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Energy Metabolism and Thermoregulation in the Golden Lion Tamarin (*Leontopithecus rosalia*)

Abstract

Energy metabolism and body temperature were examined in *Leontopithecus rosalia*, the golden lion tamarin. Total standard metabolic rate (SMR), defined as the metabolic rate of resting, fasted animals within thermoneutrality and during the inactive (nighttime) phase, averaged 381.5 ± 65.2 ml $O_2 \cdot h^{-1}$ (mass-specific metabolic rate 0.520 ± 0.089 ml $O_2 \cdot g^{-1} \cdot h^{-1}$). This value ranges from 73 to 89% of the expected SMR for animals of this body size depending on the predictive equation used. Active-phase resting metabolic rate within thermoneutrality was significantly greater than SMR, averaging 509.0 ± 44.6 ml $O_2 \cdot h^{-1}$ (0.709 ± 0.062 ml $O_2 \cdot g^{-1} \cdot h^{-1}$). Thermal conductance during the inactive phase was 20.3 ± 2.7 ml $O_2 \cdot h^{-1} \cdot ^\circ C^{-1}$ (0.029 ± 0.003 ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot ^\circ C^{-1}$) or 70% of that during the active phase (28.5 ± 3.2 ml $O_2 \cdot h^{-1} \cdot ^\circ C^{-1}$, 0.042 ± 0.004 ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot ^\circ C^{-1}$). These values are about 85% of the mammalian predicted value. Body temperature fluctuated substantially between day ($39.6^\circ C$) and night ($37.4^\circ C$). However, none of these differences between circadian phases are unusual for primates (or, indeed, mammals) of similar body size. Although the metabolic rate of *Leontopithecus* is lower than the predicted one, it is higher than those rates reported for small nocturnal primates with similar food habits. *Leontopithecus*' modest rates of energy turnover may reflect a combination of phylogenetic constraints, feeding ecology and/or an energy-saving tactic that comprises part of a strategy to maximize reproductive effort. Although callitrichids are often cited as having rapid growth and high reproductive effort, the moderately low SMR of *Leontopithecus* is consistent with its intrinsic rate of natural increase, which is 90-94% of that expected for a mammal of its body size.

Key Words

Callitrichidae

Leontopithecus

Energy use

Metabolism

Thermoregulation

Body temperature

Introduction

Constraints on the ability to obtain and allocate energy have been proposed as crucial proximate selective factors in the evolution of social organization, behavior and life history traits of New World primates in the family Callitrichidae (Platyrrhini) [1–3]. Most prominent among those characteristics presumably influenced by energy use is a high reproductive effort as evidenced by (1) an unusual (among primates) habit of producing twins, (2) a relatively large litter mass (up to 25% of maternal body mass [4]) and (3) the capacity for more than one litter per year. Other aspects of callitrichid biology, such as huddling together at night, facultative hypothermia or torpor in response to cool ambient temperatures and cooperative rearing of young suggest that trade-offs in allocation of energy among thermoregulation, activity and reproduction have played a major role in the evolution of callitrichid sociality and behavior. In addition, because callitrichids feed primarily on ‘high-quality’ [5] food items such as fruit, invertebrates and gums, it has been inferred that they have high energy requirements [5–7]. Although high energy use is consistent with high reproductive effort [8–10], the existing data on energy use in callitrichids actually suggest that they have low, not high, energy requirements relative to other mammals of similar body mass [11–15]; low energy requirements suggest constraints on energy availability and may be inconsistent with high reproductive effort [8, 9]. Unfortunately, there are too few data on energy use by callitrichids to permit direct comparison of energy use, reproductive effort and behavior; moreover, most of those data are either incomplete or difficult to interpret.

This paper is the first in a series on energy use in the golden lion tamarin, *Leontopithecus rosalia*. *Leontopithecus*’ biology is probably

the best known of any species in the Callitrichidae; its behavior, reproduction and ecology have been studied extensively both in captivity and the wild [1, 2, 12, 15–17]. However, little is known about how this species uses energy [12, 15, 18]. Thus, the main purposes of this first paper are to characterize energy metabolism and thermoregulation of *L. rosalia*, to evaluate those data with regard to the species’ behavior, diet and reproductive tactics and to compare that strategy of energy use to those of other small mammals, particularly primates, with similar ecological traits.

