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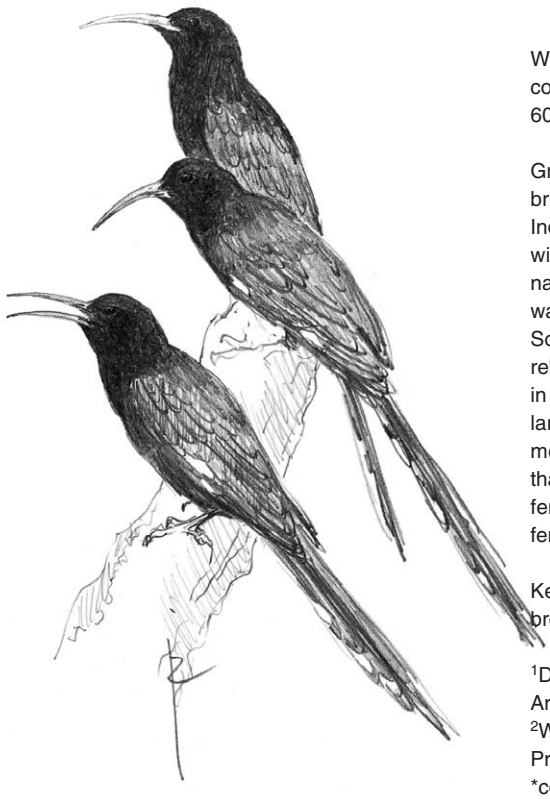
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Field metabolism and water influx of communal roosting Green Woodhoopoes *Phoeniculus purpureus*

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Williams J.B. & Du Plessis M. 2013. Field metabolism and water influx of communal roosting Green Woodhoopoes *Phoeniculus purpureus.* Ardea 101: 60–64.

Green Woodhoopoes (Phoeniculidae: *Phoeniculus purpureus*) are cooperative breeding birds that live throughout the year in groups of 2 to 16 individuals. Individuals roost in groups in cavities at night. The energy savings associated with communal cavity roosting has been implicated as an important determinant of survival in woodhoopoes. We measured field metabolic rate (FMR) and water influx of free-ranging adult woodhoopoes living in different group sizes in South Africa. We tested the hypotheses that woodhoopoes have a low FMR relative to other species of similar body mass, and that woodhoopoes roosting in small groups have a higher FMR than do individuals spending the night with large groups. For a male and females woodhoopoes, FMR differed from allometric predictions by –44.5% and –44.2%, respectively, supporting the idea that woodhoopoes have a markedly reduced FMR. Our data also indicated that females in small groups tended to have an elevated FMR compared with females in larger groups, but no such trends were identified for males.

Key words: woodhoopoes, field metabolic rate, water influx rate, cooperative breeding

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A species of open savannah woodlands in sub-Saharan Africa, Green Woodhoopoes *Phoeniculus purpureus* are cooperative breeding birds that live throughout the year in groups of 2 to 16 individuals, although groups larger than 7 are less common (Ligon & Ligon 1978, Du Plessis 1992). Throughout their range, woodhoopoes roost communally in tree cavities, despite the fact that they cannot excavate them (Du Plessis & Williams 1994). Dependence on cavity roosting appears critical for their survival by either reducing energy costs of thermoregulation of individuals, especially during winters, or protection from nocturnal predation, or a combination (Ligon & Ligon 1978, Du Plessis 1989, Williams *et al.* 1991).

The energy savings associated with communal cavity roosting has been implicated as an important determinant of survival in woodhoopoes (Boix-Hinzen & Lovegrove 1998). At inland locations in South Africa, adults in small roost groups (2–3) suffered disproportionately higher mortality during winter than ones living in larger groups (>7) (Williams *et al.* 1991, Du Plessis & Williams 1994). Communal cavity roosting can lower overall energy expenditure because (1) individuals experience less convective heat loss, (2) because group members warm the air in the cavity and thus reduce the gradient between body temperature (T_b) and air temperature (T_a), and (3) because heat transfer to the environment is reduced as individuals huddle together while roosting (Withers & Jarvis 1980, Williams *et al.* 1991, Du Plessis & Williams 1994, Boix-Hinzen & Lovegrove 1998). Depending on the architecture of the cavity and nighttime T_a, laboratory studies suggest that individuals can save up to 35% on their energy expenditure by roosting with conspecifics at low T_a (Du Plessis & Williams 1994, Boix-Hinzen & Lovegrove 1998). Such savings could contribute to the fitness of woodhoopoes thereby becoming a selective force for sociality in this species.

