

RESEARCH ARTICLE

Resting Energy Metabolism of Goeldi's Monkey (*Callimico goeldii*) is Similar to That of Other Callitrichids

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The resting metabolic rates (RMRs) of six adult Goeldi's monkeys (*Callimico goeldii*) were measured using standard methods of open circuit respirometry during both the active (daytime) and inactive (nighttime) circadian phases for this species. One subject was measured both while she was pregnant and after she delivered a full-term, stillborn infant. Inactive-phase RMR within thermal neutrality (above 27.5°C) averaged 288.5 ± 30.8 ml O₂/hr; active-phase RMR within thermal neutrality averaged 416.3 ± 60.9 ml O₂/hr. These values are 74.6% and 107.6%, respectively, of the mammalian expected for animals of this body mass. During the inactive phase, metabolic rate increased an estimated 4.3% for every degree decline in temperature below 27.5°C. The RMR in Goeldi's monkey is similar quantitatively and qualitatively to those of other captive callitrichids that have been studied, with active-phase RMR being at or slightly above the mammalian expected, and inactive-phase RMR being significantly reduced. We propose that this circadian pattern of RMR is a consequence of small body size, and is not a specific metabolic adaptation within the Callitrichidae. Thus we predict that metabolic studies measuring both circadian phases in other small primates will also find this pattern of reduced RMR during the inactive phase. The inactive-phase RMR within thermal neutrality of the pregnant female was not different from that measured after the stillbirth, despite an almost 15% difference in body mass. During pregnancy, however, the female was more metabolically responsive to temperature below thermal neutrality, and had a lower upper critical temperature (i.e., was less tolerant of heat). *Am. J. Primatol.* 60:57–67, 2003. © 2003 Wiley-Liss, Inc.

Key words: metabolic rate; Callitrichidae; circadian phase; primates

Contract grant sponsor: PHS; Contract grant number: RR2022.

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Received 16 September 2002; revision accepted 21 April 2003.

DOI 10.1002/ajp.10078

Published online in Wiley InterScience (www.interscience.wiley.com).

INTRODUCTION

The Goeldi's monkey (*Callimico goeldii*) is a small (ca. 500 g), New World primate that is similar in morphology, ecology, and behavior to members of the genera *Cebuella*, *Callithrix*, *Saguinus*, and *Leontopithecus*. Many authors place *Callimico* with these other four genera in the monophyletic family Callitrichidae [Martin, 1992; Schneider and Rosenberger, 1996]; however, others have placed *Callimico* within its own family, the Callimiconidae [Hershkovitz, 1977]. Molecular evidence supports a close phylogenetic relationship between *Callimico* and the undisputed callitrichids, although the exact relationship is still in question [Schneider & Rosenberger, 1996; Horovitz et al., 1998; Pastorini et al., 1998; Dornum & Ruvolo, 1999]. Based on molecular, morphological, and fossil evidence, Schneider and Rosenberger [1996] argued strongly that these five genera form a monophyletic unit, though they classified them at the subfamily level (Callitrichinae). In this work we refer to the five genera as "callitrichids" based on evidence that they form a monophyletic taxon, but without comment as to whether the taxonomic unit should be a family or subfamily.

One significant difference between *C. goeldii* and the other callitrichids is the number of offspring produced per year. Female *C. goeldii* typically produce a single offspring once per year. Other callitrichids regularly produce twin offspring, and many species are capable of producing two such litters per year. The high (for a primate) reproductive output of most callitrichids has been suggested to cause severe energetic and nutritional stress on reproductive females, and thus to underlie the adaptive significance of many aspects of callitrichid social behavior—most notably their system of cooperative infant care [Garber et al., 1984; Tardif et al., 1993]. *C. goeldii* exhibits many of these infant-care behaviors, although perhaps to a lesser extent compared to other callitrichids [Tardif, 1994; Schradin & Anzenberger, 2001]. Therefore, comparisons of *Callimico* with other callitrichids could increase our understanding of the adaptive significance of these and other aspects of callitrichid reproductive and social behavior [Tardif, 1994].

