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SHORT COMMUNICATION

Field metabolic rate, water flux and food consumption by free-living silky anteaters (*Cyclopes didactylus*) in Panama

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Abstract Wild silky anteaters (*Cyclopes didactylus*) were studied in Panama during the dry season using doubly-labeled water (DLW) to measure field metabolic rates (FMR) and water intake rates (WIR), and to estimate feeding rates. Their daily requirements for energy, food and water were low: only one- to two-thirds of those of typical eutherian mammals with the same body size. Anteaters' body-size-adjusted requirements were similar to, but higher than, those of sympatric three-toed sloths, another xenarthran species. Xenarthrans in general may have unusually low metabolic intensities and nutritional needs. Silky anteaters were strictly nocturnal, arboreal and myrmecophagous, and had relatively low body temperatures (31.5 ºC).

Keywords: *Cyclopes didactylus*, daily energy expenditure, drinking behavior, feeding rate, field metabolic rate, silky anteater

Tasa metabólica de campo, flujo de agua y consumo de alimentos de Serafines del platanar (*Cyclopes didactylus*) silvestres en Panamá

Resumen Se estudiaron serafines del platanar (*Cyclopes didactylus*) en Panamá durante la estación seca con agua doblemente marcada (DLW) para medir las tasas metabólicas de campo (FMR), la tasa de ingesta de agua (WIR) y para estimar las tasas de alimentación. Sus requerimientos diarios de energía, alimento y agua fueron bajos: correspondían a uno a dos tercios de los valores típicos para mamíferos euterios de tamaño corporal similar. Los requerimientos de los serafines, ajustados por el tamaño corporal, fueron similares pero más altos que los registrados en otra especie de Xenarthra simpátrica, el perezoso de tres dedos. Los xenartros en general pueden tener intensidades metabólicas y necesidades nutricionales inusualmente bajas. Los serafines del platanar fueron estrictamente nocturnos, arbóreos y mirmecófagos, y tenían una temperatura corporal relativamente baja (31,5 ºC).

Palabras clave: *Cyclopes didactylus*, comportamiento de consumo de agua, gasto diario de energía, serafín del platanar, tasa de alimentación, tasa metabólica de campo

The silky, or pygmy, anteater (*Cyclopes didactylus*) is sympatric with the three-toed sloth (*Bradypus variegatus*) on Barro Colorado Island in Lake Gatun, Panama. Both are in the Magnorder Xenarthra which, as a group, may have unusually low resting energy requirements (Irving *et al*., 1942; McNab, 1978, 2002). In free-living three-toed sloths, we found that field metabolic rates (FMRs), which include costs of activity, thermoregulation, digestion, and other costs of living above resting metabolic rates, were also unusually low (Nagy & Montgomery, 1980). We hypothesized that silky anteaters may also have comparatively low field metabolic rates. In addition, diet may influence resting or basal metabolic rates as well as field metabolic rates in mammals in general (see reviews by Speakman, 1997; Cruz-Neto & Bozinovic, 2004). Accordingly, we hypothesized that silky anteaters (insectivores) would have higher body-mass-adjusted FMRs than the folivorous sloths living in the same habitat. The study described here included measurements of field metabolic rates, and water influx and efflux rates, along with estimates of feeding rates. We also determined body temperatures and recorded daily time budgets, which allowed us to estimate the energetic costs of sleeping and activity.

Free-ranging silky anteaters living in the rain forest around the Smithsonian Tropical Research Institute's field station on Barro Colorado Island, Panama were studied near the end of the dry season (April) in 1977. Animals were captured by noosing them while they slept in trees during the daylight hours. After an anteater was captured, a small radio-transmitter with whip antenna was taped to its tail temporarily to facilitate relocation and recapture (Montgomery *et al*., 1973). Five individuals were recaptured on one to four occasions during different times of the day for measurement of body temperature (rectal, 1 cm deep) using a calibrated Tele-thermometer® (YSI) equipped with a blunt flexible probe. Ambient (shaded air) temperatures were measured adjacent to the anteaters immediately after measuring rectal temperatures.

