COMMUNAL CAVITY ROOSTING IN GREEN WOODHOOPOES: CONSEQUENCES FOR ENERGY EXPENDITURE AND THE SEASONAL PATTERN OF MORTALITY

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ABSTRACT.—Green Woodhoopoes (*Phoeniculus purpureus*) roost in cavities in groups throughout the year. It has been proposed that the energy savings achieved by roosting with conspecifics in a cavity could enable birds in poor body condition to remain normothermic during inclement weather. We tested the hypothesis that woodhoopoes conserve energy by roosting with conspecifics in cavities and found that a woodhoopoe roosting with four conspecifics can reduce its nighttime energy expenditure by 30% or more when the minimum ambient temperature is about 5°C. In areas where nocturnal temperatures sometimes drop below freezing, such energy savings are associated with mortality patterns among adults during winter. Our data support the idea that energy considerations may have been important in the evolution and/or maintenance of sociality in this species. *Received 14 August 1992, accepted 25 November 1992.*

GREEN WOODHOOPOES (*Phoeniculus purpureus*; also known as Red-billed Woodhoopoes) are cooperative breeders that live in groups of 2 to 12 individuals (Ligon and Ligon 1978). Woodhoopoes obligately roost communally in cavities throughout their range even though they are unable to excavate these holes themselves. This dependence appears critical for their survival by either providing energetic benefits to individuals, protection against predators, or both (Ligon and Ligon 1978, 1988, Ligon et al. 1988, Du Plessis 1989a, b, Williams et al. 1991). The energy savings associated with communal cavity roosting have been implicated as an important driving force in the evolution of sociality in this species (Williams et al. 1991). In an earlier paper, Williams et al. (1991) reported that Green Woodhoopoes maintained normothermic body temperatures at ambient temperatures from −10° to 40°C. However, birds that were in apparently poor body condition, as judged by their unusually low body mass, exhibited body temperatures slightly below 39°C, even at moderate ambient temperatures. We reasoned that birds in depressed body condition will be unable to thermoregulate at low ambient temperatures, but that they can do so when roosting in cavities with conspecifics. We suggested that

cavity roosting may be particularly critical to first-year birds, and that it may also be important to adults that have experienced periods of food shortage. In this paper we examine the energetic benefits of Green Woodhoopoes' communal cavity-roosting behavior.

METHODS

We captured two groups of Green Woodhoopoes (five and six birds each) on Silverdale Farm near Kidd's Beach (32°02'S, 27°40'E) in the eastern Cape Province of South Africa. They were then transported to the University of Cape Town, where groups were housed separately in large outdoor flight aviaries (see Williams et al. 1991). Experiments were performed on nonmolting birds over a period of 2.5 months beginning in October 1989.

Measurement of roost-cavity temperatures.—We constructed three nest boxes, with inner dimensions simulating those of cavities used by woodhoopoes under natural conditions (50 × 12 × 12 cm; see Du Plessis 1989a), and placed them in the flight aviary used to house the group of six birds. The three nest boxes were positioned 150 mm apart at a height of 1.75 m with their entrances facing the same way. Coarse wood chips were glued to the insides of boxes so that woodhoopoes could cling to the sides of cavities if they chose to do so. Six thin insulated copper-constantan thermocouples were prepared and tested against a standardized Wescor digital thermometer (model TH-65) to assure identical reading of the same temperature. Each thermocouple was fixed in the center of a plastic tube to ensure that birds could not physically touch the former; numerous small holes were then drilled over the entire surface of each plastic tube.

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Two thermocouples were placed in each of nest boxes 1 and 2, one near the lower back and one near the top front of each box. Temperature readings were averaged in these two boxes. Only one thermocouple was placed in the middle of nest box 3, which was used as a control. Another thermocouple was positioned near the three nest boxes (and at the same height) to measure ambient air temperature. The output of thermocouples was monitored by a Campbell datalogger (model CR10), which registered temperature once per minute and recorded the mean at 10-min intervals. Roost-box temperatures were recorded on 20 days in 1990 during June and July, two of the coldest months in Cape Town. When the three nest boxes were empty, mean temperatures among them differed by no more than 0.3°C.