Because the energy and nutritional costs of reproduction are hypothesized to underlie much of callitrichid social structure, basic information on energy metabolism and expenditure is crucial to furthering our understanding of these animals. This research was designed to compare resting metabolic rates (RMRs) of *C. goeldii* with those of callitrichids previously studied. The null hypothesis is that *Callimico* will not differ from the other callitrichids, due to the phylogenetic, morphological, and ecological similarities among these species. An alternative hypothesis is that the higher costs of reproduction in the callitrichid species that twin have favored the evolution of energy-saving mechanisms that are absent in *Callimico*.

One feature of energy metabolism common to all callitrichid species studied thus far is a large decline in both body temperature and RMR during the inactive (night) period. The nighttime RMR within thermoneutrality is 30–40% lower than daytime RMR [Petry et al., 1986; Power, 1991; Thompson et al., 1994]. This decline in metabolism is equivalent to approximately 10% of daily maintenance energy for captive nonreproductive adults [Power, 1991]. We measured night (inactive-phase) RMR at a variety of ambient temperatures and day (active-phase) RMR within thermal neutrality in six adult *Callimico* (three males and three females). These data enable us to compare basic energy metabolism in this species with previous data from other callitrichid species.

METHODS

Standard methods of open circuit respirometry were used to measure day and night RMR in three male and three female adult *C. goeldii*. The methodology employed was identical to that used to measure RMR of pygmy marmosets (*Cebuella pygmaea*) [Power, 1991] and golden lion tamarins (*Leontopithecus rosalia*) [Thompson et al., 1994].

Definitions

Thermal neutral zone (TNZ).

The TNZ is the range of temperatures in which an animal's RMR is invariant with temperature. The upper and lower limits to the TNZ are termed the upper (T_{UC}) and lower (T_{LC}) critical temperatures, respectively.

RMR.

The RMR is the heat production of a healthy, adult, nonreproductive, postabsorptive animal that is resting comfortably. For animals (such as primates) that have consistent, prolonged periods of inactivity, a distinction should be made between active-phase RMR and inactive-phase RMR. If the measurement is made at an ambient temperature within the thermal neutral range for that species, and during the circadian time period when the animal is normally inactive (inactive-phase RMR), the measurement is termed the standard metabolic rate (SMR) [Aschoff and Pohl, 1970; McNab, 1978; Thompson et al., 1994]. The SMR is analogous to the basal metabolic rate (BMR) in humans, and is an estimate of the lowest rate of energy metabolism.

Respiratory quotient (RQ).

The RQ is the ratio of carbon dioxide produced to oxygen consumed by an animal [Maynard et al., 1979]. The RQ will vary depending on the ratios of the substrates being metabolized (carbohydrate, protein, or fat). Different RQs are associated with different values for energy produced per liter of oxygen consumed or liter of carbon dioxide produced.

Procedures

The animals were housed in two groups: a family group of four adult animals, and an adult pair that had never reproduced. Animals had no access to natural sunlight; room lights were on a 12:12 cycle, with lights out at 7:00 P.M. and lights on at 7:00 A.M.

The animals were caught in a modified version of their plexiglass nest box, which had screen mesh at either end to allow free air flow. The nest boxes had been previously weighed, and were reweighed with the animal inside. The animal's weight was determined by the difference. The nest box with the animal inside was placed within a larger plexiglass respirometry chamber. The respirometry chamber was placed within a water-jacketed chamber attached to a recirculating water bath. By varying the temperature of the water flowing through the jacket, the ambient air temperature was varied from 20°C to 32°C, a range appropriate to the natural history of these animals. A negative pressure system was used in which room air was drawn through the respirometry chamber and then through a Beckman model 870 CO₂ analyzer (Beckman, Fullerton, CA). Water vapor and carbon dioxide were removed from a subsample of the airstream and passed through one chamber of an Ametek S3A-II dual channel oxygen

analyzer (Ametek, Paoli, PA). Dry, CO₂-free room air was passed through the other chamber to provide a continuous baseline. Animals remained in the chambers for 3–6 hr during each measurement.