Two radio-tagged anteaters were given doubly labeled water (DLW) (Nagy, 1980) in order to measure FMRs and water flux rates over time intervals lasting 3–4 days. The decline in hydrogen isotope concentration in a doubly labeled animal over time is a measure of the rate of water movement (gain and loss) through its body. The oxygen isotope traces both water and CO_2 loss, so the difference in the washout rates of the two isotopes is a measure of CO_2 production, or metabolic rate (Lifson & McClintock, 1966). An anteater was weighed (to ±1 g), a small (0.5 ml) blood sample was taken for measurement of background isotope levels, and the animal was given an intra-peritoneal injection of sterile water containing 0.9% NaCl, 90 atom % oxygen-18 and 0.10 milliCurie tritium per ml. After waiting at least 6 h for the labeled water to mix thoroughly in the body water space, another small blood sample was taken, and the animal was released where captured. The animal was recaptured three or four days later, weighed, and a blood sample taken before it was released again the next day. One of the animals was recaptured after 3.5 more days of free-living to obtain a third DLW measurement. Blood samples were analyzed at the University of California, Los Angeles, and rates of CO_2 production and water flux were calculated from isotope washout rates (Nagy, 1980; Nagy & Costa, 1980; and see details in Nagy & Montgomery, 1980). Body water volumes, required in the DLW calculations, were estimated as 0.754 l/kg body mass, which is the mean water content (determined as isotope dilution space; Nagy, 1980) of two injected anteaters. Labeled anteaters were radio-located frequently while they were free-ranging, and times spent active and resting, and distances moved, were estimated.

Diet was determined by sampling stomach contents (via intubation) of five marked silky anteaters on Barro Colorado Island. Feeding rates were estimated three ways. First, recaptured anteaters were placed in cloth bags to collect all feces voided over the next 24 hours. They remained relaxed and quiet while in these bags. The feces were dried and examined microscopically, and were found to consist nearly entirely of ants of over two dozen morpho-species. The numbers of ant heads in each morpho-species seen were recorded. Then, samples of each morpho-species were collected in the field, and the fresh and dried mass of the individual ants were measured to obtain average dry and live body masses per ant head for each ant morpho-species seen in *Cyclopes* feces. Daily food intake by a given anteater was estimated by multiplying the numbers of heads of each morpho-species of ant in its 24-h feces collection by the average fresh and dry mass per head of that ant type, and adding these together. Secondly, feeding rates were estimated from field metabolic rates (in units of kJ/d) by calculating the mass of ants required to provide that amount of metabolizable energy. We calculated that the overall ant diet was 76% water (from fresh and dry masses of our ant morpho-species samples), that the ant dry matter was 90% digestible (from our data on dry matter per ant head in food samples and in feces samples), that 90% of the digested dry matter was available for energy metabolism (metabolizable energy ≈ 90% of assimilable energy; Nagy, 2004a), and that the metabolizable dry matter was mainly protein, having 23 metabolizable kJ/ metabolizable g dry matter (Nagy, 1980). These values yielded the conversion factors of 0.22 g fresh food consumed per kJ metabolized, and 0.054 g dry matter of food consumed per kJ metabolized. Third, we estimated feeding rates from water intake rates, by assuming that all water taken in by silky anteaters was part of the food, either the preformed water already in the food (its succulence) or water formed later during oxidation of the nutrients in the food (metabolic water). For these calculations, we assumed that the metabolizable dry matter in ants yielded 0.098 ml metabolic water per g fresh ant food, and 0.41 ml metabolic water per g dry matter of ant food (conversion factors from Nagy, 1983). Thus, total water in the anteater's food (preformed plus metabolic) was 0.858 ml/g fresh matter, and 3.58 ml/g dry matter, which yield the conversion factors of 1.17 g fresh food consumed/ ml water intake and 0.28 g dry food consumed/ml water intake.

The body temperatures of four adult and one juvenile silky anteater in the field averaged only 31.5 ºC (SD=0.7 ºC; 14 measurements on five anteaters). This was about 5.1 ºC (SD=0.5 ºC) above ambient (shaded air) temperatures measured at the same time, but about 6 ºC below the body temperature of 37 ºC that is typical of eutherian mammals (McNab, 2002). However, silky anteaters had body temperatures that were similar to those in the three-toed sloths living in the same habitat (Montgomery & Sunquist, 1978). Our data were too sparse to detect possible daily variation in body temperatures of silky anteaters.