Biology and Energy Use of Golden Lion Tamarins

Golden lion tamarins are diurnal omnivores that feed predominantly on fruit and seeds but also consume noticeable amounts of invertebrates and small vertebrates such as amphibians [16]. In captivity, adult body mass ranges from about 550 to 850 g, with males having a tendency to be larger. In the wild, the mean body mass of males is 620 g while that of females is 598 g [J. Dietz, pers. commun.]. Wild social groups typically comprise 5–9 individuals, with several adults of both sexes and offspring. Normally, only one female within the group breeds, typically producing a set of twins each year [16, 17]. All adult-sized group members may carry infants, and, during travel, infants are carried predominantly by group members other than the mother [17]. Presumably, this behavior frees the mother from the energetic and foraging burdens associated with carrying offspring and permits a greater reproductive effort than if the mother were solely responsible for infant care [3, 19–21].

Unlike most other primates, all members of a callitrichid social group sleep huddled together [16, 17, 22–24]. In the case of golden lion tamarins, the group usually sleeps within a tree hole [16, 17, 24]. Although huddling has

been suggested to perform an antipredator function [22, 24, 25], there are thermoregulatory and energetic consequences of this behavior that likely are of adaptive significance. The geographical range of *L. rosalia* is farther from the equator, and thus presumably more thermally seasonal, than that of any other callitrichid except its congener, the black lion tamarin, *L. chrysopygus*. Thus, because golden lion tamarins are exposed to seasonal ambient temperatures as low as 8°C [26], thermoregulatory costs should be high relative to other callitrichids. Direct and indirect heat exchange during huddling may mitigate the allocation of energy to thermoregulation, in response to low ambient temperatures [27–29], and thus make more energy available for reproduction [8].

Callitrichids may also use circadian shifts in body temperature, basking and facultative hypothermia or shallow torpor as tactics to reduce thermoregulatory expenses in response to moderate or low ambient temperatures. There are numerous anecdotal reports that many callitrichid species display morning lethargy and lack of coordination that could be attributed to either circadian or facultative hypothermia [22, 24, 30]. Moreover, at least some species can withstand significant bouts of unregulated hypothermia at very low ambient and body temperatures [30].

In this paper, we examine resting and standard metabolic rates (RMR and SMR), thermoregulation and circadian patterns of body temperature (T_b) and metabolism with respect to the role of energy metabolism and thermoregulation in the biology of the golden lion tamarin.

Methods

Definitions

Standard Metabolic Rate. The heat production of a healthy, adult, nonreproductive, fasted (postabsorptive) animal, resting comfortably at an ambient temperature within the thermal neutral zone for that species, during the circadian time period when the species is normally inactive [31, 32]. The SMR is analogous to the basal metabolic rate reported in other studies on primates [33, 34].

Resting Metabolic Rate. The heat production of an animal at rest and postabsorptive, but not under the strict temperature and temporal conditions defined for the SMR [8, 35].

Thermoneutrality. The range of temperatures over which an animal does not alter heat production in response to changes in ambient temperature. The upper and lower bounds to the thermal neutral zone are called the upper and lower critical (T_{uc} and T_{lc}) temperatures respectively.

Thermal Conductance. The rate of increase of RMR with declining ambient temperature below thermoneutrality. This quantity estimates the energetic cost of thermoregulation with declining ambient temperature.

Procedures

Indirect calorimetry was used to determine SMR and RMR for 5 male and 1 female adult *L. rosalia*. Animals were housed at the Department of Zoological Research, National Zoological Park, Washington, D.C., USA, on a 24-hour light-dark cycle, with 11 h of light and 13 h of dark, and at air temperatures of 21–27°C. Food and water were provided ad libitum except that access to food was not permitted for at least 6 h prior to any measurement. All measurements were made during 1990–1992.

Standard methods of open-circuit respirometry [35] were used to determine oxygen consumption during the active (day, alpha phase) and inactive (night, rho phase) phases of the day. Oxygen consumption was measured with animals in a rectangular Plexiglas chamber (30 cm × 40 cm × 30 cm) lined on three sides with unfinished plywood. A negative-pressure, open-flow system pulled room air through the chamber. Chamber flow ranged from 1,200 to 5,200 ml·min⁻¹ to provide an appropriate deflection on the chart recorder. Outlet airflow from the chamber was metered, then H₂O and CO₂ were removed via columns of indicating silica gel and soda lime (6–12 mesh). Percent oxygen in the outflow air was measured using either a Beckman Model 755 paramagnetic oxy-

gen analyzer or an Ametek S-3A/II oxygen analyzer attached to a Miniscribe strip-chart recorder with full-scale output of 1.00% O₂. The system was calibrated after each determination of oxygen consumption using N₂ gas [36].

Chamber temperature (T_c) was regulated by placing the chamber within a water-jacketed, insulated stainless-steel chamber connected to a temperature-controlled water bath. This permitted T_c to be varied from 9 to 33 ± 0.2 °C, a range similar to that the species encounters in its natural habitat. T_c was measured with a type K thermocouple inserted in the top of the Plexiglas chamber and attached to an Omega 871 digital telethermometer.