Five to seven nighttime measurements were made for each of the six animals at chamber temperatures ranging from 20.1°C to 31.4°C. All nighttime measurements were made between 10 P.M. and 5 A.M., with the majority made between 10 P.M. and 1 A.M.. One daytime (between 9 A.M. and 4 P.M.) measurement was made for each animal at approximately 29.5°C ($\pm 0.2^\circ\text{C}$). The parameters measured were: air temperatures of the respirometry chamber and the water-jacketed chamber using copper-constantin thermocouples, the air flow rate through the chamber using mass-flow meters (Omega Engineering, Stamford, CT), the oxygen concentrations of room air and the air leaving the chamber, and the carbon dioxide concentration of the air leaving the chamber. From these measurements, the oxygen consumption and carbon dioxide production of the animal within the chamber as a function of ambient temperature were calculated. From these data the TNZ, RMR as a function of temperature, and RQ were determined.

In this research RMR was calculated as total metabolic rate (ml O₂/hr), following the argument of McNab [1999] that total metabolic rate is the ecologically and evolutionarily relevant concept, and that mass-specific metabolic rate is derivative in nature. Although in McNab's [1999] view, the two parameters are "two sides of the same coin," Hayes [2001] pointed out that despite the fact that there is a simple relationship between the allometric scaling coefficients of these parameters (mass specific coefficient = total coefficient - 1), the two parameters do not necessarily have to be correlated. Thus, the two parameters may measure different concepts. Total metabolic rate is directly related to energy expenditure, which is the parameter of interest in the current study. Mean mass-specific metabolic rates are also reported; however, note that multiplying the mean mass specific metabolic rate by the mean mass will not give the same value as the mean metabolic rate. This is not due to rounding errors, but rather to the fact that averaging a set of metabolic rates divided by their respective masses is not mathematically equivalent to dividing average total metabolic rate by the average mass [Power, 2000].

One female was pregnant during the study. Before the end of the study she delivered a full-term but stillborn infant. Five measurements of inactive-phase RMR were made on this animal during the last 2 months of gestation, and six additional inactive-phase measurements and one active-phase measurement were made after the stillbirth.

All values are presented as mean \pm SEM. Linear regression is used to estimate the increase in energy expenditure per decline in temperature below thermal neutrality, and to estimate the allometry of metabolic rate within thermal neutrality for callitrichid primates, using these data and previously published data.

RESULTS

The nonpregnant animals in the study averaged 547 ± 40 g, with a range of mean body mass of 357–618 g (Table I). The smallest animal was a reproductive male that had sired two other animals in the study. This animal had always been small. The pregnant female averaged 681 ± 14 g during the last 2 months of gestation, compared to an average of 598 ± 8 g after the stillbirth.

Lower critical temperature was estimated to be 27.5°C. Above this temperature the regression of RMR with temperature was not significant. The

upper limit of thermal neutrality could not be determined, but was above 31.4°C (except for the pregnant individual). All animals had higher RMR below 27.5°C, averaging 123% of RMR within thermal neutrality. Because core body temperatures were not measured, thermal conductance could not be determined. However, the slope of the regression line below 27.5°C was significantly negative, and implied an increase in RMR of 4.3% for every 1°C decline in temperature (Fig. 1).

Within thermal neutrality, inactive-phase RMR (equals standard metabolic rate, SMR) was less than active-phase RMR for all animals (Table I), with a mean among individuals of 71.7% of average active-phase RMR. Within thermal neutrality the average inactive-phase RMR was 288.5 ± 30.8 ml O₂/hr (0.527 ± 0.017 ml O₂/hr/g) and active-phase RMR was 416.3 ± 60.9 ml O₂/hr (0.749 ± 0.072 ml O₂/hr/g). These values are 74.6% and 107.6% of the predicted value for mammals of this mean mass (547 g), respectively [Kleiber, 1975].

