

RESEARCH ARTICLE

Energy Intake, Energy Expenditure, and Reproductive Costs of Female Wild Golden Lion Tamarins (*Leontopithecus rosalia*)

KIMRAN E. MILLER^{1*}, KAREN L. BALES^{2,3}, JADIR H. RAMOS⁴,
AND JAMES M. DIETZ¹

¹Department of Biology, University of Maryland, College Park, Maryland

²Department of Psychology, University of California–Davis, Davis, California

³California National Primate Research Center, Davis, CA

⁴Associação Mico-Leão-Dourado, Caixa, Brazil

Callitrichid females are often described as energetically constrained. We examined the energy budgets of 10 female wild golden lion tamarins (GLTs, *Leontopithecus rosalia*) in an effort to understand how energy intake and expenditure might influence physical condition and therefore reproductive performance. We used focal animal sampling to record behavioral data and conducted energy analyses of foods consumed by GLTs to estimate intake and expenditure. We used two-tailed Wilcoxon signed-rank tests to compare intake in the reproductive vs. nonreproductive period and expenditure in the reproductive vs. nonreproductive period. Energy intake decreased during the reproductive period compared to the nonreproductive period. While total expenditure did not vary significantly across the two periods, females spent more time and therefore expended significantly more energy engaged in energetically inexpensive behaviors (i.e., sleeping or being stationary) during the reproductive period compared to the nonreproductive period. We suggest that reproductive female GLTs may adopt a reproductive strategy that includes high intake prior to pregnancy and lactation, and energy conservation during pregnancy and lactation. *Am. J. Primatol.* 68:1037–1053, 2006. © 2006 Wiley-Liss, Inc.

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INTRODUCTION

Energy budgets may be more meaningful than activity budgets in assessing the costs and benefits of behaviors. Energy budgets consider variation in the rates

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*Correspondence to: Kimran (Miller) Buckholz, Ph.D., Biology Department, Montgomery College, 51 Mannakee St., Rockville, MD 20850. E-mail: bocolobo00@yahoo.com

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at which an individual consumes different types of food, food consumption among individuals [Janson, 1988; Miller, 1997], and the rates of energy expended in different behaviors (e.g., traveling vs. being stationary). The efficiency with which animals obtain, process, and allocate energy is expected to influence their chances of survival and reproductive success [Blay & Yuval, 1997; Koteja, 1996]. Energy budgets may be used to assess the costs of reproductive events (e.g., pregnancy, lactation, and infant carrying), since energy intake and expenditure may be influenced by these reproductive events [Kirkwood & Underwood, 1984; Leutenegger, 1980; Tardif, 1994; Terborgh, 1983; Terborgh & Goldizen, 1985]. Energy budgets may also be used to test the relationship between reproductive costs and the degree of reproductive suppression [Creel & Creel, 1991].

Reproductive events, such as pregnancy and lactation, may influence energy expenditure. Females of the family Callitrichidae (marmosets, tamarins, and lion tamarins), small forest-dwelling primates, have been described as energetically constrained due to high litter-to-maternal-weight ratios and energy expended in pregnancy, lactation, and infant carrying [Goldizen, 1987; Kirkwood & Underwood, 1984; Leutenegger, 1980; Price, 1992b; Sánchez et al., 1999; Tardif, 1994]. Also, individuals that carry infants while traveling have a reduced ability to leap, and increased energy expenditure per unit distance traveled [Schradin & Anzenberger, 2001; Tardif, 1997]. Factors other than reproductive events, such as thermoregulation, may also influence energy expenditure [Karasov, 1992].

Reproductive events (e.g., pregnancy, lactation, and infant carrying) and external factors (e.g., risk of predation while carrying infants, and low resource availability) may also limit energy intake. Pregnant and lactating *Cebus capucinus* meet the increased energy demands of reproduction by increasing time resting and decreasing time foraging compared to nonreproductive females [Rose, 1994]. Female golden lion tamarins (GLTs, *Leontopithecus rosalia*) do not forage while nursing their young, perhaps because the presence of infants limits the adult's range of motion (K. Bales, unpublished data, personal observation). Female callitrichids also spend less time foraging and feeding while carrying infants [Price, 1992b; Tardif, 1994; Terborgh & Goldizen, 1985], which may also lower the risk of predation on the young [Caine, 1993; Price, 1992b; Tardif, 1997].

If energy intake is limited and/or expenditure is increased during reproductive events, animals may offset these costs with strategies that include increasing their intake before the onset of costly reproductive events [Di Bitetti & Janson, 2000]. A reproductive female's condition (e.g., body weight) before pregnancy or during parturition may influence her reproductive success. Several studies have demonstrated a relationship between female condition and the rate of offspring production or other measures of reproductive success [Kirkwood, 1983; Mori, 1979; Tardif & Jaquish, 1997]. For example, Tardif and Jaquish [1997] reported that female common marmosets (*Callithrix jacchus*) with higher body weights also experienced more ovulations in each ovulatory cycle. Additionally, Tardif et al. [2001] found that small marmoset mothers that were rearing twins lost more weight than large mothers that were rearing twins. The energy reserves of small mothers were inadequate to meet the demands of lactation, and as a result the small mothers produced milk with lower energy values than that of large mothers. The timing of improvement in a female's condition (e.g., by energy reserves) may play an important role in reproductive success. Results from several studies on wild GLTs suggest that energy intake may influence female fitness, since nonpregnant/early pregnant body weight significantly predicted the number of live-born offspring [Bales et al., 2001], the amount of maternal carrying of offspring [Bales et al., 2002], and female lifetime

reproductive success [Bales et al., 2003]. Kirkwood [1983] also found that improved nutrition was related to increased litter sizes in cotton-top tamarins (*Saguinus oedipus*).

Since previous studies have indicated that female callitrichid condition before or at conception is crucial for reproductive success, we sought to explore the proximate mechanisms by which energy intake and expenditure influence female condition. We quantified the energy budgets of female GLTs to address the following questions: 1) how do energy intake and energy expenditure differ in the period of reproductive events vs. other periods, and 2) what factors other than reproductive costs (e.g., energy reserves, resource availability, thermo-regulation, and reproductive strategies) potentially influence energy budgets?

MATERIALS AND METHODS

Study Site and Subjects

The study was conducted from March 1998 to March 1999 (excluding April 1998) in Poço das Antas Biological Reserve (22°30'-33' S, 42°15'-19' W), Rio de Janeiro State, Brazil. The reserve is a 6,300 ha remnant of the Atlantic coastal rainforest [Dietz & Baker, 1993]. During the study the dry season months included April–August 1998, and the wet season months included March 1998 and September 1998–March 1999. Precipitation and temperature were recorded daily [Miller & Dietz, 2005].