Animals remained in the chamber for 2–4 h. By inspection, minimal metabolism was taken as the planimetered area of the lowest continuous 30-min time period. To ensure that the animal had acclimated to the chamber, the selected time period was at least 1 h after the animal had been placed within the chamber. Oxygen consumption was calculated using the formula of Fedak et al. [36] and is reported at standard temperature, pressure dry. Body mass was measured immediately before and following each measurement.

The respiratory quotient, the ratio of CO₂ production to oxygen consumption [37], was estimated from 8 simultaneous measurements of CO₂ production and oxygen consumption for 2 animals (4 measurements each for individuals BA and MM) during the inactive phase at T_c above the T_{lc}.

Core T_b were monitored on 2 adult males housed in a group of 7 animals, and an adult male and female from a group of 4 animals; these 4 animals were not included in the oxygen consumption study. T_b was measured using temperature-sensitive radio transmitters (SM1-Temp A, AVM Instruments Inc.) implanted in the peritoneum. Prior to implantation, all transmitters were calibrated from 36 to 42 °C, at intervals of 0.5 °C, by recording their pulse rates while submerged in a temperature-controlled water bath. Pulses were counted for 5 min using a radio receiver (AVM Instruments Inc.) and a digital timer. Nonlinear regression was used to develop a quadratic function relating pulse rate to water temperature.

The T_b of each animal was determined by counting pulses for two 5-min intervals each hour of the day. The same receiver and digital timer used in calibrating the transmitters were used to collect the data. Room air temperature and, at night, nestbox temperature (T_{nb}) were recorded before and after T_b.

Most measurements of T_b were made while the animals were with their respective groups in their normal cages. To examine the effect of changing T_c on T_b, the

animals from the group of 4 were monitored over several nights while resting in their nestbox within the double-walled constant-temperature chamber. In this way T_b for the 2 animals with transmitters in this group was measured at T_{nb} ranging from 13.9 to 33.3 °C.

Statistical Analyses

Convention is to report and analyze oxygen consumption as specific (mass-specific) metabolic rates (ml O₂·g⁻¹·h⁻¹) [38]. This approach is convenient because it seemingly adjusts for effects of body mass, thus permitting comparisons and graphical presentations that appear to be mass independent. However, because the allometry of metabolic rate has consistently been shown to be less than unity, specific metabolic rates are not 'mass independent'. A more appropriate approach to analysis of these data is to treat mass as a covariate. Thus, while for comparative purposes we present data as both specific and total metabolic rate (ml O₂·h⁻¹), all analyses were conducted using total metabolic rate with mass as a covariate [38].

T_{lc} was estimated by piecewise regression of the residuals from a linear regression of RMR with body mass on T_c [35]. T_{lc} was the temperature above which the slope of the residuals with respect to T_c did not differ from zero.

Mean RMR within thermoneutrality for individuals were compared between the active (RMR) and inactive (SMR) phases using paired-sample t tests. Within the activity phase, the relationship between RMR and body mass was examined using Pearson product-moment correlation on the untransformed data and linear regression on log-transformed data. Below thermoneutrality, RMR was compared between activity phases using one-way and two-way analysis of covariance with T_c and body mass as the covariates and activity phase and individual as grouping variables.

Wet thermal conductance (= total heat transfer coefficient [35]) was estimated using linear regression of oxygen consumption on T_c below the respective T_{lc} values [39]. Active- and inactive-phase thermal conductances for individuals were compared using paired-sample t tests.

Active- and inactive-phase T_b was compared across the 4 individuals using two-way Anova. Mean T_b was compared between active and inactive phases by t test. The relationship between T_b and ambient temperature was explored using Pearson product-moment correlation.

Data are reported as means ± standard error (SEM) where n = number of measurements and N = number of individuals.