Mean RQ for these measurements was 0.75 ± 0.02 , which corresponds to 4.74 ± 0.04 kcal per liter of oxygen consumed [Maynard et al., 1979]. Thus, the average energy expenditure due to RMR within thermal neutrality was calculated to be 1.97 kcal/hr during the active phase, and 1.37 kcal/hr during sleep. Based on a 12-hr active/inactive cycle, those estimates correspond to 40.1 kcal/day expended via RMR. This represents a 15.2% reduction in estimated daily energy expenditure via RMR based on 24 hr of active-phase RMR (47.3 kcal/day).

Inactive-phase RMR within thermal neutrality of the pregnant female (349 ± 8 ml O₂/hr) was not different from her nonpregnant values (345 ± 6 ml O₂/hr).

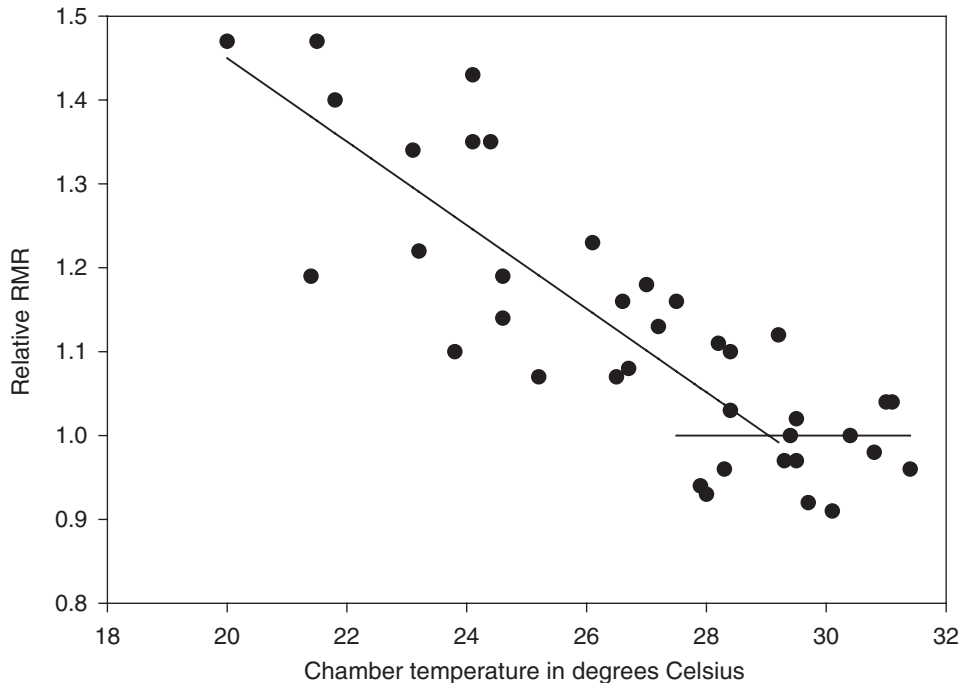


Fig. 1. Inactive-phase (nighttime) RMR of individual *Callimico goeldii* by temperature, expressed as a fraction of each animal's mean RMR within thermal neutrality (above 27.5°C). The data from 040 during pregnancy is excluded. The regression equation for the data below 27.5°C is: $2.289 - .043 \times \text{temperature}$ ($R^2 = 0.446$, $F = 16.287$, $P = 0.001$).