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In this study we tested the idea that woodhoopoes would have a low field metabolic rate (FMR) and water influx rate (WIR) compared with other non-cavity roosting species, and the hypothesis that individuals roosting with fewer conspecifics would have an elevated rate of metabolism. Using the doubly labeled water method (Speakman 1997), we measured the field metabolic rate (FMR) and water influx of free-ranging adult woodhoopoes living in different group sizes. We have found support for the idea that woodhoopoes have a markedly reduced FMR. Support for the second hypothesis was equivocal with females in small groups having a significantly higher FMR than females in larger groups, but no such trends were evident in males.

Study area

We studied Green Woodhoopoes in the Kubusi River Valley (32°32'S, 27°47'E), South Africa, in a 45-km^2 area during the winter of 1993, May–June. The vegetation of this region has been described by Du Plessis (1992). Most individuals of the groups that we studied had been previously banded and their territories marked (Du Plessis 1992). We determined the age and sex of birds based on their plumage, body mass, and bill coloration (Du Plessis 1992).

Natural history of Green Woodhoopoes

Green Woodhoopoes breed cooperatively and together defend a territory year-round (Ligon & Ligon 1978, Fry *et al.* 1988, Du Plessis 1992). Large groups tend to separate when roosting at night, often by sex (Fry *et al.* 1988). Woodhoopoes eat insects and other invertebrates that they capture by probing beneath bark and into crevices. The roost cavities selected by woodhoopoes vary in dimensions, and in their thermal quality, factors which add to variation to energy savings attributable to communal roosting.

Doubly labeled water

Measurements of FMR and water flux were obtained by means of the doubly labeled water (DLW) technique, in which the rate of decline of an isotope of hydrogen in the body water pool provides a measure of water flux (Nagy & Costa 1980), and the loss rates of both a hydrogen isotope and ^{18}O yield an estimate of CO_2 production (Lifson & McClintock 1966, Nagy 1980, Speakman 1997). Our procedures for using the DLW method have been detailed elsewhere (Williams 1987, Williams & Dwinnel 1990, Williams & Du Plessis 1996). In brief, groups of woodhoopoes were captured by placing a net over their roost hole before dawn, and waiting for their exit (Du Plessis 1992). After capture, we injected them with 0.35–0.40 ml of a mixture of tritiated water (1.1×10^4 Bq/ul) and 95 atom percent 18O, a quantity sufficient to raise initial levels of O-18 to >6000 ppm above background. After a 1-h period for equilibration of isotopes, we removed a 100 microliter blood sample from the brachial vein. Birds were then weighed with a Pesola scale that had been calibrated against a Mettler P2100 laboratory balance, banded if they were not already, and released. We recaptured birds 24 or 48 h later, took a second blood sample, weighed and released them.

Blood samples were microdistilled to obtain pure water (Wood *et al.* 1975), then assayed in three separate 10-μl aliquots for tritium activity. The O^{18} content was measured in triplicate in the laboratory of Dr. K. Nagy, University of California, Los Angeles. We calculated water influx using equation 6 of Nagy (1975) and rates of CO_2 production using $rCO_2 = (N/2.078)(k_o - k_d) - 0.0062 \times k_d \times N$, where rCO_2 is carbon dioxide production (moles/h), N is the average moles of body water, and k_o and k_d are isotope turnover rates (Speakman 1997). This equation assumes that 25% of the total water loss is subject to fractionation (Speakman 1997). In all cases background levels of isotopes, determined from blood samples of un-injected individuals ($n = 3$), were subtracted from values prior to calculations.

Estimates of water flux using isotopes of hydrogen are on average within ±10% of values obtained by standard laboratory methods (Nagy & Costa 1980) and estimates of CO_2 production as given by DLW are within 8–10% (Williams & Nagy 1984, Speakman 1997). Energy expenditure for an endotherm can be calculated from CO_2 production when the composition of the diet is known (Gessaman & Nagy 1988, Weathers & Sullivan 1989). We used a conversion factor of 24.6 kJ (per l CO_2) (Williams & Prints 1986). To adjust FMR for body mass (adjFMR), we divided FMR by $mass^{0.57}$ where the exponent comes from slope of equation for log FMR versus log mass for woodhoopoes.