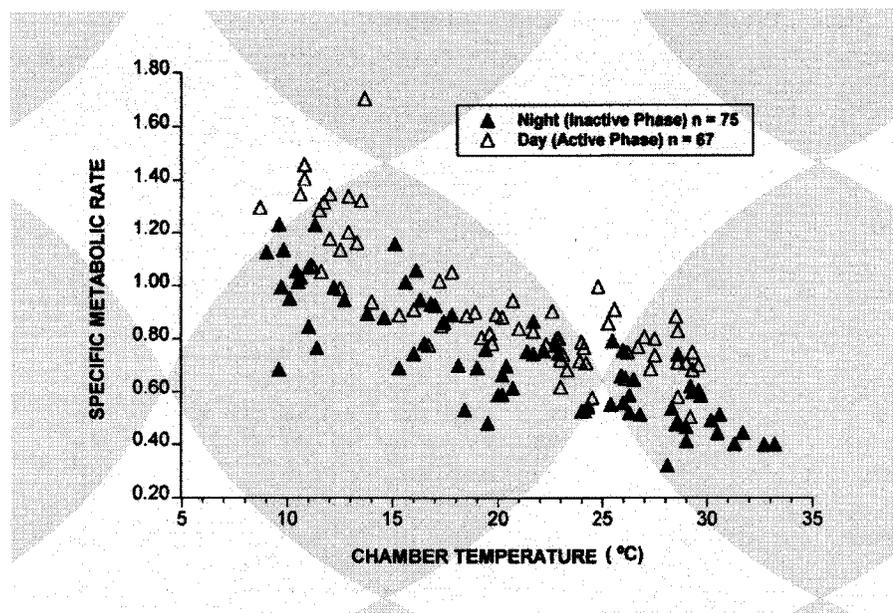


Fig. 1. Specific metabolic rate ($\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) as a function of T_c for active and inactive phases. $N = 6$ individuals (table 1), $n =$ number of measurements.

Results

Metabolic Rate

The pattern of mass-specific oxygen consumption as a function of T_c was similar to that reported for most mammals (fig. 1). Piecewise regression identified 4 breakpoints for the inactive phase: 28.1, 24, 19.5 and 12.7°C. Because (1) the coefficient for T_c above 28.1°C was not significantly different from zero and (2) inclusion of values below 28.1°C always resulted in a significant slope ($p < 0.05$), $T_{lc} = 28.1^\circ\text{C}$ for the inactive phase. A single breakpoint of 18.5°C was identified for the active phase. However, all regressions that included data below 25.5°C resulted in coefficients for T_c that were significantly different from zero ($p < 0.05$). For active-phase data above 25.5°C, the coefficient of T_c was not significant ($p > 0.1$). Therefore, the active-

phase T_{lc} was estimated to be 25.5°C. T_c did not exceed 30 or 33.2°C during the active and inactive phases, respectively. Both of these values appear to be below the respective upper critical temperatures for this species.

Within thermoneutrality, SMR was less than active-phase RMR (table 1, $p = 0.004$). Mean active phase RMR was $509.0 \pm 44.6 \text{ ml O}_2 \cdot \text{h}^{-1}$ (mass-specific metabolic rate $0.709 \pm 0.062 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) which is 108% of Kleiber's [40] predicted basal metabolic rate for animals of this size. Mean SMR averaged $381.5 \pm 65.2 \text{ ml O}_2 \cdot \text{h}^{-1}$ (mass-specific metabolic rate $0.520 \pm 0.089 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) which is only 79% of Kleiber's predicted. Comparisons with other published predictive equations for mammals [41, 42] gave similar results, with values ranging from 99 to 120% of expected value for active-phase RMR, and from 73 to 89% of the mammalian expected

Table 1. Mean SMR and RMR in thermoneutrality

Individual	Sex	Phase	n	Mass	Total RMR	Specific RMR	Percent of predicted ¹			
							ref. 40	ref. 41	ref. 42	ref. 43
BA	M	A	4	798.0±59.9	542.5±109.7	0.680±0.137	106	98	118	107
		I	6	858.0±13.7	345.0±34.4	0.402±0.040	64	59	71	64
DO	M	A	6	549.0±11.1	435.5±52.6	0.793±0.096	112	102	125	116
		I	2	565.0±7.1	378.0±51.9	0.669±0.092	95	87	107	98
HE	M	A	2	830.0±28.3	557.0±64.2	0.067±0.077	105	98	118	106
		I	1	780.0	432.0	0.554	86	79	96	98
JJ	M	A	3	657.5±10.1	472.0±23.6	0.718±0.036	106	97	119	109
		I	2	693.0±9.9	325.5±10.1	0.470±0.015	70	65	79	72
TB	M	A	2	802.5±19.1	549.0±15.3	0.684±0.019	106	99	119	108
		I	2	826.5±10.6	497.5±14.4	0.602±0.017	94	88	106	95
MM	F	A	2	669.5±6.4	497.5±1.0	0.743±0.001	111	101	124	113
		I	5	676.0±8.7	310.5±35.1	0.459±0.052	68	63	77	70
Mean		A		718.0±100.5	509.0±44.6	0.709±0.062	108±2.7	99±1.8	120±2.9	110±3.5
		I		733.0±99.8	381.5±65.2	0.520±0.089	79±12.6	73±11.7	89±14.3	83±14.4

A = Active phase; I = inactive phase.

¹ Expected calculated as $3.42 \cdot BW^{0.75}$ [40], expected calculated as $5.30 \cdot BW^{0.696}$ [41], expected calculated as $3.24 \cdot BW^{0.741}$ [42], expected calculated as $2.42 \cdot BW^{0.80}$ [43], with BW = body weight.

value for SMR (table 1). Comparison with a recent predictive equation for primates [43] found active-phase RMR for golden lion tamarins to be 110% and SMR only 83% of the expected value.