TABLE I. Mean Values (\pm SEM) for Body Mass and RMR of the Animals in the Study

Animal ID	Sex	Mean body mass (g)	Inactive RMR (ml O ₂ /hr)	Active RMR (ml O ₂ /hr) (n = 1 for all subjects)
038	♀	537 \pm 5	244 \pm 13	274
039	♂	357 \pm 6	183 \pm 11	249
040 pregnant	♀	681 \pm 14	349 \pm 8	Not measured
040 not pregnant	♀	598 \pm 8	345 \pm 6	513
041	♂	558 \pm 5	245 \pm 6	327
042	♀	615 \pm 14	336 \pm 19	560
043	♂	618 \pm 12	378 \pm 11	575

This was true despite a >80 g difference in average body mass between those measurements. Thus, her average mass-specific inactive-phase metabolic rate was lower when she was pregnant (0.512 ml O₂/hr/g vs. 0.577 ml O₂/hr/g, respectively). There were qualitative differences in RMR between the pregnant and nonpregnant states (Fig. 2). When the female was pregnant, the RMR was substantially increased over minimal levels at 31°C, a temperature that was within thermal neutrality for all other animals. In addition, when she was pregnant the RMR was increased below the lower critical temperature more consistently than it was after the stillbirth.

Using the data from the sources in Table II for callitrichid species, the linear regressions of ln(body mass) vs. ln(RMR) for both inactive ($F = 138.27$, $df = 5$, $P < 0.001$, $R^2 = 0.965$) and active ($F = 50.48$, $df = 6$, $P = 0.001$, $R^2 = 0.892$) phase RMR within thermal neutrality were highly significant. The coefficients for body mass were 0.863 and 0.792 for inactive- and active-phase RMR, respectively. The 95% confidence intervals for both coefficients included both 0.75 and 1 (0.659–1.067 and 0.506–1.079 for inactive- and active-phase RMR, respectively). The equations for estimating RMR within thermal neutrality in callitrichids from these data are:

$$1.19 \times (\text{body mass})^{0.863} \quad \text{inactive-phase RMR} = \text{SMR}$$

$$2.72 \times (\text{body mass})^{0.792} \quad \text{active-phase RMR}$$

DISCUSSION

Although there is debate about the precise phylogenetic position of *C. goeldii* relative to the other genera within the Callitrichidae, there is broad agreement that *C. goeldii* is the closest extant genus to the callitrichids, if not a callitrichid itself. These data indicate that *C. goeldii* is similar in energy metabolism to previously studied callitrichids (Fig. 3). The active- and inactive-phase RMRs of *C. goeldii* are similar to those of other callitrichids if scaled to body size by mass to the three-fourths power. Using the regression equations derived from the data presented in Table II, the estimated inactive- and active-phase RMRs for a callitrichid of 547 g would be 275.5 ml O₂/hr and 401.5 ml O₂/hr, respectively, which are very similar to the actual results reported here. The findings of Kálin et al. [in press] on 10 *C. goeldii* (mean body mass = 557 g, lower critical temperature = 27°C, mean SMR = 278 ml O₂/hr) provide independent evidence supporting our findings for *C. goeldii*. They also conclude that energy metabolism and thermoregulatory patterns in *C. goeldii* are similar to those in other callitrichids. In general, callitrichids, including *Callimico*, appear to have active-