The subjects were 10 adult females in seven groups. Eight females gave birth during the study and were classified as reproductive, while two did not and were classified as nonreproductive. Most groups (six of seven) contained only one reproductive female, and all groups contained one or two non-natal adult males and one or two litters of offspring. Fertile copulations took place from May–July and births occurred in October–November. GLTs typically have two general birth peaks: a major peak in September–November and a minor peak in December–March [Dietz et al., 1994].

Data Collection and Analysis

We observed one group per day. We randomly chose each focal animal and observed the animal during a 15-min focal period using continuous focal animal sampling [Martin & Bateson, 1993]. The behaviors for which we collected data are listed in Table I and defined in Miller and Dietz [2005]. We quantified resource availability for the GLTs using transects [Miller & Dietz, 2005]. We quantified energy expenditure and intake from plants and animal prey for the females during four periods (Table II): dry season/not reproductive (DRY/NR; May–July), dry season/pregnant (DRY/P; August), wet season/pregnant or lactating (WET/PL; September–December), and wet season/not reproductive (WET/NR; January–March). We defined the DRY/NR period as the time (during the dry season) when a female was not pregnant or lactating, or when a female was in the first 2 months of pregnancy. In a previous study, Bales et al. [2001] found no significant changes in the weight gain of female GLTs during the first 2 months of pregnancy. We assumed that females in the first 2 months of pregnancy would experience minimal costs due to pregnancy (also see Kirkwood and Underwood [1984]). We counted back from the birth date of the infant to determine the period of pregnancy, using an average duration of pregnancy of 130 days [Kleiman, 1978]. The definitions for all four periods are provided in Table II.

TABLE I. Behaviors and Associated Calculations of Energy Expenditure

Behavior	Calculation of energy expenditure (kcal/day)
Inactive (sleep)	Inactive phase BMR/hour × # hours sleeping/day
Stationary ^a	1.7 × active phase BMR/hour × # hours stationary/day
Eat animal prey, eat plant; groom ^a	1.7 × active phase BMR/hour × # hours in behavior/day
Search for prey	2.4 × active phase BMR/hour (avg. of 1.7,3) × # hours searching/day
Stationary-play ^b	3 × active phase BMR/hour × # hours in stationary-play/day
Travel ^c	[(((10,700 × (weight kg) ⁻⁶⁸⁴) J/km × (distance traveled km/day))/ (1000 J/1 kJ))/4.18 kJ/kcal] + (active phase BMR × # hours traveled)

^aAdapted from Taylor et al. [1970]; Taylor [1977].

^bAdapted from Karasov [1981].

^cAdapted from Taylor et al. [1982]; Altmann [1998]; Steudel [2000]. Travel includes walking/running, chasing another animal and playing while walking/running.

TABLE II. List of Abbreviations and Associated Definitions Used in the Text

DRY/NR	Time period when female is not pregnant or lactating or when female is in first two months of pregnancy, during dry season
DRY/P	Time period when female is in last two months of pregnancy, during day season
WET/PL	Time period when female is in last two months of pregnancy or when she is lactating, during wet season
WET/NR	Time period when female is not pregnant or lactating, during wet season
Energy intake calculations	
GE (gross energy)	Amount of energy that is consumed from food items
DE (digestive energy)	GE minus energy lost in feces
ME (metabolizable energy)	DE minus energy lost in urine
A	Number of food items eaten per month
B	g of dry matter per food item
C	Kcal/g of dry matter per food item
D	Kcal consumed per month
E	Hours visible per month minus hours spent eating exudates that month
F	Average number of hours spent consuming food type/day
G	Kcal consumed per day
H	Kcal consumed from frogs
Energy expenditure calculations	
I	Hours spent in an activity per month
J	Average number of hours awake per day

We compared energy intake in the season assumed to be the least reproductively costly (DRY/NR) with intake in the season assumed to be the most costly (WET/PL). We compared energy expenditures during the same two periods. Energy costs and protein and mineral requirements have been found to increase during pregnancy and lactation [Coelho, 1974; Dunbar & Dunbar, 1988],

with lactation being more costly than pregnancy or infant carrying [Oftedal, 1985; Tardif & Harrison, 1990]. We considered the WET/PL period to be the most reproductively costly because all of the females were in the last 2 months of pregnancy or lactating, and extensively carrying the young. We considered the DRY/NR period to be the least reproductively costly period because none of the females were in the costly last 2 months of pregnancy or lactating, and all of the previous year's infants were independently traveling.

We used two-tailed Wilcoxon signed-rank tests [Siegel, 1956] for all comparisons (GraphPad InStat version 4.00 for Windows 95; GraphPad Software, San Diego, CA). We compared daily energy intake and expenditure values for eight reproductive females during the DRY/NR vs. WET/PL periods. We did not have sufficient data to compare intakes and expenditures during the other two periods. The small number of nonreproductive females made it impossible to statistically compare reproductive and nonreproductive females, so we made qualitative comparisons. Additionally, we compared energy expenditures for reproductive females during the DRY/NR and WET/PL periods for the two categories of behaviors in which the females had the greatest average energy expenditure (i.e., being stationary and sleeping).

Determining Energy Intake

Examining energy intake involves calculating the gross energy (GE), digestive energy (DE), and metabolizable energy (ME) [Blaxter, 1989; Hudson & White, 1985] (Table II). We used the following formula to calculate GE intake per plant species for each GLT per month:

$$A_{\text{plant}} \times B_{\text{plant}} \times C_{\text{plant}} = D_{\text{plant } 1}, \quad (1)$$

where A_{plant} (Table II) represents the number of hours spent consuming plant species 1 per month/average number of hours needed to consume one fruit of species 1, B_{plant} represents the number of grams of dry matter of the fruit part(s) eaten (e.g., skin or pulp) in one fruit, and C_{plant} represents the number of kcal per gram of dry matter of the fruit part(s) eaten. Therefore, $D_{\text{plant } 1}$ represents the total kcal consumed per month when eating species 1. We used the following formula to calculate GE intake from all plant species for each GLT per day:

$$\frac{D_{\text{plant}}}{E} \times F_{\text{plant}} = G_{\text{plant}}, \quad (2)$$

where D_{plant} represents the total kcal consumed from all plant species per month, E represents the number of hours the animal was visible per month, F_{plant} is the average number of hours spent consuming plants per day, and G_{plant} is the total plant kcal (GE) consumed per dawn-to-dusk day. We calculated F_{plant} by multiplying the number of hours the animal was awake during the average wet or dry season day (dawn to dusk) by the percentage of time spent consuming plants. We calculated the percentage of time spent consuming plants using the following computation: total number of hours spent consuming plants per month/ (number of hours visible per month minus number of hours spent eating exudates per month).