We manipulated the number of birds roosting in a given nest box by moving them after dark. Birds did not seem perturbed by these disturbances and immediately settled into their "new cavity." We observed no voluntary bird movement out of or between cavities after dark. We recorded nest-box temperature of roosting groups of one to six birds. Whenever measurements were taken, we made sure the one nest box was unoccupied (control) so that we could distinguish thermal benefits of the shelter alone from those attributable to metabolic heat generated by roosting birds.

Measurement of oxygen consumption.—Rates of oxygen consumption (VO_2) were determined for postabsorptive birds at night (2000–0200) by standard flow-through respirometry methods (see Williams et al. 1991). Metabolic chambers, 12 cm in diameter, were lined with a layer of 0.4-mm corrugated paper on which birds could cling vertically. Inner dimensions of metabolic chambers were similar to those that woodhoopoes used under natural conditions (Du Plessis 1989a). Flow rates were monitored continuously with rotameters to assure constancy, but were measured several times during each hour-long trial with 500-ml and 1,000-ml glass bubble meters (Levy 1964). Air was metered through the chambers at a rate of about 1,500 ml/min for single birds, and increased to about 2,000 ml/min for groups. Trials were run between −10° and 20°C, and a thermocouple was placed inside the metabolic chamber.

We continuously monitored VO_2 during each trial with the aid of a BBC Acorn computer and commercially available data-acquisition software (Lighton 1985). After birds were exposed to a given temperature for a 1-h period, we recorded the fractional oxygen concentration of the airstream when the trace on the computer screen remained constant for at least 10 min. In practice, birds were quiescent during most experiments and made irregular movements only after being exposed to subzero temperatures for several hours. We assumed the thermal equivalence of VO_2 to be 20.08 J/ml O_2 (Schmidt-Nielsen 1983).

Oxygen consumption was measured for individuals, trios, and groups of five birds at given temperatures. Trials were run with trios and groups using the same birds as for individual measurements. These measurements were expressed as the rate of oxygen consumption per unit body mass (ml O_2 g^{-1}h^{-1}). At the end of each 1- to 2-h trial, we measured deep-core temperature (T_b) of all individuals immediately after removing them from the metabolic chambers by insertion of a thermocouple into the proventriculus.

Estimating effect of wind on nighttime energy expenditure.—We used Bakken's (1990) equation to calculate the standard operative temperature (T_{es}) at wind speeds that birds would experience if they roosted in the open:

$$T_{es} = T_b - (1 + 0.26u^{0.5})(T_b - T_e), \qquad (1)$$

where T_b is the bird's body temperature, u is the wind speed, and T_e is operative temperature. We assumed that at nighttime T_e equalled T_a (see Bakken 1990).

Demographic and weather data.—One of us (M.A. Du P.) studied Green Woodhoopoes at two sites in the eastern Cape Province, South Africa, between 1981 and 1989. At Morgan's Bay (32°43'S, 28°19'E), 29 groups were monitored in a 33-km² area, whilst 26 groups were monitored in the Kubusi River Valley (32°32'S, 27°47'E) in a 45-km² area. Most individuals from both the coastal and inland woodhoopoe groups were banded with numbered aluminum bands (provided by SAFRING) and a unique combination of colored plastic bands (see Du Plessis 1992). For the purposes of this paper, we examined survivorship data only for individuals in groups of five or less, as members of larger groups were sometimes constrained from roosting together by cavity dimensions (Du Plessis 1989b). During several hundred observations of roosting behavior, woodhoopoes invariably roosted together when groups consisted of five or fewer individuals. As group size increased, the likelihood of groups splitting into two or more roosting subunits increased (Du Plessis unpubl. manuscript). We considered group size at the time when a death occurred to include the bird that died. Adult mortality data were used only for years in which systematic, quarterly searches were made for dispersers in areas surrounding the study sites, in addition to routine within-in-site censuses (1984–1988). We obtained ambient temperature data measured at the weather stations of Ocean View Farm and Mgwali Village, which are situated at the same elevation and within 15 km from each of the woodhoopoe study sites.