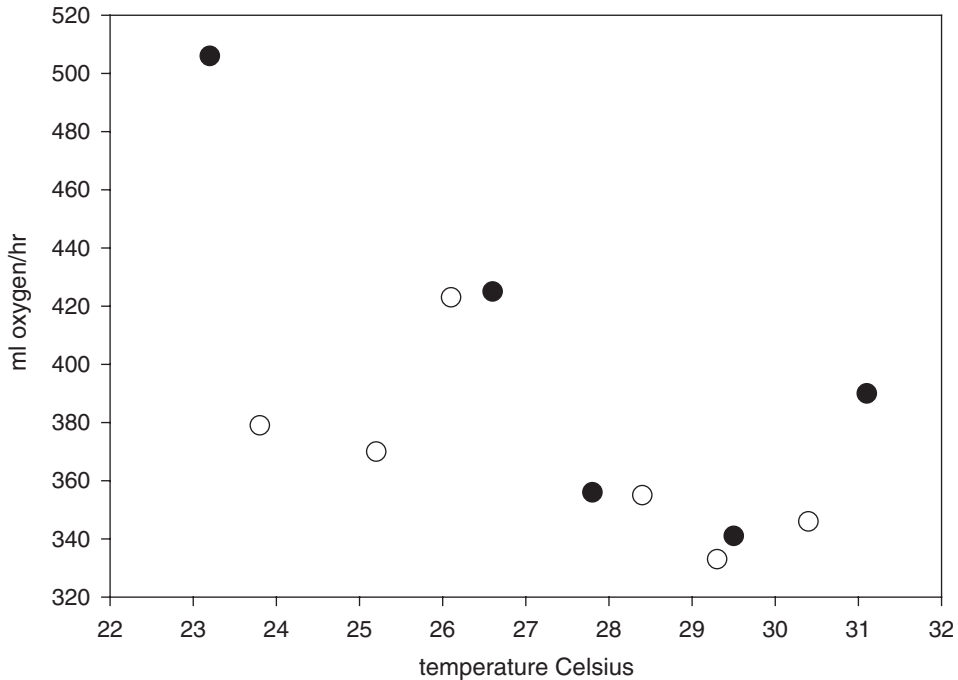


Fig. 2. Inactive-phase RMR as a function of ambient temperature for animal 040, both while she was pregnant (filled circles) and after she gave birth to a stillborn infant (open circles).

phase RMRs that are approximately equal to the mammalian predicted using Kleiber's [1975] relationship [Morrison and Middleton, 1967; Petry et al., 1986; Power, 1991; Thompson et al., 1994; Stonerook et al., 1994] (this study), but have inactive-phase RMRs (SMR) that are significantly lower [Petry et al., 1986; Power, 1991; Thompson et al., 1994; Genoud et al., 1997; Kälín et al., in press] (this study).

Although neither of the allometric scalings of RMR among callitrichids estimated in this work are statistically different from 0.75, they, like many coefficients for the allometry of energy metabolism among callitrichids, are numerically higher than this value. For example, Power [1991] estimated the allometry of digestible energy intake among five species of callitrichids to be 0.893, and Kälín et al. [in press] estimated an intraspecific allometry in *C. goeldii* of 0.86. However, again neither of these values were statistically different from 0.75. Stonerook et al. [1994] found that mean active-phase RMR of wild *Saguinus oedipus* (mean body mass = 296 g) was 60% of the mean value for captive animals (mean body mass = 500 g), implying a linear relationship between active-phase RMR and body mass. In contrast, Thompson et al. [1994] reported intraspecific allometries for *Leontopithecus rosalia* of 0.607 and 0.439 for active- and inactive-phase RMRs, respectively. We do not yet have sufficient data to assess whether the allometry of energy metabolism within callitrichids differs from that of primates in general.

These data support the hypothesis that the circadian pattern of energy metabolism seen in the callitrichids is either a phylogenetic property of being a callitrichid primate, or a function of their small body size (allometry). It seems