The methodology used to collect the data for the above calculations and the kcal values of the plant species are detailed in Miller and Dietz [2005]. To calculate consumption rates (A_{plant} in Eq. [1]), we recorded data on all individuals that were visibly consuming each plant species and calculated the average rates of consumption for each species. Energy consumed from exudates

was minimal due to the low percentage of time spent consuming exudates (1% [Miller & Dietz, 2005]). Therefore, kcal consumed from exudates and time spent consuming exudates were not included in the calculation of GE intake. Females fed from 41 plant species and spent 9% of their feeding time consuming plant material that could not be identified or was identified but could not be analyzed for energetic content ($n = 4/41$ species). To estimate the energy content of fruits consumed for which no kcal data existed, we calculated an average kcal/g of dry matter (0.97 kcal/g of dry matter, $SE = \pm 0.31$, $n = 22$ species) and an average time necessary to eat one fruit (already available for four identified species; 29.6 sec, $SE = \pm 9.4$, $n = 21$ species). To calculate these averages, we square-root transformed the average kcal/g of dry matter (available for 26 species) and the average time spent eating one fruit (available for 22 of 26 species) for each of 26 species on which females spent at least 1% of their plant feeding time (similarly to methodology used by Miller and Dietz [2005]). We used the Kolmogorov-Smirnov test to confirm normality. We calculated the Grubbs test statistic to identify and remove outliers [Sokal & Rohlf, 1981] ($n = 4/26$ species removed for kcal/g of dry matter, $n = 1/22$ species removed for average time spent eating one fruit). We used the times the animals left (dawn) and entered their nest sites (dusk) on 67 days of observation to calculate the average number of hours per day each group spent awake during the wet or dry season (group mean_(wet) = 10.7, $SE = \pm 0.3$, group mean_(dry) = 9.8, $SE = \pm 0.2$).

We calculated the DE from plants using Eq. [3] and an average digestive efficiency of 85.7% (i.e., 14.3% of the GE is lost in feces), a value obtained from a study of captive GLTs [Thompson et al., 1994]:

$$DE_{\text{plant}} = 0.857(\text{GE}). \quad (3)$$

In a previous study [Miller & Dietz, 2005], we identified 128 prey consumed by GLTs: 75% of the prey were orthopterans and 25% were other animals (10% roaches, 7% frogs, 4% larvae, 2% spiders, 1% lizards, and 1% walking sticks). We scored the sizes of all prey consumed by GLTs whenever possible. Since the GLTs fed primarily on orthopterans, we made the assumption that all unidentified prey scored for size were orthopterans. For identified prey for which size data were unavailable, we used average sizes calculated from our data of identified, sized prey consumed by GLTs ($n = 100$ prey; e.g., roach_(mean size) = 3.8 cm, $SE = \pm 0.6$; orthopteran_(mean size) = 4.8 cm, $SE = \pm 0.2$; frog_(mean size) = 5.6 cm, $SE = \pm 0.8$). For unidentified prey for which size data were unavailable, we assumed the prey were orthopterans and used the average orthopteran size (4.8 cm). Using data on wet weights and prey sizes from Nickle and Heymann [1996], we estimated the wet weights of invertebrate prey. We corroborated these estimates of weights and lengths from a sample of katydids we collected.

We calculated the dry weights of all orthopterans using the dry weight measure for grasshoppers (*Melanoplus femurrubrum*; 30.5% of wet weight) given in Bird et al. [1982]. For prey identified as cockroaches we used the dry weight measure for cockroaches (33.0% of wet weight) given by Allen [1989]. We used the following estimates of kcal/g of dry animal matter: 5.25 kcal (grasshopper (*M. femurrubrum*) [Allen, 1989; Bird et al., 1982]) and 5.52 kcal (American cockroach (*Periplaneta americana*) [Allen, 1989]). We used data on body size and weight from a tropical frog species (tomato frog (*Dyscophus antongilli*) www.zoo.org/educate/fact_sheets/day/tomato.htm) to determine the weights of frogs (all of which were scored for size) consumed by GLTs. We used data on frog body weight and kcal content (www.qrg.northwestern.edu/projects/marssim/

simhtml/organisms/frog/html) to estimate kcal content of frogs consumed by GLTs. We used the following formula to calculate GE intake from prey for each GLT per day:

$$\frac{(B_o \times C_o) + (B_c \times C_c) + H}{E} \times F_{\text{prey}} = G_{\text{prey}}, \quad (4)$$

where B represents the number of grams of dry matter per prey consumed per month (o = orthopteran, c = cockroach), C represents the number of kcal per gram of dry matter per prey consumed, H represents the kcal consumed from frogs per month, E represents the number of hours visible per month, F_{prey} represents the average number of hours spent consuming prey per day, and G_{prey} represents the total prey kcal (GE) consumed per dawn-to-dusk day. We calculated F_{prey} by multiplying the number of hours the animal was awake during the average wet or dry season day (dawn to dusk) by the percentage of time spent consuming prey. We calculated the percentage of time spent consuming prey using the following computation: total number of hours spent consuming prey per month / (number of hours visible per month minus number of hours spent eating exudates per month).

We calculated the DE from prey using the following formula and an average digestive efficiency of 75.4% (i.e., 24.6% of the GE is lost in feces):

$$DE_{(\text{prey})} = 0.754(\text{GE}). \quad (5)$$

This value was the average digestive efficiency of two insectivores: the pygmy hedgehog tenrec (*Echinops telfairi*) and the southern grasshopper mouse (*Onychomys t. longicaudus*) [Allen, 1989].

We calculated the total ME consumed from plants and prey per day by summing the values for DE from plants and prey per day and then subtracting 3.8% of the sum of GE from plants and prey per day to account for energy lost in urine, using the following formula:

$$\text{ME} = (\text{DE}_{(\text{plant})} + \text{DE}_{(\text{prey})}) - 0.038(\text{GE}_{(\text{plant})} + \text{GE}_{(\text{prey})}). \quad (6)$$

The average percentage of GE lost in urine (3.8%) was calculated from data on humans, rats, and pigs [Blaxter, 1989; Grodzinski & Wunder, 1975]. This value does not vary greatly among species [Blaxter, 1989]. In contrast, energy lost in feces is a major determinant of ME intake [Blaxter, 1989].

Determining Energy Expenditure

Major sources of energy expenditure for adults include maintenance, lactation, thermoregulation, heat production during pregnancy, digestion, and energy expended during daily activities [Blaxter, 1989; Karasov, 1992; Nagy & Milton, 1979]. The following is a description of how we calculated energy expenditure for these sources.

Maintenance is defined as the sum of energy required for the active-phase basal metabolic rate (BMR) while awake (= resting metabolic rate (RMR) [Thompson et al., 1994]) and the inactive-phase BMR while sleeping (~ standard metabolic rate (SMR) [Thompson et al., 1994]). In the current study we defined BMR as the heat production of an animal at rest and postabsorptive but not within the thermal neutral zone for that species. We used the following formula to calculate inactive- and active-phase BMRs per hour [Kleiber, 1961; Thompson et al., 1994]:

$$a(w)^x = \text{BMR}, \quad (7)$$

where “a” and “x” are constants, and “w” is body weight (kg). The constant “x” (= 0.6) for active-phase BMR was calculated from the log-log regression of RMR on body mass [Thompson et al., 1994]. The constant “x” (= 0.4) for inactive-phase BMR was calculated from the log-log regression of the SMR on body mass [Thompson et al., 1994].