Statistical analyses.—For measurements of VO_2 versus T_a, we calculated regressions for each individual and tested for differences among individuals by analysis of covariance (Snedecor and Cochran 1989). Finding no differences between slopes or elevations for regressions for birds within either group, we have pooled our data within groups. Data were analyzed by means of a PC-SAS computer program (SAS Institute 1985). Differences between two regression lines
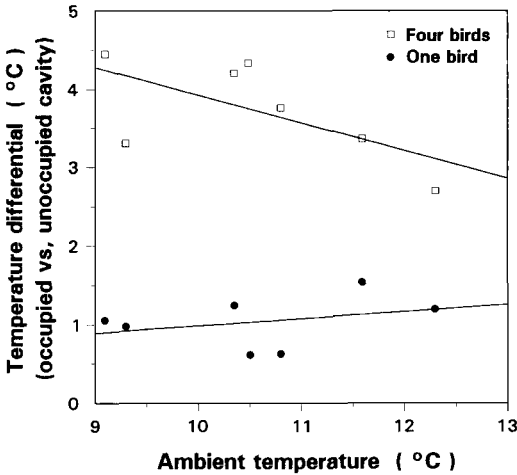
Fig. 1. Relationship between temperature differential of unoccupied cavities and those with one and four woodhoopoe occupants, respectively. Birds within each of these categories were exposed to an identical T_a, since experiments were run on same nights (n = 7 nights).
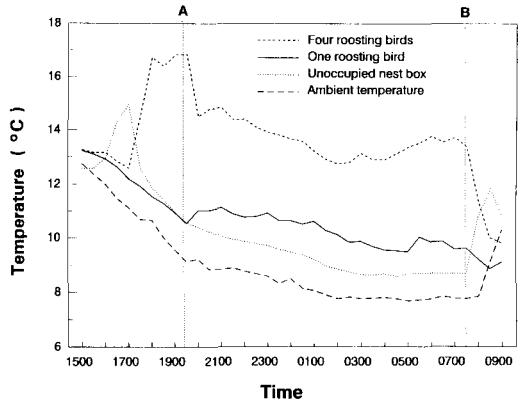

Fig. 2. Example of a night during which a woodhoopoe flock was manipulated so as to have a combination of four birds roosting together in one cavity, and a single bird in another. All five birds entered nest box 2 around 1720; a single bird was removed and placed in nest box 1 at 1930 (point A); birds left nest boxes around 0730 on following morning (point B).

were evaluated using t-tests; when comparing more than two lines we used analysis of covariance (Zar 1984). Data are presented as $\bar{x}$ ± SD.

RESULTS

During a period of nine years absolute minimum temperatures never dropped below 4.2° and −4.2°C at the Morgan's Bay and Kubusi River valley study sites, respectively. At both sites the coldest months fell between April and September.

Temperatures inside unoccupied nest boxes were on average between 0.20° and 1.45°C higher than mean ambient temperatures, with the latter ranging between 6.5° and 14.6°C (N = 18 nights, n = 144). As ambient temperature decreased, the difference between T_a and the temperature inside unoccupied nest boxes increased. The equation for temperature change (ΔT; °C) is

$$\Delta T = 1.69 - 0.10T_{a(min)} \qquad (2)$$

(N = 18 nights; r^2 = 0.30; F = 7.01; P < 0.05) and describes the relationship where $T_{a(min)}$ is the minimum ambient temperature reached each night, while the equation for the maximal nocturnal temperature change is

$$\Delta T \text{ (°C)} = 2.13 - 0.12T_{a(max)} \qquad (3)$$

(N = 18 nights; r^2 = 0.36, F = 9.09, P < 0.01).