TABLE II. Mean Body Mass and RMR (as Percent of Expected) for Small Primates

Species	Nocturnal/ diurnal	Average body mass (g)	Active RMR ^a	Inactive RMR ^a	Reference source
<i>Cebuella pygmaea</i>	Diurnal	114	93%	–	Morrison and Middleton [1967]
		124	109%	62%	Power [1991]
		153	–	66%	Genoud et al. [1997]
<i>Callithrix jacchus</i>	Diurnal	356	70%	55%	Petry et al. [1986]
<i>Saguinus oedipus</i>	Diurnal	500	121%	–	Stonerook et al. [1994]
		300	110%	–	
<i>Callimico goeldii</i>	Diurnal	547	107%	76%	This study
		557	–	71%	Kälin et al. [in press]
<i>Leontopithecus rosalia</i>	Diurnal	725	108%	79%	Thompson et al. [1994]
<i>Galago demidovii</i>	Nocturnal	68	–	78%	Dobler [1982]
<i>Galago moholi</i>	Nocturnal	156	–	79%	Dobler [1982]
<i>Galago elegantulus</i>	Nocturnal	262	–	97%	Hildwein [1972]
<i>Galago senegalensis</i>	Nocturnal	275	–	86%	Dobler [1982]
<i>Loris tardigradus</i>	Nocturnal	284	–	54%	Müller et al. [1985]
<i>Cheirogaleus medius</i>	Nocturnal	330	–	81%	McCormick [1981]
<i>Peridicticus poto</i>	Nocturnal	1,024	–	76%	Hildwein and Goffart [1975]
<i>Nycticebus coucang</i>	Nocturnal	1,160	63%	40%	Müller [1979]

^aExpressed as a percent of the mammalian expected for body mass given by the formula: $3.42 \times (\text{body mass g})^{0.75}$ [Kleiber, 1975].

unlikely that this pattern of a significant reduction in RMR during the inactive phase evolved to support their greater reproductive output. However, it remains possible that the existence of this pattern was a factor in the evolution of twinning in most of the callitrichids.

The allometry hypothesis is supported by data from a study of rodents of <1 kg body mass, in which it was found that inactive-phase RMR averaged 25% lower than active-phase RMR [Kenagy & Vleck, 1982]. Few studies have measured RMR in both phases in primates, aside from the studies on callitrichid. A study of the metabolic rate of *Nycticebus coucang* (1,100 g body mass) found that inactive-phase RMR was 36.5% lower than active-phase RMR [Müller, 1979]. The fat-tailed dwarf lemur (*Cheirogaleus medius*) (ca. 300 g) is similar in body size to many callitrichids, and has an inactive-phase RMR (daytime) of 81% of the mammalian expected. During the active phase, metabolic rate increased substantially, but the animals were active and had access to food, so true active-phase RMR could not be determined [McCormick, 1981]. These data, combined with the callitrichid data, support the hypothesis that RMR is substantially reduced in small-bodied primates during the inactive phase. However, the data can hardly be considered conclusive.

Data are available on the metabolic rates of several species of callitrichid-sized nocturnal prosimians; however, these data were all obtained during the day (the inactive phase for these animals). These results are compared with the callitrichid results in Table II. The inactive-phase RMRs of these primates, which are quite distinct in phylogeny, geography, and circadian rhythm, are remarkably similar. It seems reasonable to hypothesize that the active-phase RMRs of the small, nocturnal prosimians would also be similar to those of the callitrichids. This should raise doubts about statements that have been made in the literature

