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Total Energy Expenditure in Captive *Sapajus apella*

by

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ABSTRACT

Previous research has shown that primates have markedly lower total energy expenditure (TEE; kcal/day) than other eutherians, in that primates expend approximately 50% less energy for their mass than non-primate eutherians. However, little is known regarding interspecific variation of energy expenditure within platyrrhine primates. In this study, I investigated TEE in captive tufted capuchins (*Sapajus apella*, n=8, ages 7-36), a frugivorous and large-brained platyrrhine formerly known as *Cebus apella* (Alfaro *et al.* 2012), in order to compare their TEE with other placental mammals and primates. This study employed the doubly labeled water (DLW) method to measure TEE over a 7 – 10-day period, during which 16 – 20 hours of physical activity data was recorded via focal observation. I then compared these data to previously published TEE data collected from other primates and placental mammals. Capuchin TEE was similar ($p=0.67$) to other, less encephalized platyrrhines (*Callithrix* and *Alouatta*) in multiple regression controlling for body mass. Similar to other primates, capuchin TEE was 54% below than expected for a placental mammal of similar body mass. I discuss the effects of physical activity on daily energy requirements and the implications of these data for explaining capuchin life history.

INTRODUCTION

Sapajus apella are medium-bodied platyrrhine primates which are characterized by their large brains relative to body size, long life history patterns, and a suite of unique behavioral and manipulative traits, including, but not limited to tool use (Visalberghi and McGrew 1997; Stephan *et al.* 1988). While the behavior and ecology of capuchins have been studied extensively, capuchin energetics have not. Aside from measurements of locomotor costs in

Cebus albifrons by Taylor and Rowntree (1973), no measures of capuchin metabolism have been published.

Primates have large brains relative to body mass (Martin and Harvey 1985). Platyrrhine and cercopithecoid primates generally have the same relative brain size, with the exception of the very small bodied and metabolically slow callitrichid primates (Armstrong and Shea 1997). Specifically, capuchins tend to have relatively larger brains than other platyrrhine primates and show marked expansion of key parts of the brain, including the cerebellum, the cerebral cortex, and the thalamus (Stephan *et al.* 1988). In fact, relative to body mass, capuchins, along with *Pan*, have the highest index of brain to body size of any haplorrhine primate (Fragaszy and Bard 1997; Gibson 1986). Capuchins are also characterized by their small caecum, which could be due to their diet of fruits supplemented with seeds, nuts, leaves, and insects (Chivers and Hladik 1980; Martin 1990; Martin *et al.* 1985). Animals that tend to rely more on slow digesting plant material tend to possess larger caeca, while carnivores and insectivores tend to lack a caecum entirely (Martin 1990).

Differences in metabolic rate have been historically attributed to the allocation of energy toward different so-called “expensive organs,” such as the brain and gut (Aiello and Wheeler 1995; Isler and van Schaik 2009). However, others argue that lower TEE can be a reflection of slow life history patterns (Pontzer *et al.* 2014). Primates, in general, tend to have long life spans and an extended period of development relative to what would be expected for their body mass (Fragaszy and Bard 1997). Previous studies have shown that primates have lower daily total energy expenditure (TEE; kCal/day) for their body size than non-primate eutherian mammals (Pontzer *et al.* 2014). In fact, primates expend, on average, 50% less kilocalories than would be expected for eutherians of a similar mass (Pontzer *et al.* 2014). In addition to their relatively

large brains, capuchins stand out for their slow life history patterns. They have been known to live up to 55 years in captivity, and females experience their first birth between 4 and 7 years (Hakeem *et al.* 1996; Frigaszy *et al.* 2004).

While many studies have used basal metabolic rate (BMR; kcal/day) to understand energy budgets, this measure has been shown to obscure energy expenditure variation between taxa (Speakman 2005; Pontzer *et al.* 2014). BMR is a measure of the amount of energy that is expended while an individual is at rest, at a neutral temperature, and while the digestive system is inactive (Speakman 2005). Even at rest, the body expends energy through various processes, including circulating blood, breathing, regulating body temperature, growing and repairing cells, contracting muscles, and maintaining brain and nerve functions. TEE differs from BMR in that it takes into account energy that is expended during non-resting daily activity and digestion (Speakman 2005). Fundamentally, all energy is expended by the same biochemical process of oxidative phosphorylation regardless of whether the body is active or at rest (Speakman 2005). Although BMR does not vary greatly between taxa, TEE does vary depending on body size and life history, among other factors (Speakman 2005; Pontzer *et al.* 2014). For example, small mammals contribute approximately 40% of their TEE to BMR (Speakman 2000). Therefore, given this information, some researchers have posited that TEE is actually a better measure of life history than BMR (Speakman 2005).