Using data from Thompson et al.’s [1994] study of captive GLTs, including an average nonpregnant body weight of 0.718 kg, we calculated the constant $a_{(\text{active-phase BMR})}$ to be 2.9, using an active-phase BMR of 2.4 kcal/hr and a value of 0.6 for $x_{(\text{active-phase BMR})}$. We calculated the constant $a_{(\text{inactive-phase BMR, small group})}$ to be 2.1, using an inactive-phase BMR of 1.8 kcal/hr for groups of fewer than four GLTs [Power, 1999] and a value of 0.4 for $x_{(\text{inactive-phase BMR})}$. We calculated the constant $a_{(\text{inactive-phase BMR, large group})}$ to be 1.6, using an inactive-phase BMR of 1.4 kcal/hr for groups of four or more GLTs [Power, 1999] and a value of 0.4 for $x_{(\text{inactive-phase BMR})}$. Inactive-phase BMR varied relative to group size because animals in larger groups do not need to produce as much heat to maintain body temperatures at night due to the presence of more animals [Power, 1999]. Using values for the constant “a” that vary relative to group size is one way to account for the cost of thermoregulation indirectly. We used the calculated values for the constants “a” and “x,” in addition to monthly measures of body weight of wild GLTs collected from July 1998 to February 1999, to calculate inactive- and active-phase BMR/hr for the females (see Bales [2000] for details on collecting weight data).

Kirkwood and Underwood [1984] estimated that maintenance energy expenditure for lactating cotton-top tamarins was about twice that for nonlactating tamarins. Nievergelt and Martin [1999] found that female captive common marmosets increased their energy intake by up to 100% during lactation. Therefore, we doubled the maintenance values (active-phase BMR/hr and inactive-phase BMR/hr) for females during the months when they were lactating. The increase in heat production during pregnancy was estimated to be a constant of 18 MJ/kg of litter weight at birth, a calculation made from data obtained from a range of species, including rats and rabbits [Brody, 1945]. The average weight of GLT twins recorded 1 day after birth and the weight of a GLT singleton recorded 2 days after birth were used to estimate birth weight [Bales et al., 2002]. We calculated the heat of production for females during the last 2 months of pregnancy, when weight gains are apparent and pregnancy is most costly [Bales et al., 2001].

We calculated energy expenditure for eight daily activities (Table I). For all behaviors except sleeping and traveling, we multiplied increments of active-phase BMR (kcal/hr) by the number of hours spent on the activities per day to calculate the energy expended in those activities (kcal/day; Table I). We calculated the number of hours spent in each activity per day for each GLT using the following formula:

$$\frac{I}{E} \times J, \quad (8)$$

where I represents the number of hours spent in an activity per month, and J represents the number of hours awake during the average wet or dry season day (dawn to dusk).

For the calculation of energy expended while sleeping, we calculated the average number of hours each group spent sleeping per day during the wet or dry season (Table I). For the behavior traveling, we used a formula that included the rate of travel to calculate energy expended while traveling [Altmann, 1998;

Stuedel, 2000; Taylor et al., 1982] (Table I). We calculated the distance traveled each day (Table I) using two rates of traveling (walking at a slow or medium pace: mean = 2.84 km/hr; running: mean = 6.48 km/hr [Miller & Dietz, 2005]), the monthly percentage of time spent traveling at these two rates, and the average number of hours each group of GLTs was awake/day during the wet or dry season.

The heat increment of feeding describes the percentage of ME that is used while feeding (i.e., the cost of digestion). We used data on heat increments of feeding from a study of humans, rats, dogs, and pigs by Blaxter [1989]. We calculated an average heat increment for humans, rats, dogs, and pigs from the heat increments given when feeding at or below maintenance level and above maintenance level (21% of ME, SE = ±0.04). We summed energy expenditures for all behaviors, heat of production, and 21% of the respective ME values to obtain the energy expenditure per day.

Additionally we estimated energy expended in thermoregulation. We used data from Thompson et al. [1994], including kcal expenditure per hour in temperatures below the low critical temperature for the inactive-phase (lower bound for the thermal neutral zone during the night). We used minimum temperatures recorded at Poço das Antas to identify the nights when temperatures fell below the low critical temperature for the inactive phase (K. Miller, unpublished data).

RESULTS

We observed each female for an average of 1.5 visible hr/month (SE = ±0.1). Reproductive females had significantly greater ME intake in the DRY/NR period vs. WET/PL period (mean_(DRY/NR) = 108.2 kcal/day, SE = ±26.4, mean_(WET/PL) = 38.1 kcal/day, SE = ±10.8; Wilcoxon signed-rank test: T = 34.0, n = 8, P = 0.02, Fig. 1). Qualitatively, nonreproductive females had higher ME intakes during the WET/PL vs. DRY/NR period (mean_(WET/PL) = 90.6 kcal/day, SE = ±102.1, mean_(DRY/NR) = 34.0 kcal/day, SE = ±25.5, n = 2, Fig. 1). Qualitatively, reproductive females had higher ME intakes during the DRY/NR period and lower ME intakes during the WET/PL period compared to nonreproductive females (Fig. 1).

The average energy expenditure (DRY/NR and WET/PL periods) for the eight reproductive female GLTs was 92.7 kcal/day. The energy expended per day was

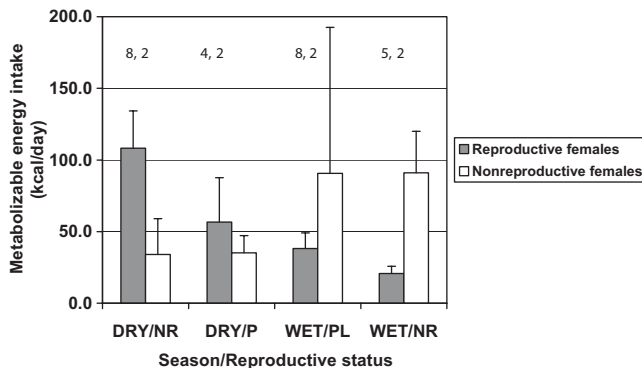


Fig. 1. Average daily intake of ME (±SE) for eight reproductive females and two nonreproductive females. See Table II for explanations of abbreviations. Sample sizes are listed at the top of the graph. Reproductive females had higher intakes of energy in the DRY/NR period than in the WET/PL period (Wilcoxon signed-rank test: T = 34.0, n = 8, P = 0.02).