In cavities containing three or four roosting birds, the temperature elevation attributable to bird occupancy was significantly greater than that for cavities containing one or two birds (Wilcoxon sign rank test, Z = 2.75, n = 10 nights, P = 0.006). Single-roosting woodhoopoes raised their cavity temperatures on average by 0.99° ± 0.40°C at mean control temperatures ranging between 9.1° and 11.6°C, but there was no correlation between temperatures of occupied (by one bird) and unoccupied (control) cavities (r = 0.29, F = 0.47, P = 0.52). However, for groups of four, there was a significantly negative correlation between temperatures of occupied (by four birds) and unoccupied (control) cavities (r = 0.94, F = 41.39, P = 0.01; Fig. 1). The typical pattern observed during a particular night when the number of birds roosting together was manipulated is presented in Figure 2.

Temperatures inside the metabolic chambers (T_{mc}) were higher than those immediately outside as a result of birds warming the cavity. However, as T_{mc} decreased, VO$_2$ (ml O$_2$ g^{-1}h^{-1}) increased, and the equation

$$VO_2 = 3.355 - 0.071T_{mc} \qquad (4)$$

(N = 10 birds, n = 71 measurements, r^2 = 0.92, F = 327.8, P < 0.0001) described the relationship for birds roosting individually,

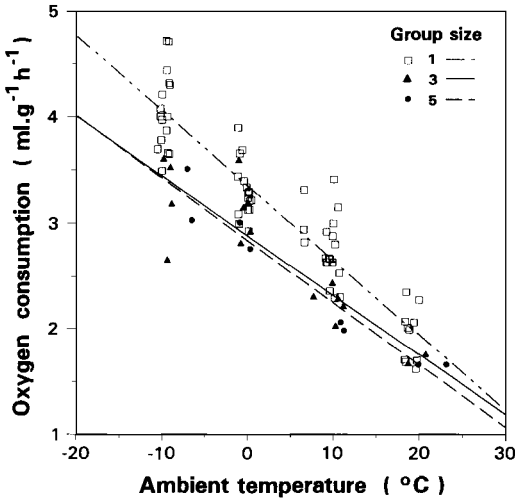$$VO_2 = 2.917 - 0.063T_{mc} \qquad (5)$$

Fig. 3. Relationship between temperature inside a metabolic chamber (simulating a roost cavity) and oxygen consumption of individuals roosting on their own, in trios, and in groups of five.

($N = 10$ birds, $n = 15$ measurements, $r^2 = 0.97$, $F = 186.4, P < 0.0001$) described the relationship for birds roosting in trios, and

$$VO_2 = 2.834 - 0.059T_{cav} \qquad (6)$$

($N = 10$ birds, $n = 8$ measurements, $r^2 = 0.97$, $F = 92.8, P < 0.0001$) represented the relationship for birds roosting in groups of five (Fig. 3). An *a posteriori* test for examining the differences between pairs of lines indicated that there were significant differences between the equations representing single roosting birds versus both groups of three and five birds (both $P < 0.001$). However, the difference between the latter two categories was not significant ($P = 0.72$).

The shelter afforded by the cavity resulted in a difference between T_a and T_c (temperature in an unoccupied cavity), and this difference increased as T_a decreased. For instance, the difference between T_c and T_a due to the shelter given by experimental nest/roost boxes at T_a of 5°C was about 1.4°C (Table 1). This temperature differential alone could result in a 3.3% reduction in energy expenditure by birds roosting inside, as opposed to roosting outside the nest box (Table 1). As T_a decreased, the absolute elevation in T_c increased, resulting in potentially relatively larger energy savings at lower ambient temperatures.