This study measured TEE using the doubly labeled water (DLW) method in capuchins (*Sapajus apella*), and compared these data with previously published data on other primates. Our goals were twofold. First, we sought to provide new data on metabolic rates for *Sapajus*. While the available measurements for primate TEE are taxonomically diverse and include a wide range of body sizes (Pontzer *et al.* 2014), they include very few platyrrhine primate species. Prior to this

study, TEE data had been collected on only the primarily folivorous *Alouatta palliata*, and the small bodied exudivorous *Callithrix jacchus* (Pontzer *et al* 2014; Harrison and Tardif 1994). The inclusion of *S. apella* within the study of primate energetics serves to further elucidate the variation within platyrrhines and the primate Order in general. Second, we tested two competing hypotheses regarding energy expenditure: that capuchins have high TEE due to their relatively large brains, or that they have low TEE due to their slow life history.

METHODS

Captive *Sapajus apella* (n=8; 4 female; 4 male; ages 7-36 years) housed in the Franklin and Marshall College Vivarium in Lancaster, PA were used in this study. The capuchins live in two separate colonies. Each colony has access to a large common enclosure, which has access to toys, climbing substrates, and platforms. Each colony also has access to a wall of two rows of eight smaller testing cubicles separate from the larger enclosure, which can be isolated or opened to other cubicles and the main enclosure. The large enclosure of one colony is 3.35 m wide by 8.50 m long and 3.05 m high and can be divided into 4 smaller enclosures by sliding doors. The other colony has access to a main enclosure measuring 3.16 m wide by 7.16 m long by 3.05 m high and can be divided into 3 smaller spaces by sliding doors. Each of the testing cubicles is 0.91 m wide by 0.91 m long and 1m high. The two main enclosures are separated by an observation room, each with one-way mirrored glass and opaque curtains so that the capuchins of one colony cannot see the other colony. Once per day the capuchins are scatter-fed fresh produce and New World Primate Diet (Lab Diet, St. Louis, MO).

Institutional IACUC approvals for this project were obtained from both Franklin and Marshall College and Hunter College prior to data collection. All of the capuchins in this study

were healthy, non-lactating adults. Age, sex, body mass, and other statistics are listed in Table 1. Prior to the experiment, handlers trained the subjects to take juice and other liquids by mouth from a syringe. Each dose of Doubly Labeled Water (DLW) was carefully measured and stored in a separate vial for each subject based on its weight before the start of this study (average = 10.8g of DLW).

Table 1. Sapajus apella Population Statistics, TEE Data, and Travel Distance Data

Subject	Age (yrs)	Mass (kg)	Fat free mass (kg)	TEE (kCal/day)	% Body Fat	Water/day (L)	Horizontal Distance (km/day)	Vertical Distance (km/day)
Jill (F)	19	2.8	2.19	205.16	21.70	0.33	4.2	0.8
Honey (F)	9	3.3	2.57	255.37	22.06	0.49	4.9	0.7
Gracie (F)	36	3.5	2.83	266.91	19.01	0.54	4.2	0.6
Money Penny (F)	7	3.7	2.89	273.62	22.02	0.39	0.8	0.3
Nicknack (M)	19	4.5	3.55	374.51	21.21	0.63	12.9	0.4
Marcel (M)	20	4.5	3.66	390.26	18.66	0.70	5.5	0.3
Casey (M)	15	5.1	4.30	501.09	15.64	0.77	6.6	0.3
Rusty (M)	18	5.2	4.31	468.64	17.19	0.67	6.7	0.4
Mean	18	4.1	3.3	342	20	0.55	5.3	0.5
St. Dev.	8.79	0.88	0.79	107.66	2.38	0.15	3.55	0.20

Total Energy Expenditure

Total daily energy expenditure (TEE, kCal/day) was calculated using the DLW method. Oxygen within the body is eliminated via water loss (H₂O) and by expiration of carbon dioxide (CO₂), while hydrogen is eliminated only by water output (Speakman 1998). Calculating the difference between the elimination of hydrogen and oxygen yields a measure of CO₂ produced, and hence energy expended, per day (Speakman 1997). By labeling water with isotopes of hydrogen and oxygen, the turnover of oxygen and hydrogen can be quantified (Speakman 1997). For this study, DLW contained the isotopes deuterium (²H) and oxygen-18 (¹⁸O) in a concentration of 10% H₂¹⁸O, 6% ²H₂O.