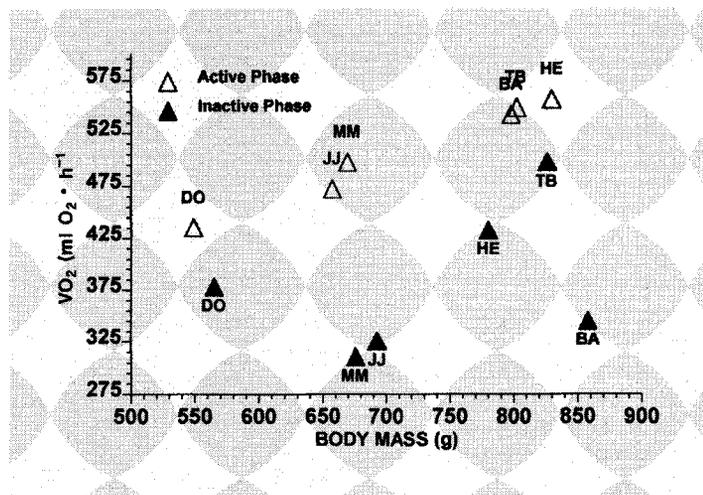
Mean active-phase RMR of individuals within thermoneutrality was strongly correlated with body mass ($r = 0.991$, $p < 0.001$). Although the estimated regression line for mean RMR during the inactive phase versus body mass was roughly parallel to the active-phase RMR regression line (fig. 2), the correlation between inactive-phase RMR and body mass was not significant ($r = 0.400$, $p > 0.1$). The log-log regression of RMR and SMR on body mass yielded coefficients of 0.607 for the active phase, which was significantly different from both zero and 0.75 (the coefficient for Kleiber's [40] much used equation; $p < 0.001$ and $p = 0.028$, respectively, $R^2 = 0.976$), and 0.439 ($R^2 = 0.160$) for the inactive phase.

The inactive-phase coefficient was not statistically significantly different from zero or 0.75 ($p > 0.1$).

Below the T_{lc} , inactive-phase RMR continued to be lower than active-phase RMR (fig. 1) relative to ambient temperature ($p < 0.001$). Body mass and T_c were significant covariates ($p < 0.001$). When both individual and activity phase were used as grouping variables in the Ancova, each was significant ($p < 0.001$). T_c was still a significant covariate ($p < 0.001$), but body mass was no longer significant ($p = 0.121$). Thus, variations in body mass did not have a significant effect on RMR within individuals but did contribute to the differences among individuals.

Thermal conductance during the inactive phase was about 70% of the value for the active phase. This difference was significant ($p = 0.038$). During the active phase, a decline of 1°C in T_c resulted in an average increase in

Fig. 2. Mean RMR and mean SMR (oxygen consumption, VO_2) as a function of mean body mass for all measurements.



RMR of $28.5 \pm 3.2 \text{ ml O}_2 \cdot \text{h}^{-1}$ ($0.042 \pm 0.004 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$) while the increase in RMR was $20.3 \pm 2.7 \text{ ml O}_2 \cdot \text{h}^{-1}$ ($0.029 \pm 0.003 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$) during the inactive phase. These conductances are both about 85% of Aschoff's [44] predicted value for mammals measured in the respective phases. However, these values for conductance must be interpreted cautiously as no subset of data extrapolated to T_b below 40°C [10].

The respiratory quotient was estimated at 0.75 ± 0.04 , $N = 2$, $n = 8$. Thus, within thermoneutrality, the mean active-phase RMR for the 6 animals in this study was estimated to correspond to $2.412 \pm 0.211 \text{ kcal} \cdot \text{h}^{-1}$ or $57.9 \pm 5.1 \text{ kcal} \cdot \text{day}^{-1}$, and the average inactive-phase RMR yielded $1.808 \pm 0.309 \text{ kcal} \cdot \text{h}^{-1}$ or $43.4 \pm 7.4 \text{ kcal} \cdot \text{day}^{-1}$. Assuming a 12-hour active 12-hour inactive cycle; total daily energy expenditure due to RMR within thermoneutrality for these individuals would average $50.64 \pm 6.2 \text{ kcal} \cdot \text{day}^{-1}$.

Below thermoneutrality, the estimated cost of thermoregulation was $0.135 \pm 0.015 \text{ kcal} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$ and $0.096 \pm 0.013 \text{ kcal} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$

during the active and inactive phases, respectively. Thus, every decline of 1°C in T_c below T_{lc} increased energy expenditure by just over 5% of either RMR or SMR within thermoneutrality.