T_{cav} (temperature change due to warming of cavity because of presence of one or more birds)

TABLE 1. Summary of contributions to temperature elevation within cavities as a result of shelter and of cavity warming due to metabolic heat[a]. Results for different ambient temperatures (T_a) and group sizes, with the proportionate energy savings achieved by roosting Green Woodhoopoes.

| No. birds | DT from T_a due to | | Effective T_c (°C) | Energy expenditure ($Jg^{-1} h^{-1}$) | Total energy saving (%) |
	Shelter	Cavity warming			
		$T_a = 5°C$			
1	1.4	1.0	7.4	56.8	5.7
3	1.4	3.5	9.9	46.0	23.6
5	1.4	6.5	12.9	41.6	30.9
		$T_a = 10°C$			
1	0.7	1.0	11.7	50.7	4.6
3	0.7	2.5	13.2	41.9	21.2
5	0.7	4.5	15.2	38.9	26.8
		$T_a = 15°C$			
1	0.4	1.0	16.4	44.0	4.3
3	0.4	1.5	16.9	37.2	19.1
5	0.4	2.5	17.9	35.7	22.4

[a] Energy-expenditure values calculated using a conversion factor of 20.08 J/ml of O_2 consumed during metabolic trials. The latter value was subtracted from calculated energy expenditure of a single woodhoopoe roosting outside confines of a cavity, thus giving amount of energy saved under a given set of conditions.

increased both with the number of birds roosting together, and with decreasing T_a. For example, at T_a of 5°C, T_{cav} was 1°C when only a single bird roosted in a nest box, but T_{cav} was 6.5°C when five birds were roosting together (Table 1). The warming of the microenvironment within the cavity at T_a of 5°C, alone, could result in energy savings of between 2.4% for single individuals and 15.9% for individuals roosting with four conspecifics (Table 1). The energy savings achieved by three birds roosting together, attributable to the close proximity of bodies, was almost identical to that for five birds; at T_a of 5°C, 11.7% of energy savings was achieved for both instances in which three and five birds roosted together (Table 1).

Overall, a bird that roosted in a cavity with four conspecifics at T_a of 5°C potentially could expend 41.6 $Jg^{-1}h^{-1}$, compared to 60.2 $Jg^{-1}h^{-1}$ if it had slept alone outside a cavity. This represents a cumulative energy savings of almost 31%.

Body temperature of roosting individuals at a variety of ambient temperatures varied between 39.0° and 41.0°C, and this was the case irrespective of the number of birds roosting to-

gether. A single individual twice registered a T_b of around 38.5°C at a T_a of 10°C, but this happened on different nights.

DISCUSSION

Roost cavities are thought to be a critical resource for Green Woodhoopoe survival and reproduction (Ligon and Ligon 1978). This notion received experimental support when Du Plessis (1989a, 1992) distributed artificial nest boxes in a woodland that previously contained neither suitable cavities, nor woodhoopoes. Five woodhoopoe groups established permanent territories in this area within two months. All roosting and nesting activities were confined to these artificial boxes, providing evidence of the importance of cavities to woodhoopoes. The dependency of Green Woodhoopoes on roost cavities has been attributed to physiological limitations (Ligon and Ligon 1978, Ligon et al. 1988), antipredatory behavior (Du Plessis 1989b), and physiological enhancement (Williams et al. 1991). Ligon and Ligon (1978) first proposed that the necessity of cavity roosting appears to be responsible for the comparatively high rate of predation on woodhoopoes in Kenya. Recently, Ligon et al. (1988) suggested a causal relationship between the apparent inability of woodhoopoes to tolerate what appear to be moderately low nighttime ambient temperatures, and the development of group living. They proposed that woodhoopoes roosted in tree cavities to avoid low ambient temperatures. This fact, combined with the scarcity of available cavities, led to the retention of young in their natal territories, thereby setting the stage for the evolution of behavioral characteristics associated with cooperative breeding.