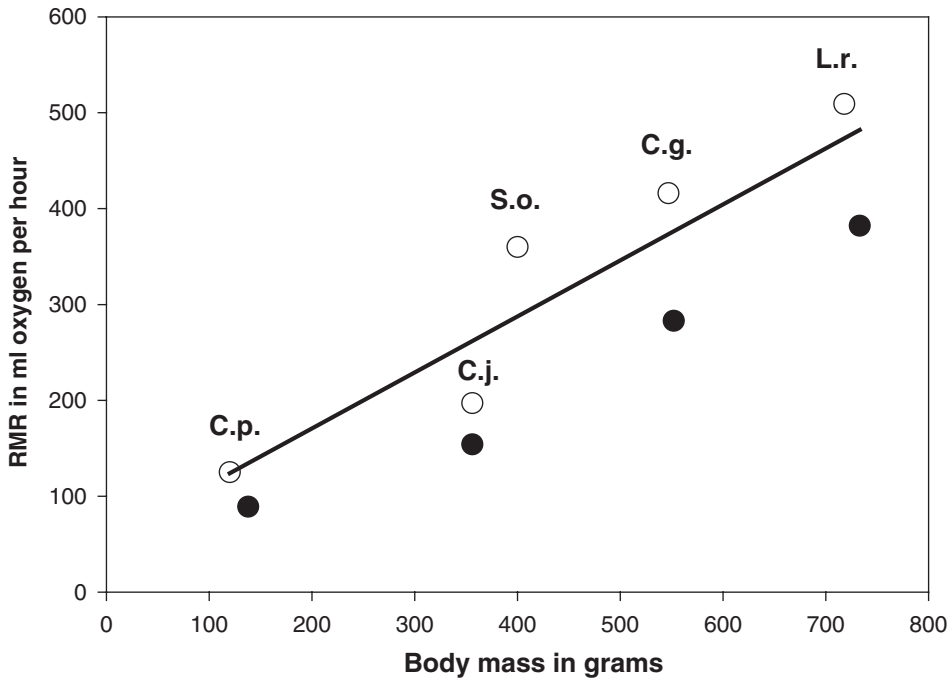


Fig. 3. Mean active (open circles) and inactive (closed circles) phase RMR within thermal neutrality for *Cebuella pygmaea* (C.p.), *Callithrix jacchus* (C.j.), *Saguinus oedipus* (S.o.), *Callimico goeldii* (C.g.), and *Leontopithecus rosalia* (L.r.). Data from sources listed in Table II; values averaged across studies. The solid line represents the mammalian expected from Kleiber [1975].

concerning the “lower” metabolic rates of prosimian primates compared to anthropoid primates.

The data from the pregnant animal are intriguing, and provide fertile ground for speculation (as do most results from a single individual). The salient facts are that inactive-phase RMR apparently does not increase, despite the additional fetal and maternal tissue, but that the female was metabolically more responsive to temperature. It is tempting to draw an analogy between the female’s apparent lower tolerance to heat and the experience of overheating that is common to many human gravidas. The increased responsiveness of her RMR at temperatures below thermoneutrality while she was pregnant could be interpreted as tighter body temperature regulation during that time. Those hypotheses could be tested via temperature transmitter implants.

One hypothesis to account for the lack of increase in inactive-phase RMR during gestation, which is also consistent with the apparent allometric effect on inactive-phase RMR discussed above, is that inactive-phase RMR is constrained by glycogen storage. In other words, the animals reduce their metabolic rate not merely to conserve energy, but to conserve a particular energy substrate that is necessary to maintain glucose metabolism. Glucose is the optimum fuel for brain and fetal tissue. Glycogen stores are finite, and callitrichids do not feed (and thus cannot replenish stores) during their inactive period. We are not aware of any data on the allometry of glycogen stores in primates. However, if the allometry of glycogen storage is greater than the approximately 0.75 power that appears to

scale primate active-phase RMR, then small primates cannot store as much glycogen proportionate to their active-phase RMR as can large primates. A physiological adaptation to that proposed allometric constraint would be a proportionately larger reduction of inactive-phase RMR with declining body size, such as seen in the callitrichid data. We propose that the reduction in RMR during the inactive phase common to all callitrichids measured to date represents an allometric effect, possibly related to glycogen storage, and is not a specific adaptation within the callitrichids. Thus we predict that a significant reduction in RMR during the inactive phase should be a common finding in metabolic studies of small primates.

In summary, the circadian pattern of the metabolic rate in *C. goeldii* is identical to that of other, previously studied callitrichid primates. Active-phase RMR is slightly (7%) above the mammalian expected, as it is for most primates. Inactive-phase RMR is reduced by about 30%, consistent with the data from common marmosets, pygmy marmosets, and golden lion tamarins. The pregnant individual apparently did not have an increased inactive-phase RMR during gestation, but she did appear to be more temperature-sensitive.

ACKNOWLEDGMENTS

We are grateful to the Department of Conservation Biology, Smithsonian National Zoological Park, for the use of the respirometry equipment.

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