Core Body Temperature

T_b values were not different between the 4 measured animals during either the active or inactive periods ($p > 0.1$) but did differ between phases ($p < 0.001$, fig. 3). Mean T_b during the active phase ($39.6 \pm 0.29^\circ\text{C}$) was significantly greater than that of the inactive phase ($37.7 \pm 0.33^\circ\text{C}$, $p < 0.001$). T_b varied little during the active phase although there was an 'anticipatory' decline immediately prior to 'lights out', which corresponded with a period of minimal activity with the animals usually in their nestbox [M. Power, pers. observation].

After an initial rapid decline to a mean of 38.3°C immediately after 'lights out', T_b declined another 0.9°C over the course of the night. Thus, the average minimal inactive-phase T_b for the 4 animals (37.4°C) was 2.2°C lower than the mean for the active

Fig. 3. Circadian pattern of T_b for 4 individuals (CHMT group) housed at room temperatures of 21–23°C. Error bars indicate standard deviation. 2 = Two measurements only.

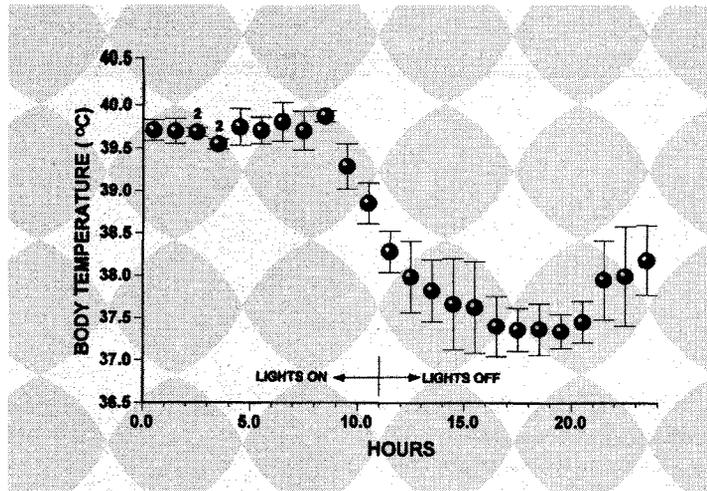
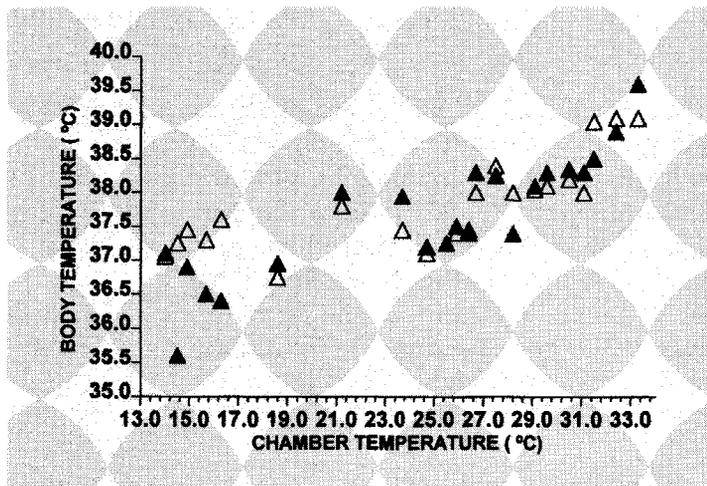


Fig. 4. T_b as a function of T_c for 1 male and 1 female with group at night. \blacktriangle = Night; \triangle = day.



phase. T_b immediately returned to the active-phase levels at 'lights on'.

Ambient (air) temperature in the cages averaged $26.4 \pm 0.9^\circ\text{C}$ during the active period and $26.2 \pm 0.6^\circ\text{C}$ during the inactive period. During the inactive period, however, the animals slept together in a nestbox where temperatures (T_{nb}) averaged $28.5 \pm 1.2^\circ\text{C}$. Mean T_{nb} is probably below the actual temperature of the air surrounding the monkeys, as the probe was not always immediately adjacent to

the huddling animals. Regardless, despite higher air temperature and T_{nb} , inactive-phase T_b of all 4 animals were significantly below T_b during the active phase.

T_b for both animals in the group of 4 animals (fig. 4) were correlated with T_{nb} ($r = 0.859$ and 0.757 , respectively, $p < 0.01$). At T_{nb} above 31.5°C , inactive-phase T_b for these individuals approached those of the active phase.