Williams et al. (1991) tested the thermoregulatory-insufficiency hypothesis on 10 wild-caught Green Woodhoopoes and found that birds in good body condition (as judged by relationship between body mass and wing length) could maintain normothermic body temperatures even at −10°C, a temperature well below that which birds would routinely encounter. Williams et al. posited that, since body condition apparently influences a woodhoopoe's ability to thermoregulate, roosting with conspecifics in tree cavities could lower daily energy requirements and place such individuals at an advantage during periods of food scarcity. They showed that adults that were in poor body

condition (two standard deviations or more below mean of body mass of free-living birds) were unable to maintain normothermic body temperatures even at moderate ambient temperatures. The findings of Ligon et al. (1988), that adults could not sustain normothermy at 19°C, lends some support for the idea that body condition is fundamentally important to the maintenance of T_b in adult woodhoopoes. All three birds used in their metabolic trials were between 8.2 to 18.3% below mean values for body mass for adult woodhoopoes in Kenya. During their first year of life, juvenile woodhoopoes in southern Africa frequently were in poor body condition (as judged by their body mass) even until they were 10 months old (Williams et al. 1991), suggesting that energy savings may be particularly important during this stage.

Energy savings attributable to communal cavity roosting.—We identified two components that may have affected the energy expenditure of individuals that roost communally in cavities (one associated with cavity roosting per se, and one associated with communal roosting): (1) shelter from the physical environment (see also Buttemer 1985); (2) warming of the microenvironment within the cavity, together with physical contact between bodies (or clumping).

The benefits associated with shelter provided by a cavity during the nocturnal phase were relatively small (5–6% energy savings at T_a of 5°C). However, the thermal properties of cavities may vary widely in the field, and attendant energy savings obtained by cavity-roosting woodhoopoes may be higher, or lower, depending on the characteristics of the cavity. When we take the effects of convective heat loss into account, the energy saving attributable to shelter provided by the cavity is magnified. For example, at an ambient temperature of 5°C, the nocturnal standard operative temperature (T_{es}) experienced by woodhoopoes roosting in the open would be 0.8 and −2.1°C at wind speeds of 0.1 and 0.5 m/s respectively (following Bakken 1990). This, in effect means that a bird roosting singly out in the open would, at a T_a of 5°C and wind speed u of 0.1 m/s, expend 64.2 $Jg^{-1}h^{-1}$, compared to 41.6 $Jg^{-1}h^{-1}$ if it had slept with four conspecifics in a cavity—an energy saving of 35.2%. At a wind speed of 0.5 m/s the energy saving would amount to 36.7%.

When several birds roost together, there is an additive elevation in temperature resulting from

metabolic heat produced within the cavity that provides a microclimate benefiting all birds simultaneously. Consequently, warming of the microenvironment plays a significant role in reducing an individual's nighttime energy expenditure. Again, the thermal properties of the cavity will influence this component of communal cavity roosting (i.e. larger savings in some cases, and smaller ones in others). In contrast to this pattern, Buttemer et al. (1987) reported that for Verdins (*Auriparus flaviceps*) the insulative properties of the nest cup were more important than the nest's retention of metabolically warmed air in forestalling heat loss by the roosting bird.

Huddling behavior has been shown to reduce the metabolic cost of thermoregulation, at constant body temperature, for birds and mammals (Pearson 1960, Baudinette 1972, Glasser and Lustick 1975, Pinshow et al. 1976, Withers and Jarvis 1980, Chaplin 1982). We found that the woodhoopoes had clumped during the course of all the metabolic trials, and propose that the component of communal roosting attributable to the physical contact between bodies of individuals played a significant role in the conservation of energy during the course of a night. Energy savings, however, reached a plateau with trios, as there was no statistically significant difference between metabolic rates of birds roosting in trios versus fives when the effects of cavity warming were experimentally controlled. Similar results were reported for European Starlings (*Sturnus vulgaris*) in which the metabolic rate of birds roosting singly was significantly higher than for birds roosting in pairs and quads, but there was no difference between metabolic rates of individuals in the latter two categories (Brenner 1965). We suggest that our results are attributable to physical constraints of the cavity in which we conducted our metabolic experiments, since the diameter of our metabolic chambers allowed physical contact between a maximum of only three birds (pers. obs.). This must also be the case under natural conditions, as our metabolic chambers simulated the "mean measurements" of cavities used under natural conditions.

