at a T_a of 40°C (the equation of Calder and King predicts 53.0%).

Ratios of EWL to $\dot{V}O_2$ increased monotonically with increasing temperatures (Fig. 3). Differences between sexes were insignificant, hence we combined data to yield the equation EWL/$\dot{V}O_2$ (mg $H_2O \cdot h^{-1}$/ml $O_2 \cdot h^{-1}$) = $0.55e^{0.053(T_a)}$ (n = 47, $r^2 = 0.87$, $F = 298.8$, $P < 0.0001$).

Dry thermal conductance ($\dot{H}_d$) measures heat flux from the body core to the environment encompassing heat flow through the body, feathers, and air boundary layer. Between 0 and 30°C, $\dot{H}_d$ was unrelated to T_a for either sex and averaged 31.7 ± 4.3 mW·°C^{-1} for males and 32.5 ± 4.7 mW·°C^{-1} for females (Fig. 4). These values are indistinguishable ($t = 0.58$, $P > 0.5$). Above 30°C, $\dot{H}_d$ rapidly escalated reaching nearly 80 mW·°C^{-1} at the highest temperatures.

DISCUSSION

Among birds, explanations for the evolution of group living and attendant phenomena such as cooperative breeding often emphasize ecological circumstances that have mandated delayed dispersal of young (Selander 1964, Brown 1978, Koenig and Pitelka 1981, Woolfenden and Fitzpatrick 1984). A widely held notion is that living in expanded social units occurs when some limiting factor renders successful reproduction after dispersal improbable (Emlen 1982). For permanently territorial species, earlier writers often invoked habitat saturation as the impetus for living with conspecifics. The critical resource was presumably a shortage of unoccupied breeding territories (Emlen 1982). Recent studies have implicated other factors besides habitat saturation as important in the evolution of group living in some species (Rabenold 1984, Stacey and Ligon 1987).

In Green Woodhoopoes, roost cavities have been identified as a critical limiting resource that may have led to group living (Ligon and Ligon 1978). When artificial roost boxes were placed in a woodland that was unoccupied by woodhoopoes, 5 flocks established permanent territories in the area within 2 months (du Plessis 1990a). These birds always roosted in the boxes provided—evidence of the importance of suitable roosting cavities to woodhoopoes. Their dependency on roosting cavities has been related to antipredatory behavior (du Plessis 1990b) and also to physiological limitations (Ligon and Ligon 1978, Ligon et al. 1988). The thermoregulatory insufficiency hypothesis was proposed as a resolution to the paradox that woodhoopoes sleep in cavities despite the associated high risk of mortality. Woodhoopoes were thought to roost in the cavities because of their inability to cope physiologically with low night-time temperature.

The hypothesis was buoyed when Ligon et al. (1988) studied the laboratory metabolism of three Green Woodhoopoes borrowed from zoos. Woodhoopoes consumed oxygen at rates ostensibly similar to allometric predictions when exposed to 30.5°C and 27°C. As temperatures were decreased to 19°C, birds elevated their $\dot{V}O_2$ coincident with becoming active in the chambers. Despite increased activity, birds were hypothermic, evidence proffered in support of the thermoregulatory insufficiency hypothesis.

From 97 determinations of $\dot{V}O_2$ on 10 wild-caught Green Woodhoopoes at ambient temperatures ranging from −10°C to 40°C, we found no support for the idea that Green Woodhoopoes are incapable of generating sufficient heat by shivering thermogenesis to maintain normothermic body temperatures. As ambient temperature declined, birds linearly elevated their oxygen consumption while maintaining their body temperatures. Even at −10°C, a temperature rarely encountered by this species (du Plessis 1990b), birds remained normothermic.

Though our data cast doubt on the thermoregulatory insufficiency hypothesis, the possibility remains that energy considerations have played a role in the development of sociality in woodhoopoes. If body condition influences the capacity of woodhoopoes to thermoregulate, as we suggest, then roosting with conspecifics in insulated cavities could lower energy requirements and place these individuals at an advantage during periods of food scarcity. Suppose independent juveniles forage much less efficiently, have a higher field metabolic rate, and live closer to the body condition boundary than do adults, as has recently been found for Yellow-eyed Juncos (*Junco phaeonotus*; Weathers and Sullivan 1989). During inclement weather, young birds may experience problems of energy balance, which depresses body condition. By sleeping with family members in insulated roost cavities, these birds might save a significant amount of energy, lower their daily energy expenditure (Kendeigh 1961), and enhance their chances of survival. Because appropriate roost cavities are scarce, juveniles that disperse and sleep individually in exposed sites would experience a higher risk of death by starvation than individuals that remain in the natal territory. The possibility exists then that energy savings through group roosting has been an important determinant in the evolution of sociality in woodhoopoes. The energetic advantages of roosting with conspecifics need not be restricted to juveniles. Adults that experience periods of reduced body condition might also increase their fitness (e.g. through enhanced survival) by roosting with flock members. Our hypothesis predicts that (1) birds (adults or juveniles) in depressed body condition will be unable to thermoregulate at low ambient temperatures, (2) birds in depressed body condition will maintain normal body temperatures when they roost in cavities with conspecifics, and (3) juveniles live closer to the body condition boundary than do adults.