Discussion

RMR and SMR

Relative to its body size, the SMR of *Leontopithecus* is moderately low compared to that predicted for either mammals in general or primates of similar body size (table 1). This is consistent with data for other callitrichids, all of which fall below the various allometric equations (table 2). Despite suggestions that small primates generally feed on high-quality food and therefore must have high energy requirements, most small primates have SMR that are lower than predicted by allometric equations. For example, some species of *Galago*, *Aotus*, *Arctocebus*, *Nycticebus*, *Perodicticus* and *Tarsius* have SMR ranging from about 42 to 71% of expected value [33]. Other mammals with food habits characterized as containing mostly fruit but with some vertebrate and invertebrate components also have moderately low to low SMR. For example, in a comparison of 43 terrestrial carnivores, all 7 frugivore-omnivores had SMR lower than the allometric relationship for that group, ranging from 54 to 82% of the expected value [46]. Thus, *Leontopithecus* would seem to have an SMR that is typical of a mammal with its food habits.

McNab [34, 46, 47] contends that characterization of food quality should include not only energy content, but also 'roughage' and availability: high-energy foods may be rare or come in difficult-to-digest packages (e.g. ants and termites [48]). McNab suggests that, in general, frugivore-omnivore diets may actually be of low quality because the components are relatively unpredictable in time and space [34, 51]. Low SMR appears to be a common evolutionary correlate of a frugivorous-omnivorous diet, presumably because it reduces daily energy expenditure in the face of an unpredictable resource [34, 46–48]. Evidence exists that *Leontopithecus* and other callitrichids are energy limited, despite the 'high quality' of individual food items. Size of ranging area and habitat type are both correlated with reproductive success in wild *Leontopithecus* [21], and this is compatible with McNab's suggestion that while the individual items in a frugivore-omnivore's diet may be of high quality, their temporal and spatial pattern may not provide a diet that is predictable in quality or quantity over the short term (e.g. days).

Low thermal conductance during the inactive phase is also consistent with low SMR [33, 34, 46, 48]; it is a tactic that reduces the

Table 2. RMR and SMR of callitrichids

	N	Mass	RMR	SMR	Kleiber [40]
<i>Cebuella pygmaea</i> [12]	3	125.4	139.5		109.00
	4	121.5		77.8	62.00
<i>Cebuella pygmaea</i> [13]	2	116.8	113.5		93.00
<i>Callithrix jacchus</i> [14]	?	c. 190	152		
<i>Callithrix jacchus</i> [11]	5	356	197	154	70.00
					53.00
<i>Saguinus oedipus</i> [45]	12	500	436		121.00
<i>Leontopithecus rosalia</i> (this study)	6	718	509		107.00
	6	733		381.5	79.00

energy allocated to thermoregulation. However, minimal conductance was not precisely determined in that no subset of data extrapolated to a realistic T_b [10, 33, 44]. The absence of decreasing conductance and increasing metabolism so typical of many species (e.g. *Tarsius* [33]) below thermoneutrality suggests that these data may not represent true minimal conductance. As suggested by the data for 2 animals subjected to a range of T_c (fig. 4), T_b during the respirometry measurements may not have been constant at lower T_c values. If conductance is low in *Leontopithecus*, the situation may be unusual in that unlike other species that apparently achieve lowered conductance through pelage that appears rigid and dense (high number of follicles per surface area, e.g. *Tarsius* [33]), *Leontopithecus* fur is fine, long and wispy, and much less dense than might be expected. There are nearly bare areas on the ventral surfaces of the limbs and abdomen, and most regions of the body readily reveal the skin surface when the pelage is either physically brushed away or subjected to air currents. The long shaggy fur may represent a compromise between insulation against seasonally cool and cold temperatures versus the need to dump heat when faced with the high ambient temperatures and high relative humidity that characterize the daylight hours during much of the year in this species' natural habitat.

Captive golden lion tamarins, living in a social group, reduce their T_b several degrees from the active to inactive phase. Moreover, there is more variability in T_b during the inactive phase (fig. 3), suggesting that at lower ambient temperatures at least some individuals may allow T_b to drop even further in an effort to conserve energy (fig. 4).

The observed reduction in T_b during sleep in golden lion tamarins and other callitrichids [18, 35, 49] is consistent with various observations concerning callitrichid behavior and

physiology. Field researchers have commented upon the sluggishness of tamarins after dark [22, 23]. Captive common marmosets are completely inactive when it is dark [11, 50]. Captive golden lion tamarins and pygmy marmosets are difficult to arouse at night [M. Power, pers. observation]. Heart rate declines substantially at night in both saddle-back and cotton-top tamarins [35] and in common marmosets [51].

Most endotherms display a decline in both RMR and T_b from the active to inactive phase of the 24-hour day [31]. Callitrichids, including this study, have SMRs that range from 62 to 79% of active-phase RMR (table 2). This circadian variation in RMR is comparable to that reported for other small mammals as well as birds [52]. Thus, *Leontopithecus* does not display an unusual circadian pattern of metabolism. Rather, this study provides further evidence that RMR of most small primates, and probably most small mammals, differ substantially between the active and inactive phases.