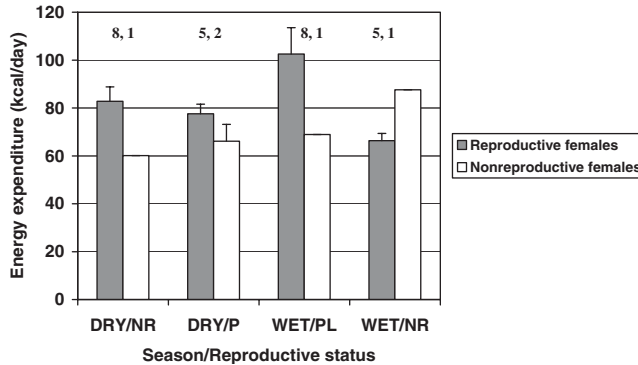


Fig. 2. Average daily energy expenditure (\pm SE) for eight reproductive females and two nonreproductive females. See Table II for explanations of abbreviations. Sample sizes are listed at the top of the graph. There was no difference in the amount of energy expended in the DRY/NR vs. WET/PL period (Wilcoxon signed-rank test: $T = 9.0$, $n = 8$, $P = 0.25$).

twice the daily BMR (inactive- and active-phase BMRs). There was no difference in the energy expenditure of reproductive females in the DRY/NR period vs. WET/PL period (mean_(DRY/NR) = 82.8 kcal/day, SE = ± 6.3 , mean_(WET/PL) = 102.5 kcal/day, SE = ± 11.2 ; Wilcoxon signed-rank test: $T = 9.0$, $n = 8$, $P = 0.25$; Fig. 2). Qualitatively, reproductive females tended to expend more energy in the WET/PL period than nonreproductive females (mean_(reproductive female) = 102.5 kcal/day, SE = ± 11.2 , $n = 8$; mean_(nonreproductive female) = 68.9 kcal/day, $n = 1$; Fig. 2). Qualitatively, it is unclear whether there was a difference between the energy expenditures of reproductive and nonreproductive females during the DRY/NR period (mean_(reproductive female) = 82.8 kcal/day, SE = ± 6.3 , $n = 8$; mean_(nonreproductive female) = 60.1 kcal/day, $n = 1$; Fig. 2).

Reproductive females expended more energy while stationary and while sleeping in the WET/PL vs. DRY/NR period (stationary: Wilcoxon signed-rank test: $T = 1.0$, $n = 8$, $P = 0.02$; sleeping: Wilcoxon signed-rank test: $T = 3.0$, $n = 8$, $P = 0.04$; Fig. 3). Although being stationary and sleeping are the least energetically demanding behaviors, the GLTs spent the most amount of time and therefore expended the most amount of energy in these behaviors. Energy expended in the behaviors being stationary and sleeping during the WET/PL period accounted for 63% of the daily energy expended (38% and 25%, respectively), while the most energetically costly behaviors (travel and stationary-play) accounted for respectively 7% and 0.1% of the daily energy expended. We did not test for seasonal differences in energy expended in other behaviors, since the percent of daily energy expended in the other behaviors ranged from 0.1% to 9% during the DRY/NR and WET/PL periods. Our estimates of energy expended due to thermoregulation ranged from 6 to 19 kcal/night and averaged 15.4 kcal/night in the dry season.

Our data collection allowed for 44 calculated measures of average daily net energy gain (ME intake minus expenditure) for the 10 females. The WET/PL period had the highest percentage of negative values (90%). The DRY/NR period had the lowest percentage of negative values (63%). For the DRY/NR and WET/PL periods, female GLTs averaged 25% DE from prey and 75% DE from plants (SE = ± 0.04 , $n_{(female)} = 10$). Qualitatively, reproductive females (unlike nonreproductive females) doubled their percentage of DE from prey in the WET/PL period vs. DRY/NR period (Table III).

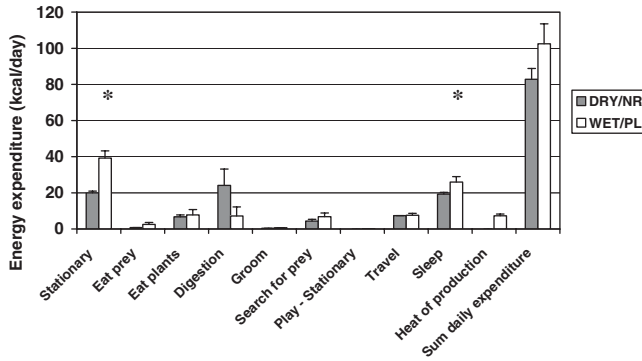


Fig. 3. Average daily energy expenditure (\pm SE) for eight reproductive females in each of 10 categories. The sum daily energy expenditure is also given. Asterisks denote significant differences between the WET/PL and DRY/NR periods. Reproductive females expended more energy while being stationary and while sleeping in the WET/PL period than in the DRY/NR period (stationary: Wilcoxon signed-rank test: $T = 1.0$, $n = 8$, $P = 0.02$; sleeping: Wilcoxon signed-rank test: $T = 3.0$, $n = 8$, $P = 0.04$).

TABLE III. Average Percent DE From Prey and Plants During the DRY/NR and WET/PL Periods for Reproductive and Nonreproductive Female GLTs During March 1998–March 1999

	DRY/NR		WET/PL	
	Prey % DE	Plant % DE	Prey % DE	Plant % DE
Reproductive female ID				
291	6	94	45	55
436	1	99	52	48
524	70	30	15	85
603	21	79	49	51
651	0	100	28	72
663	2	98	32	68
703	0	100	5	95
721	14	86	53	47
Nonreproductive female ID				
689	31	69	7	93
720	35	65	37	63
Overall average	18	82	32	68
Average reproductive	14	86	35	65
Average nonreproductive	33	67	22	78

DISCUSSION

In this study, we focused on the following questions: 1) how do energy intake and expenditure differ in the reproductive vs. nonreproductive period, and 2) what factors other than reproductive costs (e.g., energy reserves, resource availability, thermoregulation, and reproductive strategies/constraints) potentially influence energy budgets? We discuss our expenditure and intake results, and their relationship to factors other than reproductive costs, below.

Our estimate of average daily energy expenditure (92.7 kcal; DRY/NR and WET/PL periods) for the eight reproductive female GLTs was twice that of their daily metabolic rate, which is similar to previous results [Nagy & Milton, 1979]. Expenditures were similar to those observed in other studies of wild primates, including *Alouatta palliata* (355 kJ/kg/day (85 kcal/kg/day) [Nagy & Milton, 1979]) and *Papio cynocephalus* ($354 M^{0.75}$ kJ/day + $65.3M^{0.684}$ kJ/day, where M = body weight (kg) [Altmann, 1998]). Altmann's [1998] estimate included energy required for basal metabolism and locomotion, and if applied to a 650 g wild GLT is estimated at 305 kJ/day (73 kcal/day).