Body masses remained rather constant over the approximately four-day DLW measurement periods, and averaged 269 g per animal (**Table 1**). Rates of water gain and water loss were nearly equal, and averaged about 21 ml/d, while field metabolic rates averaged 120 kJ/d. The small sample sizes and large confidence intervals (near 20%) for these average rate values suggest some caution in interpreting the following calculations that are based on these rates. The three different estimates of feeding rate were surprisingly similar: 19.3 g fresh food eaten/d (based on 24-h fecal collections), 24.1 g eaten/d (from FMR measurements), and 26.3 g eaten/d (from water intake rates; **Table 1**).

The generally good agreement between feeding rates based on FMR (which we believe are the most reliable) and those based on water influx rates indicates that nearly all water intake can be accounted for by water in the food alone (preformed water plus metabolically produced water). This suggests that silky anteaters did not drink much free water during our measurements, even though there were rain showers nearly every day of the study. The water economy index (WEI) for free-living anteaters was calculated as the water intake rate, 21 ml/d, divided by the FMR, 120 kJ/d, to yield a value of 0.17 ml water intake per kJ of energy expenditure. This value is at the upper end of the range expected for an animal eating a carnivorous diet and not drinking any free water – 0.08 to 0.17 ml/kJ (Nagy, 2004b). This comparison further supports the suggestion that silky anteaters did not drink much water during our study period.

Table 1. Body masses and rates of mass change, water influx, water efflux, field metabolism, and estimated food consumption in free-living silky anteaters during the dry season on Barro Colorado Island, Panama. FMR=Field metabolic rate.

Animal number	5	9	9	Mean (SD)
Age, sex	Adult female	Adult male	Adult male	
Days elapsed	3.4	4.1	3.5	3.7 (0.38)
Body mass, g	241	279	286	269 (24)
Mass change rate, %/d	-0.12	+0.65	-1.65	-0.37 (1.17)
Water in, ml/d	18.7	20.1	22.9	20.6 (2.1)
Water out, ml/d	18.9	18.7	26.6	21.4 (4.5)
FMR, kJ/d	97.2	112.6	148.7	120 (26)
Food intake, g fresh/d (from feces)	12.3	22.9	22.7	19.3 (6.1)
Food intake, g fresh/d (from H_2O in)	21.9	23.5	26.8	24.1 (2.5)
Food intake, g fresh/d (from FMR)	21.4	24.8	32.7	26.3 (5.4)
Food intake, g dry/d (from FMR)	5.25	6.08	8.03	6.45 (1.43)

Table 2. Time-activity budgets, and estimated energy budgets of silky anteaters during the dry season on Barro Colorado Island, Panama. BMR=Basal metabolic rate. FMR=Field metabolic rate.

Animal number	5	9	9	Mean (SD)
Age, sex	Adult female	Adult male	Adult male	
Time sleeping, h/d	11.3	13.4	13.1	12.6 (1.1)
Time active/foraging, h/d	12.7	10.6	10.9	11.4 (1.1)
Distance traveled, m/d	56	73	99	76 (22)
Cost while sleeping, kJ/d	25.1	35.3	35.4	31.9 (5.9)
Cost while active, kJ/d	71.5	77.3	113.3	87.4 (22.7)
Cost of basal metabolism during activity period, kJ/d	28.9	27.9	29.4	28.7 (0.8)
Added cost of being active (above resting), kJ/d	42.6	49.4	83.9	58.6 (22.1)
Activity MR/BMR ratio	2.47	2.77	3.85	3.03 (0.73)
FMR/BMR ratio	1.80	1.78	2.29	1.96 (0.29)