Leontopithecus and other callitrichids differ from other low-SMR species in several ways. First, the behavior of most low-SMR species is slow and deliberate. Although many are capable of rapid locomotion, most adhere to an economy of movement that is broken only when a perceived threat is both proximate and imminent. The archetypal low-SMR species are sloths although many small marsupials, ant and termite feeders and many small primates (e.g. *Tarsius*, *Loris*, *Perodicticus*) are slow moving and deliberate. Second, McNab [42] has suggested that low SMR, particularly in conjunction with arboreality, is associated with low muscle mass and that the latter is the basis for the sluggish behavior of many low-SMR species. However, *Leontopithecus* is very active and has a relatively high muscle mass [Thompson and Grand, unpubl. data]. Third, *L. rosalia* and other callitrichids

are diurnal while many low-SMR species are crepuscular or nocturnal. Activity levels, for example flight in response to predators (diurnal) versus stealth and crypticity (nocturnal), may differ greatly.

Low SMR is inconsistent with either a high rate of reproduction or a high reproductive effort [8, 9]. The reproductive biology of *Leontopithecus* has consistently been compared to that of other primates but seldom compared to other mammals of similar size. Since most biologists agree that many important reproductive parameters vary allometrically both within and across groups, it is important to examine the energetic aspects of *Leontopithecus* biology with regard to both its phylogeny and its absolute body size (mass). Henneman [9] and others have reported that specific SMR is loosely correlated with the intrinsic rate of natural increase while others suggest a positive relationship between reproductive effort and SMR [8, 9, 47, 50]. The argument here is that SMR generally reflects the ability to allocate energy to reproduction [8, 9], perhaps because low SMR reflects energy limitation that is manifested by avoidance of high expenditures or because the limit on energy allocation to reproduction is a factorial increase over SMR [8, 9, 47]. Using a range of body mass from 650 to 750 g, *Leontopithecus*' rate of natural increase, calculated after Hennemann [9], ranges from 91 to 95% of that predicted by Hennemann. Moreover, at 79% of Kleiber's predicted SMR, *Leontopithecus*' rate of natural increase seems just about what Henneman's analysis would predict.

The data from this study enable us to examine the contribution of RMR to the total energy budget at different ambient temperatures in captive golden lion tamarins. In order to examine the costs of RMR and thermoregulation relative to total energy expenditure, we compared values for total daily RMR (under the assumption of constant temperature

between 20 and 30°C, and 12 h each of active and inactive phases) with average maintenance values for daily gross energy intake (= 133.5 kcal·day⁻¹), and an estimate of daily metabolizable energy intake (= 109.8 kcal·day⁻¹) for singly housed golden lion tamarins from Power [12]. The estimate of metabolizable energy was derived from gross energy, apparent energy digestibility, total protein intake and apparent protein digestibility [Power, unpubl. data] under the assumption that all protein digested is metabolized (i.e. no growth occurred).

Depending on ambient temperature, estimated total RMR was equivalent to 37.9% (at 30°C) to 49.6% (at 20°C) of average gross energy intake and 46.1% (at 30°C) to 60.3% (at 20°C) of estimated metabolizable energy intake. Thus, RMR probably accounts for roughly half of the metabolizable energy intake of captive, singly housed golden lion tamarins.

The extent of the energy 'savings' realized by golden lion tamarins from reducing RMR during sleep also depends on temperature. Within nighttime thermoneutrality (above 28°C), the difference between SMR and RMR is estimated to be 7.25 kcal or 6.6% of metabolizable energy. Below 25.5°C, the estimated energy difference between nighttime and daytime RMR decreases to 4.36 kcal·day⁻¹ or 4.0% of metabolizable energy.

To put these figures in perspective, the estimated metabolizable energy equivalents for carbohydrate, protein and fat for golden lion tamarins are 4.0, 4.1 and 9.0 kcal·g⁻¹, respectively. Assuming that typical orthopteran prey in the wild is similar in size and body composition with crickets such as are fed to this species in captivity, the differences between inactive- and active-phase RMR are equivalent to the metabolizable energy contents of 23 and 14 orthopteran prey at ambient temperatures above 28 and below

25.5°C, respectively. This emphasizes the important behavioral consequences, such as the potential effect on foraging time, of subtle aspects of the overall strategy of energy use.

Leontopithecus and other small primates should serve as a reminder that the varied

strategies and tactics of energy use displayed by mammals other than primates [32, 34, 42, 54] are also present among the primates. In the absence of data, primatologists should be especially cautious about inferring energy requirements for any given species.

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