Other studies have reported values for ME intake (kcal/kg/day) for wild nonreproductive primates (e.g., 85.2 for *Alouatta palliata* [Nagy & Milton, 1979] and 63.9 for *Macaca fuscata* [Nakagawa, 1989]). The average daily ME intake (DRY/NR and WET/PL periods) for the eight reproductive GLTs in the current study was 73.2 kcal. It is difficult to make comparisons with previous studies because the data from those studies were collected during only one season. Interspecific variation exists in the seasonality of food consumption and the feeding strategies used to ameliorate reproductive costs [Di Bitetti & Janson, 2000]. As a result, study duration and the feeding strategy of a species can dramatically influence observed intake rates. Additionally, energy intake varies with lifestyles and diet preferences (e.g., terrestrial vs. arboreal and folivore vs. frugivore).

For reproductive females, the daily ME intake was 2.8 times greater during the DRY/NR period than during the WET/PL period, while there was no significant difference in total daily expenditure across the two time periods. Reproductive females had the greatest average daily net energy gain during the DRY/NR period (25.4 kcal), while they had the lowest average daily net energy gain (-64.4 kcal) during the WET/PL period.

Energy Reserves

Females may increase their energy intake during the DRY/NR period to maximize energy storage prior to conception. Each reproductive female in the current study gave birth to twins during the first birth peak, except for one female in the one group that contained two reproductive females (a mother-daughter duo). The mother gave birth to a singleton during the month in which she was losing her alpha ranking to her daughter. Evidence that may support the relationship between energy reserves and birth peaks for GLTs comes from a population of reintroduced, food-provisioned GLTs in Brazil, and other food-provisioned species [e.g., Loy, 1988; Lyles & Dobson, 1988]. No wild female GLTs in the current study gave birth during the second birth peak. There were 16 instances (for which maternal ID and offspring birthdate were known) in which 15 females in the population of reintroduced, food-provisioned GLTs gave birth (during March 1998–March 1999). Three of the 15 females gave birth to twins during the second peak (December 1998–March 1999; B. Beck, personal communication). This observed difference in births between wild and food-provisioned females was not due to variation in the age structure of the females [Bales et al., 2001]. Low intakes of energy by wild reproductive females during the WET/PL vs. DRY/NR period (Fig. 1) may explain the lack of a second birth peak in the wild population. It would be useful to obtain frequent measures of fat storage by females relative to birth frequency over several years to address the potential relationship among intake, energy storage, and reproductive success.

Resource Availability

The limited availability of food resources during the wet vs. dry season may influence lower energy intake during the wet season. Miller and Dietz [2005] found that the average daily rainfall per month significantly predicted GLTs' percentage of time spent feeding on plants 2 months later. GLTs tended to consume more food during the dry season than in the wet season, in part due to rainfall in the preceding wet-season months [Miller & Dietz, 2005]. Other studies [e.g., Chapman, 1988] have demonstrated a lag in the response of tropical vegetation productivity to rainfall. In the current study, reproductive females had the lowest intakes of energy during the wet-season months (WET/PL and WET/NR periods; Fig. 1).

Contrary to the results in the current study, reproductive female callitrichids in captivity often increase their time spent feeding and energy intake when nursing [Kirkwood & Underwood, 1984; Price, 1992a; Sánchez et al., 1999]. Generally, captive females have access to more food and are able to feed ad libitum during this costly period, whereas wild females may not have ample resources available at this time. The second birth peak for wild GLTs may occur in years when relatively abundant food resources are available in the initial months of the wet season, and intake during the WET/PL period exceeds expenditure (similarly to the DRY/NR period; Figs. 1 and 2). Additional data on resource availability, precipitation, and intake during the DRY/NR and WET/PL periods would provide useful information with which to test the relationship among resource availability, intake, and birth frequency in the first and second peaks. The large increase in prey intake by reproductive females in the WET/PL vs. DRY/NR periods (unlike nonreproductive females; Table III) warrants further examination of the relative need for prey during reproductive vs. nonreproductive periods, and the seasonal availability of prey.

Thermoregulation

It is unlikely that thermoregulation during the relatively cold dry season (DRY/NR period) caused the elevated energy intakes during the dry season. We estimated that the GLTs averaged only 15.4 kcal expended per night during the dry season. Since the difference between the estimated average ME intakes during the DRY/NR period and WET/PL period is 70.1 kcal/day, it is unlikely that energy expended in thermoregulation explains the observed increase in energy intake during the dry season.

Strategies and Constraints

An increase in time spent being stationary and/or a decrease in time spent consuming food is often indicative of an energy-conserving strategy [Dasilva, 1992; Rose, 1994]. Data from Miller and Dietz [2005] indicate that GLTs spend more time being stationary and less time consuming plant matter during the wet-season months than in the dry-season months. Data from the current study indicate that reproductive females expend most of their energy in the behaviors being stationary and sleeping, as opposed to more energetically costly behaviors, during the WET/PL period (Fig. 3). Additionally, reproductive females expend more energy in the behaviors being stationary and sleeping during the WET/PL vs. DRY/NR period. It appears that reproductive female GLTs use an energy-conserving strategy during the wet season when they are gestating, lactating, and carrying infants.

Time and energy spent being stationary may be influenced by infant carrying [Digby & Barreto, 1996; Price, 1992a; Tardif & Harrison, 1990] or nursing, since carrying infants is costly, and nursing and traveling by the mother can be mutually exclusive (e.g., in GLTs; K. Bales, personal communication). Reproductive females spent an average of 5.7 hr/day being stationary during the DRY/NR period, and 7.6 hr/day being stationary in the WET/PL period. If reproductive females spent more time being stationary in the WET/PL period because they were nursing, then time spent nursing added to time spent being stationary in the DRY/NR period should approximate time spent being stationary in the WET/PL period. Females spend approximately 16% of their time nursing (1.7 hr/day) in the first month after the birth of their young [Bales et al., 2002]. If 1.7 hr/day nursing is added to the average time reproductive females spent being stationary in the dry season (5.7 hr/day), the sum (7.4 hr/day) approximately equals the amount of time reproductive females spent being stationary in the first month after the birth of their young (7.9, SE = ± 0.48). Time spent being stationary during the last month of pregnancy averaged 7.5 hr/day (SE = ± 0.57). Pregnancy may influence time and energy spent being stationary due to the physical awkwardness of traveling while pregnant [Schradin & Anzenberger, 2001].

Reproductive females appeared to employ a different feeding strategy compared to nonreproductive females during the nonreproductive period (DRY/NR), and consumed 3.2 times the energy ingested by nonreproductive females (Fig. 1). As mentioned previously, this excess consumption by reproductive females could serve to improve their condition before the probable onset of gestation and lactation [Bales et al., 2001, 2002, 2003; Kirkwood, 1983; Tardif & Jaquish, 1997; Tardif et al., 2001].