Statistics

Computations were performed using SPSS 19.0 for Windows (SPSS, Chicago). In 10 cases we injected more than one individual in a group (2–3), so we used Repeated Measures ANCOVA to investigate differences in FMR and WIR between sexes. We tested interaction terms and removed them from the model when insignificant. Differences between means of males and females were determined by *t*-test. Values are presented ± 1 SD unless otherwise specified.

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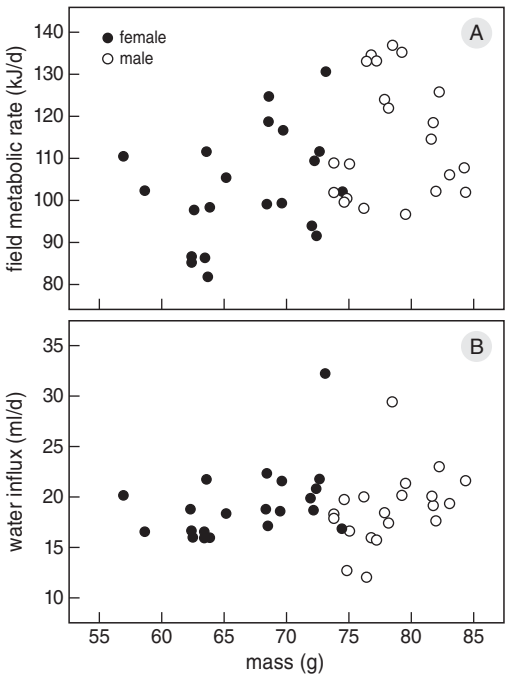


Figure 1. (A) Field metabolic rate (kJ/d) as a function of body mass (g) for Woodhoopoes. (B). Water influx (ml/d) as a function of body mass (g) for Woodhoopoes.

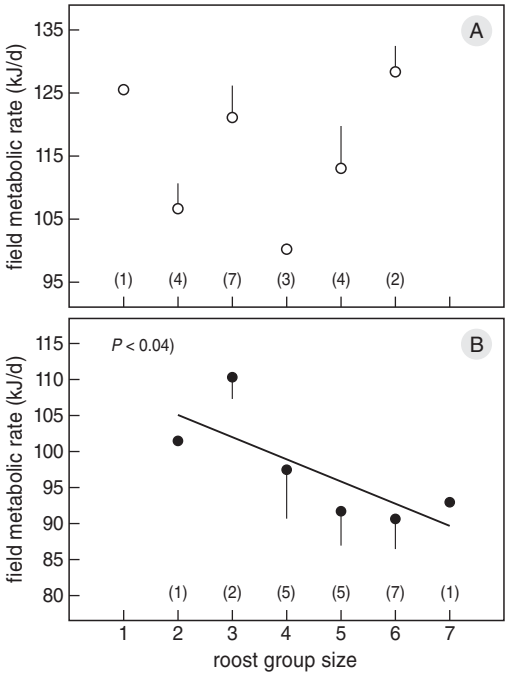


Figure 2. Field metabolic rate (kJ/d) as a function of roost group size for (A) male woodhoopes, and (B) for females. Bar represent ±1SE. Numbers in parentheses indicate numbers of individuals measured in each group.

Field metabolic rate versus body mass

We measured the field metabolic rate of 42 adult Green Woodhoopoes, 21 males and 21 females, members of 14 different groups of 1–7 individuals. Mass-specific CO_2 production was significantly correlated with body mass: ml CO_2 (/g/h) = 3.67 – 0.15×mass (g) (R^2 = 0.12, F = 5.3, $P < 0.03$, n = 42) when both males and females were considered, but not when sexes were considered separately. The relationship between FMR and body mass for males and females combined was log kJ/d = 0.97 + 0.573×log mass (R^2 = 0.19, F = 9.5, $P < 0.004$, n = 42; Figure 1A). With body mass averaging 78.6 ± 3.4 g, males expended energy at an average rate of 114.6 ± 14.0 kJ/d (n = 21), whereas females that weighed on average 66.9 + 5.02 g had a significantly lower FMR of 103.0 ± 13.0 kJ/d (n = 21)(t = 2.8, $P < 0.009$, n = 42). Obtained by dividing FMR by mass$^{0.57}$, normalized values for FMR were 9.52 ± 1.1 and 9.39 ± 1.1 for males (n = 21) and females (n = 21), respectively, values not significantly different (t-test, $P > 0.7$).

An allometric prediction for males for FMR was 206.8 kJ/d, whereas for females it was 184.6 kJ/d (Tieleman & Williams 2000). The average FMR that we measured differed from allometric prediction by –44.5% and –44.2%, respectively.