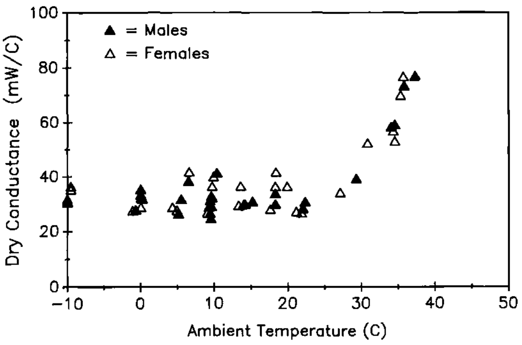

Fig. 4. Dry thermal conductance as a function of ambient temperature in Green Woodhoopoes.

We tested the third prediction by plotting

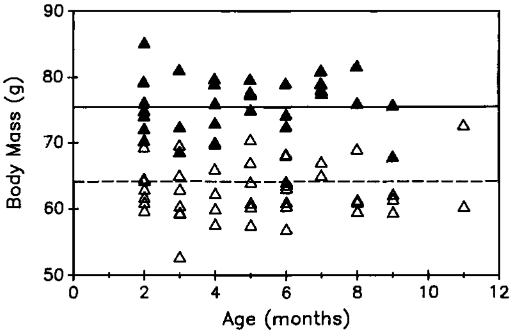

Fig. 5. Body mass as a function of age in juvenile Green Woodhoopoes. The solid line represents a body mass 2 SD below the mean for adult field-caught males, and the dashed line represents a body mass 2 SD below the mean for adult field-caught females. Juvenile males = ▲, juvenile females = △.

body masses of juveniles for the ages 2–11 months (Fig. 5). Juveniles often fall below the body condition boundary even when nearly 12 months of age. Males seem to maintain a better body condition than females do (38% of the males were below the line vs. 63% of the females). This may account for the observation that males disperse more often than females during their first year of life (du Plessis 1990b).

Data presented by Ligon et al. (1988) may lend credence to our idea that body condition is fundamentally important to the maintenance of T_b in woodhoopoes, and ultimately to their survival. Males from Kenya weigh on average 77.3 g; females weigh 64.0 g (Ligon and Davidson 1988). The two males and one female in the laboratory study of Ligon et al. (1988) weighed 71.0, 66.1, and 52.3 g, respectively. These values are −8.2, −14.5, and −18.3% below mean values for woodhoopoes in Kenya, which implies that their birds may have been in a nutritionally impoverished condition.

A seminal observation leading to the derivation of the thermoregulatory insufficiency hypothesis was that woodhoopoes in Kenya exhibit high mortality rates (40% per annum for males, 30% for females; Ligon and Ligon 1978) compared with other species. Though the evidence was circumstantial, most mortality was ascribed to nocturnal predation at the roost cavity. We recommend caution in accepting that woodhoopoes generally have high mortality rates and that most predation occurs at the roost cavity. Data from an intensive 8-yr study on woodhoopoe populations in southeastern Africa showed a mean annual mortality rate ca. 20% for both sexes (du Plessis 1990b), values similar to data for other cooperatively breeding birds (Skutch 1966, Woolfenden 1973).

Further, we find little support for the notion that predation at roost cavities accounts for most mortality in woodhoopoes. In 54 flocks followed over 8 yr, du Plessis (1990b) documented only one clear case of predation at the root cavity. Additionally, predation upon nestlings in cavities was rare in both Kenya and southeastern Africa (Ligon and Ligon 1978, du Plessis 1990b). If predation on nestlings in cavities is rare, why would adults experience just the opposite? We remain unconvinced that woodhoopoes typically experience high mortality because they sleep in cavities.

Our measurements of basal metabolism were ca. 25% higher than values predicted by equations of Aschoff and Pohl (1970), and our measurements were higher than the values reported by Ligon et al. (1988) for two males and one female. Though these authors reported that average $\dot{V}O_2$ of woodhoopoes fell within 5% of predicted values, inspection of their data shows that 2 of 3 individuals deviated significantly from the Aschoff and Pohl equation by +26.7% and −18.9%. Values for only 1 male fell within 2.7% of the Aschoff and Pohl prediction.

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