According to our calculations of daily net energy gain, the females most often fell short of their energetic requirements during the WET/PL period, and most often exceeded their energetic requirements during the DRY/NR period. Calculating variance in net energy gains over time, as opposed to calculating averages of net energy gains over time, may more accurately indicate energetic limitations and warrants further examination.

CONCLUSIONS

We realize that one weakness of our study is that we did not weigh the GLTs multiple times each month. Additionally, we recognize that systematic data on infant carrying would improve the accuracy of our energy expenditure calculations. We did account for energetic expenditure due to lactation, which is more costly than infant carrying [Ofstedal, 1985; Tardif & Harrison, 1990]. Consistent data on infant carrying and nursing would also provide additional insights into variation in energy intake. We recognize that our energy calculations included several extrapolations from studies of other species. For example, we probably underestimated GLT prey digestive efficiency by using an average digestive efficiency (75.4%) from two much smaller species (tenrec and mouse). When they were available we used values for GLTs or other callitrichids (e.g., maintenance values when lactating, values for the constants in the BMR calculations, body weights, plant digestive efficiency, and wet weights of prey).

The estimates of energy budgets in the current study are the first known estimates for a wild callitrichid, and are some of the few estimates available for a wild primate. As a result, this study may be considered an initial attempt to relate energy budgets to reproductive costs for wild callitrichids. Our data on intake indicate that reproductive female GLTs may utilize a strategy that includes

increased food intake prior to pregnancy and lactation. Miller and Dietz [2005] found that more than half of the adult fruit trees observed did not fruit during the year of this study, which may be an indication of the uncertain temporal availability of fruit resources used by GLTs (see also Ferrari and Lopes Ferrari [1989]). The possibility of temporally unstable fruit resources may necessitate increased consumption by reproductive females in periods preceding gestation and lactation. Our data on expenditure indicate that reproductive females may conserve energy during pregnancy and lactation, since they spent significantly more time in energetically inexpensive behaviors (i.e., being stationary or sleeping) during that time than in the DRY/NR period. The specific amounts of time spent being stationary during the last month of pregnancy and during the first month of nursing vs. during the DRY/NR period suggest the existence of time budget constraints (increased time spent being stationary), possibly imposed by pregnancy and lactation. Limited food resources during pregnancy and lactation may also influence energy conservation. Future research may investigate the relationship between variance in net energy gains and the degree to which costs associated with reproduction are ameliorated. For example, in cooperatively breeding social systems, reproductive costs may be lower for reproductive females in high-quality territories and/or in groups with many helpers as compared to females in low-quality territories or small groups.

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REFERENCES

- Allen ME. 1989. Nutritional aspects of insectivory. Ph.D. dissertation, Michigan State University, East Lansing, MI. 116p.
- Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press. 609p.
- Bales KL. 2000. Mammalian monogamy: dominance, hormones, and maternal care in wild golden lion tamarins. Ph.D. dissertation, University of Maryland, College Park, MD. 128p.
- Bales KL, French JA, Dietz JM. 2002. Explaining variation in maternal care in a cooperatively breeding mammal. *Anim Behav* 63:453–461.
- Bales K, O'Herron M, Baker AJ, Dietz JM. 2001. Sources of variability in numbers of live births in wild golden lion tamarins (*Leontopithecus rosalia*). *Am J Primatol* 54: 211–221.
- Bales KL, O'Herron MM, Baker AJ, Dietz JM. 2003. Are lion tamarins a good model for the Trivers-Willard hypothesis? *Am J Primatol* 60(Suppl 1):40.
- Bird DM, Ho S, MacDonald DP. 1982. Nutritive values of three common prey items of the American kestrel. *Comp Biochem Physiol A* 73:513–515.
- Blaxter K. 1989. Energy metabolism in animals and man. Cambridge: Cambridge University Press. 336p.
- Blay S, Yuval B. 1997. Nutritional correlates of reproductive success of male Mediterranean fruit flies (Diptera: Tephritidae). *Anim Behav* 54:59–66.
- Brody S. 1945. Bioenergetics and growth. New York: Reinhold Publishing Co. 1023p.
- Caine N. 1993. Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: the role of predation pressures. In: Rylands A, editor. *Marmosets and tamarins: systematics, behaviour and ecology*. Oxford: Oxford University Press. p 200–219.
- Chapman C. 1988. Patterns of foraging and range use by three species of neotropical primates. *Primates* 29:177–194.