Field metabolic rate versus group size

When we analyzed the relationship between average FMR and roost group size, we found no significant trends for males (Fig 2A), but for females, there existed a negative correlation between average FMR and roost group size (Figure 2B; one-tailed test, r = 0.76, $P < 0.04$). These findings for females are consistent with the idea that individuals in small groups tend to have a higher FMR compared with those in larger groups. No such trend was evident for males. In an ANCOVA with FMR as the dependent variable, roost size and sex as fixed factors, and body mass as a covariate, we found no significant differences between groups (F = 1.01, $P > 0.4$, n = 42) or between males and females (F = 2.1, $P > 0.15$). In a regression analysis using all the data instead of mean values, females in smaller groups tended to have a higher FMR, but this relationship was not significant (F = 4.1, P = 0.057, n = 21). For males, we found no trends between FMR and roost group size (F = 0.2, $P > 0.6$).

Water flux

Male Woodhoopoes had an average water influx of 18.9 + 3.7 ml H_2O/d (n = 21) and females 19.3 + 3.6 ml H_2O/d (n = 21), values statistically indistinguish-

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able (Figure 1B; $t = 0.31$, $P > 0.7$). For male woodhoopoes averaging 78.6 g, an allometric prediction for water influx was 33.3 ml H_2O/d, whereas for a 66.9 g female, it was 29.6 ml H_2O/d (Tieleman & Williams 2000). The average values for water flux that we have measured differed from allometric prediction by –43.2% and –34.8%, respectively. Water influx did not correlate with body mass, FMR, for either sex, or with sexes combined.

Discussion

Our results support the idea that woodhoopoes have a low FMR relative to other species of similar body mass. This finding is consistent with the idea that they save energy during the night while roosting in cavities with conspecifics as has been shown in the laboratory (Du Plessis & Williams 1994). We found that the FMR of males and females differed from allometric prediction by –49.6% and –49.2%, respectively. These data are in agreement with laboratory studies that suggest energy savings of up to 35% as a result of roosting with conspecifics at low T_a (Du Plessis & Williams 1994, Boix-Hinzen & Lovegrove 1998).

Our conclusions are predicated, in part, on the assumption that woodhoopoes have a BMR similar to other species of the same body mass. Williams *et al.* (1991) measured the BMR of individual postabsorptive woodhoopoes in their thermal neutral zone as 58 kJ/d for individuals averaging 75.9 g, whereas allometric prediction yields a value of 59.5 kJ/d (Tieleman & Williams 2000). Our values of BMR deviated from prediction by –2.5% suggesting that woodhoopoes do not have a depressed rate of basal metabolism (see Boix-Hinzen & Lovegrove 1998 for an alternative view).

We have found support for the idea that female woodhoopoes roosting in small groups during winter have a higher FMR than do individuals spending the night within large groups. Although the evidence for this conclusion is weaker than one would like, the data are at least consistent with the idea.

In conclusion, free-living woodhoopoes had a remarkably low FMR compared with other birds of similar body mass, a result that is consistent with the idea that roosting in cavities and huddling with conspecifics saves considerable energy during the night. Although FMR for males did not vary relative to group size, females living in small groups had a higher FMR than did females living in large groups.

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Samenvatting

Groene Kakelaars *Phoeniculus purpureus* zijn coöperatieve broeders die het hele jaar in groepen leven. 's Nachts slapen kakelaars in holen in groepen van 2 tot 16 individuen. De energiebesparing die het gezamenlijke overnachten in een hol oplevert, kan een belangrijke bijdrage leveren aan de overlevingskansen van de vogels. In dit artikel wordt de dagelijkse energie-uitgave ("field metabolic rate", FMR) en waterbalans van vrij levende Groene Kakelaars in de vallei van de Kubusi Rivier in Zuid-Afrika gemeten. De auteurs testen de hypotheses dat kakelaars een lagere FMR hebben dan andere soorten met hetzelfde lichaamsgewicht en dat de FMR afneemt met toenemende groepsgrootte. Mannetjes en vrouwtjes hadden een lagere FMR (respectievelijk 44,5% en 44,2%) dan voorspeld op basis van hun lichaamsgewicht. Dit bevestigt de hypothese dat kakelaars opmerkelijk weinig energie per dag uitgeven. De metingen gaven aan dat vrouwtjes in kleinere groepen een hogere FMR hebben dan vrouwtjes die in grotere groepen slapen, maar voor mannetjes was deze trend niet aantoonbaar. (YIV)

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