Time budget and activity budget observations on telemetered, free-ranging silky anteaters showed that they were strictly arboreal and strictly nocturnal. They spent 12.6 hours per day (the daylight hours; **Table 2**) sleeping, curled up in the shade, hanging on lianas or small branches well below the canopy. They were active all night (11.4 hours per day), moving nearly constantly but slowly, and stopping briefly to feed at many ant colonies along their routes. They moved an average of 76 m each night. We used McNab's (1984) value for basal/resting metabolic rate (BMR) of silky anteaters to calculate the energy expenditures for sleeping anteaters and for the basal expenses during the activity period. Added costs of being active were determined by subtraction (**Table 2**). While active at night, anteaters were spending energy about three times as fast as when they were sleeping and were presumed to be at BMR. Over a 24-h period their FMR averaged 1.96 times BMR (**Table 2**).

Comparison with sloths and other mammals: The average field metabolic rate of free-living silky anteaters was only 38% [(120/316) kJ/d times 100] of the FMR expected for a eutherian mammal weighing 269 g (Nagy *et al*., 1999). Their water flux rates averaged only 66% [(21/31.7) ml/d times 100] of that expected for a typical eutherian mammal (Nagy & Peterson, 1988), and their feeding rates averaged only 42% [(26.3/62.3) g fresh food/d times 100], on average, of that predicted for a 269 g eutherian mammal (Nagy, 2001). Sympatric three-toed sloths (data from Nagy & Montgomery, 1980) had FMRs that were 28% [(600/2154) kJ/d times 100] of that expected for a 4080 g eutherian mammal, their water flux rates averaged only 53% [(155/293) ml/d times 100] of the predicted rate, and their feeding rates averaged 35% [(61/176) g dry food/d times 100] of that expected (predictions derived from references cited above). Thus, both of these xenarthrans had unusually low energy, water, and food requirements. This supports our first hypothesis, that silky anteaters also had quite low energy, water and food needs for a mammal of their size. We suspect that xenarthrans in general may have unusually low FMRs and food requirements.

The observations that silky anteaters had apparently higher size-adjusted relative FMRs than sloths (38% vs. 28% of predicted for a eutherian), higher size-adjusted relative water fluxes (66% vs. 53%), and higher size-adjusted relative feeding rates (42% vs. 35%) supports the dietary effect hypothesis of McNab (1986) that, as insectivores, silky anteaters should have relatively higher resource requirements than do the folivorous three-toed sloths (but see Cruz-Neto & Bozinovic, 2004). Unfortunately, the small sample sizes available for silky anteaters preclude adequate statistical comparisons at this time, so these differences remain suggestive only.

The FMR/BMR ratio of 1.96 for silky anteaters is similar to that of 1.80 for three-toed sloths (Nagy & Montgomery, 1980). This indicates that both of these xenarthrans were not working very hard to maintain themselves in the rain forest. Similarly, howler monkeys (*Alouatta palliata*) living in the same forest, which have a much higher size-adjusted BMR and FMR, close to those of typical eutherians, had an FMR/BMR ratio of 1.98 (Nagy & Milton, 1979). These large monkeys were using energy much faster than the xenarthrans for both resting and being active, but their relative intensity of work (above BMR) to maintain themselves was about the same. All three of these arboreal mammals living on Barro Colorado Island have energetically conservative life styles. Many species of eutherian mammals, marsupial mammals, and birds have FMR/BMR ratios that are well above 2.0, and some species in all three taxa have FMR/BMR ratios between 5 and 7, all while maintaining constant body mass in their natural habitats (Peterson *et al*., 1990).

In summary, silky anteaters (mean body mass 269 g), studied in the field in Panama during the dry season, had energy, food and water requirements that were only one-third to two-thirds of those expected for a typical free-living eutherian mammal of their body size. Their reduced resource requirements resulted mainly from a reduced basal metabolic rate and low body temperature (31.5 °C), and a sedentary, nocturnal, arboreal life style, moving only about 76 m per night while foraging. They ate only ants, mainly from arboreal ant colonies. The very low energy, food and water needs of these anteaters were similar to those of another xenarthran living in the same forest: the three-toed sloth. There are indications that the apparently higher body-size-adjusted resource needs of silky anteaters (myrmecophagous) compared with those of three-toed sloths (folivorous) may be related to diet differences.

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