- Coelho AM. 1974. Socio-bioenergetics and sexual dimorphism in primates. *Primates* 15: 263–269.
- Creel SR, Creel NM. 1991. Energetics, reproductive suppression and obligate communal breeding in carnivores. *Behav Ecol Sociobiol* 28: 263–270.
- Dasilva GL. 1992. The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *J Anim Ecol* 61: 79–91.
- Di Bitetti MS, Janson CH. 2000. When will the stork arrive? Patterns of birth seasonality in neotropical primates. *Am J Primatol* 50: 109–130.
- Dietz JM, Baker AJ. 1993. Polygyny and female reproductive success in golden lion tamarins, *Leontopithecus rosalia*. *Anim Behav* 46:1067–1078.
- Dietz JM, Baker AJ, Miglioretti D. 1994. Seasonal variation in reproduction, juvenile growth, and adult body mass in golden lion tamarins (*Leontopithecus rosalia*). *Am J Primatol* 34:115–132.
- Digby LJ, Barreto CE. 1996. Activity and ranging patterns in common marmosets (*Callithrix jacchus*): implications for reproductive strategies. In: Norconk MA, Rosenberger AL, Garber PA, editors. Adaptive radiations of neotropical primates. New York: Plenum Press. p 173–185.
- Dunbar RIM, Dunbar P. 1988. Maternal time budget of gelada baboons. *Anim Behav* 36: 970–980.
- Ferrari SF, Lopes Ferrari MA. 1989. A re-evaluation of the social organisation of the Callitrichidae, with special reference to the ecological differences between genera. *Folia Primatol* 52:132–147.
- Goldizen AW. 1987. Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behav Ecol Sociobiol* 20:99–109.
- Grodzinski W, Wunder BA. 1975. Ecological energetics of small mammals. In: Golley FB, Petrusewicz K, Ryszkowski L, editors. Small mammals: their productivity and population dynamics. Cambridge: Cambridge University Press. p 173–204.
- Hudson R, White R. 1985. Bioenergetics of wild herbivores. Boca Raton, FL: CRC Press. 314p.
- Janson CH. 1988. Food competition in brown capuchin monkeys (*Cebus apella*): quantitative effects of group size and tree productivity. *Behaviour* 105:53–76.
- Karasov WH. 1981. Daily energy expenditure and the cost of activity in a free-living mammal. *Oecologia* 51:253–259.
- Karasov WH. 1992. Daily energy expenditure and the cost of activity in mammals. *Am Zool* 32:238–248.
- Kirkwood JK. 1983. Effects of diet on health, weight and litter-size in captive cotton-top tamarins (*Saguinus oedipus oedipus*). *Primates* 24:515–520.
- Kirkwood JK, Underwood SJ. 1984. Energy requirements of captive cotton-top tamarins (*Saguinus oedipus oedipus*). *Folia Primatol* 42:180–187.
- Kleiber M. 1961. The fire of life: an introduction to animal energetics. New York: John Wiley. 454p.
- Kleiman DG. 1978. Characteristics of reproduction and sociosexual interactions in pairs of lion tamarins (*Leontopithecus rosalia*) during the reproductive cycle. In: Kleiman DG, editor. The biology and conservation of the Callitrichidae. Washington, DC: Smithsonian Institution Press. p 181–190.
- Koteja P. 1996. Limits to the energy budget in a rodent, *Peromyscus maniculatus*: the central limitation hypothesis. *Physiol Zool* 69:981–993.
- Leutenegger W. 1980. Monogamy in callitrichids: a consequence of phyletic dwarfism? *Int J Primatol* 1:95–98.
- Loy J. 1988. Effects of supplementary feeding on maturation and fertility in primate groups. In: Fa JE, Southwick CH, editors. Ecology and behavior of food-enhanced primate groups. New York: A.R. Liss, Inc. p 153–166.
- Lyles AM, Dobson AP. 1988. Dynamics of provisioned and unprovisioned primate populations. In: Fa JE, Southwick CH, editors. Ecology and behavior of food-enhanced primate groups. New York: A.R. Liss, Inc. p 167–198.
- Martin P, Bateson P. 1993. Measuring behaviour: an introductory guide. 2nd ed. Cambridge: Cambridge University Press. 222p.
- Miller KE, Dietz JM. 2005. The effects of individual and group characteristics on feeding behaviors in wild *Leontopithecus rosalia*. *Int J Primatol* 26:1291–1319.
- Miller LE. 1997. Methods of assessing dietary intake: a case study from wedge-capped capuchins in Venezuela. *Neotropical Primates* 5:104–108.
- Mori A. 1979. Analysis of population changes by measurement of body weight in the Koshima troop of Japanese monkeys. *Primates* 20:371–397.
- Nagy KA, Milton K. 1979. Energy metabolism and food consumption by wild howler monkeys (*Alouatta palliata*). *Ecology* 60: 475–480.
- Nakagawa N. 1989. Bioenergetics of Japanese monkeys (*Macaca fuscata*) on Kinkazan Island during winter. *Primates* 30:441–460.
- Nickle DA, Heymann EW. 1996. Predation on Orthoptera and other orders of insects by tamarin monkeys, *Saguinus mystax mystax*

- and *Saguinus fuscicollis nigrifrons* (Primates: Callitrichidae), in north-eastern Peru. *J Zool Lond* 239:799–819.
- Nievergelt CM, Martin RD. 1999. Energy intake during reproduction in captive common marmosets (*Callithrix jacchus*). *Phys Behav* 65:849–854.
- Oftedal OT. 1985. Pregnancy and lactation. In: Hudson R, White R, editors. *Bioenergetics of wild herbivores*. Boca Raton, FL: CRC Press. p 215–238.
- Power M. 1999. Aspects of energy expenditure of Callitrichid primates: physiology and behavior. In: Dolhinow P, Fuentes A, editors. *The nonhuman primates*. Mountain View, CA: Mayfield Publishing Co. p 225–230.
- Price EC. 1992a. Changes in the activity of captive cotton-top tamarins (*Saguinus oedipus*) over the breeding cycle. *Primates* 33:99–106.
- Price EC. 1992b. The costs of infant carrying in captive cotton-top tamarins. *Am J Primatol* 26:23–33.
- Rose LM. 1994. Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). *Int J Primatol* 15:95–114.
- Sánchez S, Peláez F, Gil-Bürmann C, Kauhmann W. 1999. Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *Am J Primatol* 48:99–111.
- Schradin C, Anzenberger G. 2001. Costs of infant carrying in common marmosets, *Callithrix jacchus*: an experimental analysis. *Anim Behav* 62:289–295.
- Siegel S. 1956. *Nonparametric statistics for the behavioural sciences*. Tokyo: McGraw-Hill. 312p.
- Sokal RR, Rohlf F. 1981. *Biometry*. New York: W.H. Freeman and Company. 859p.
- Studel K. 2000. The physiology and energetics of movement: effects on individuals and groups. In: Boinski S, Garber PA, editors. *On the move: how and why animals travel in groups*. Chicago: University of Chicago Press. p 9–23.
- Tardif SD, Harrison ML. 1990. Estimates of the energetic cost of infant transport in tamarins. *Am J Phys Anthropol* 81:306.
- Tardif SD. 1994. Relative energetic cost of infant care in small-bodied neotropical primates and its relation to infant care patterns. *Am J Primatol* 34:133–143.
- Tardif SD. 1997. The bioenergetics of parental behavior and the evolution of alloparental care in marmosets and tamarins. In: Solomon NG, French JA, editors. *Cooperative breeding in mammals*. Cambridge: Cambridge University Press. p 11–33.
- Tardif SD, Jaquish CE. 1997. Number of ovulations in the marmoset monkey (*Callithrix jacchus*): relation to body weight, age and repeatability. *Am J Primatol* 42:323–329.
- Tardif SD, Power M, Oftedal OT, Power RA, Layne DG. 2001. Lactation, maternal behavior and infant growth in common marmoset monkeys (*Callithrix jacchus*): effects of maternal size and litter size. *Behav Ecol Sociobiol* 51:17–25.
- Taylor CR, Schmidt-Nielsen K, Raab JL. 1970. Scaling of energetic cost of running to body size in mammals. *Am J Physiol* 219:1104–1107.
- Taylor CR. 1977. The energetics of terrestrial locomotion and body size in vertebrates. In: Pedley TJ, editor. *Scale effects in animal locomotion*. New York: Academic Press. p 127–141.
- Taylor CR, Heglund NC, Maloiy GMO. 1982. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J Exp Biol* 97:1–21.
- Terborgh JW. 1983. *Five New World primates: a study in comparative ecology*. Princeton: Princeton University Press. 260p.
- Terborgh JW, Goldizen AW. 1985. On the mating system of the cooperatively breeding saddle-backed tamarin (*Saguinus fuscicollis*). *Behav Ecol Sociobiol* 16:293–299.
- Thompson SD, Power ML, Rutledge CE, Kleiman DG. 1994. Energy metabolism and thermoregulation in the golden lion tamarin (*Leontopithecus rosalia*). *Folia Primatol* 63:131–143.