Fitness consequences of communal cavity roosting.—We analyzed the seasonal pattern of mortality experienced by individuals living in groups of different sizes. Our predictions were that during the autumn and winter months, individuals (i.e. both juveniles and adults) living

TABLE 2. Summary of seasonal occurrence (by quarter) of juvenile and adult Green Woodhoopoe deaths in relation to group size at two southern African study sites. First and fourth quarters represent warm spring and summer months, while second and third quarters represent colder autumn and winter months.

Group size	Quarter died		P^a
	First and fourth	Second and third	
Juveniles on coast			
Small (3 and 4)	11	8	ns
Large (5 and 6)	10	14	ns
Juveniles inland			
Small (3, 4 and 5)	25	10	*
Large (6 and 7)	21	5	**
Adults on coast			
Small (2 and 3)	8	21	*
Large (4 and 5)	13	24	ns
Adults on coast			
Small (2 and 3)	4	21	**
Large (4 and 5)	14	20	ns

^{a} Chi-square test. ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$.

in large groups should experience proportionately lower mortality than those in smaller groups, and that this pattern should be accentuated at the inland study site, as nocturnal temperatures were consistently lower there.

Demographic data obtained over a period of nine years for Green Woodhoopoes at two sites in the eastern Cape Province, South Africa, provide a test of these hypotheses (Du Plessis 1989a). Over a nine-year study period, survivorship of breeders, nonbreeding adults, and first-year birds was not influenced by group size at either of the study sites (Du Plessis 1989b). During their first year of life, coastal woodhoopoes showed an even distribution of mortality over warm and cold seasons for both group-size categories, whereas inland birds from both categories suffered significantly higher mortality during the warmer months. The difference in the pattern of the seasonal distribution of deaths in relation to group size was not significant at either site (both $P > 0.25$; Table 2).

Seasonal mortality of first-year birds, therefore, did not conform to the predicted pattern. The high mortality rate of inland juveniles during the warm months is likely due to deaths that occur during the first three months of life (Du Plessis 1989b). At the inland site, foraging woodhoopoe groups moved more frequently and over greater distances than their coastal

counterparts. These differences were attributed both to the presence of smaller trees and sparser vegetation at the inland site than at the coast, and this presumably resulted in more frequent occurrences of localized resource depletion, thus necessitating more frequent group movements. Juveniles remained weak flyers for at least two to three months after fledging, and predation by raptors was the most frequent cause of death at this stage (Du Plessis 1989b).

Among adults, individuals living in small groups consistently suffered disproportionately high mortality during the winter months, whereas this was not the case for ones living in large groups (both $P > 0.05$). The difference in the pattern of the seasonal distribution of deaths in relation to the number of individuals present in such groups was significant only at the inland site (coast, $X^2_1 = 0.86$, $P > 0.90$; inland, $X^2_1 = 5.58$, $P < 0.05$; Table 2).

The seasonal pattern of adult mortality at the inland site was consistent with our predictions. First, it is likely that the proportionately higher survival of individuals living in large groups is related to the energetic benefits obtained by way of roosting communally in cavities during the winter months. We suppose that strong-flying adults do not run the same risks as fledglings during frequent, and relatively long, group movements. Second, the difference in the pattern of seasonal adult mortality between groups of different sizes was significant only at the inland site, and we suggest that this may largely be a function of the significantly lower nocturnal ambient temperatures that woodhoopoes experience there compared to ones at the coastal site. Absolute minimum temperatures were lower inland than at the coast, and group sizes at the former site were significantly greater than those at the latter (Du Plessis 1989a). The combination of these two factors suggests a possible link in Green Woodhoopoes between (1) environmental constraints that act in the form of minimum nocturnal ambient temperatures and (2) the degree of sociality found in this species.

Reyer and Westerterp (1985) demonstrated for Pied Kingfishers (*Ceryle rudis*) that energy expenditure was indeed a currency for fitness as measured by both survivorship and ultimate reproductive success. For Green Woodhoopoes, the potential fitness benefits gained through energy savings attributable to communal roosting may vary between populations, but we propose that, at the very least, this plays an im-

portant role in balancing the cost-benefit equation of sociality in this species.

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