Using the DLW method, TEE was measured over a 7 – 10-day period. Baseline urine samples were collected from each of the subjects at least 24 hours, but no more than 7 days prior to administering the dosage of DLW. The samples were frozen until they could be analyzed. Handlers administered the DLW dose to each subject the night before the first post-dose urine sample was to be taken (average = 10.8g of DLW). Each DLW dose was administered at least 12 hours and no more than 24 hours prior to the first post-dose urine sample. Generally, DLW doses were administered at approximately 6:00 PM, and the first post-dose sample was taken around 8:00 AM the following morning. Subjects were isolated in the testing cubicles for DLW dose administration and urine sample collection, to ensure that that each subject took the full DLW dose and that urine samples were not contaminated by other individuals.

The DLW dose was administered to the subject by pouring the complete liquid contents into a clean, dry beaker and mixing it with a sugarless, flavored drink mix. The complete contents of the beaker were then transferred into a syringe and administered to the subject in full. Any spilled liquid was quickly absorbed with popcorn and fed to the subject. Additionally, the syringe was flushed with more juice and given to the subject. The exact time and date of dose administration, as well as notes about the general health of the subject were recorded. The weight of the vial and the beaker were taken before and after the dose was administered to ensure that the exact amount of the dose was known.

Post-dose urine samples were collected beginning at least 12 hours after the dose was administered such that four post-dose samples were collected once every 2 to 3 days over a 7 – 10-day period. To collect urine, subjects were moved into the testing cubicles using routine positive reinforcement training techniques and remained in the cubicle until they urinated. A clean, dry collection pan was placed under each cubicle to capture urine. A clean, dry 2 mL

syringe was used to collect and transfer urine to a sterile vial, which was frozen until analysis. This study did not use any urine samples that were contaminated with feces or other material.

I analyzed baseline and post-dose urine samples using cavity ring-down spectroscopy. Each urine sample was first transferred to a Vivaspin vial, filtered using carbon black, and spun in a centrifuge at 2500 rpm for 25 minutes. I then pipetted each sample into a clean tube for use in the spectroscope. The spectroscope analyzed the urine samples for oxygen-18 and deuterium enrichment using cavity ring down spectrometry (Picarro®) in the Human Evolution & Energetics Lab at Hunter College - CUNY. The slope-intercept method was used to calculate fat free mass (FFM), and the production rate of carbon dioxide was calculated with the two-pool approach (Pontzer *et al.* 2012). TEE was calculated based on CO₂ production, using equation 7.15 in Speakman (1997).

Physical Activity

Behavioral data were collected during the 7 – 10 days after the dose was administered. For each subject sampled, between 16 and 20 hours of focal behavioral data were recorded, 4 of which were recorded in the morning. Prior to the study, the perimeter and cross-sectional areas of each enclosure were measured in horizontal and vertical planes. In one-hour increments, subjects' horizontal and vertical distance traveled were recorded in meters via focal observation. Additionally, time spent traveling was recorded. Travel time excluded time spent eating, resting, and engaging in social activities, unless these behaviors coincided with moving a distance further than .25 m. Table 1 outlines the average horizontal and vertical distances traveled.

The capuchin TEE data in this study were compared to previously collected TEE primate data from the work of Pontzer *et al.* (2014) using multiple regression controlling for body mass. Body mass, FFM and TEE were log₁₀ transformed prior to analysis. The results are listed in

Table 1, and in Figures 1 and 2. TEE in capuchins was also compared with travel distance over the study period. A comparison between daily travel distance and TEE can be seen in Figure 3A.

Table 2. Comparative Primate Total Energy Expenditure (TEE) and Body Composition Data

Species	Population	N	Age (yrs)	Mass (kg)	Fat Free Mass	% Body Fat	TEE	% Expected
<i>Microcebus murinus</i> ¹⁰	Wild	18	adult	0.06	-	-	28	113
<i>Callithrix jacchus</i> ⁷	Lab	6	adult	0.47	0.39	16.95	52.22	45
<i>Lepilemur ruficaudatus</i> ²	Wild	9	adult	0.77	-	-	121	70
<i>Eulemur sp.</i> ¹¹	Wild	11	adult	1.84	1.5	17.6	146	43
<i>Lemur catta</i> ¹¹	Wild	11	adult	2.24	1.8	17.3	146	37
<i>Sapajus apella</i> ⁴	Lab	8	17.9	4.1	3.3	19.7	342	54
<i>Macaca radiata</i> ⁸	Lab	5	8.9	4.20	-	-	251	39
<i>Propithecus diadema</i> ⁷	Wild	6	adult	4.90	4.7	4.2	346	48
<i>Aloutta palliata</i> ³	Wild	5	adult	7.12	-	-	602	62
<i>Allenopithecus nigroviridis</i> ⁷	Zoo	1	adult	7.90	7.9	-	524	50
<i>Macaca mulata</i> ¹	Lab	11	20	14.40	9.8	-	607	36
<i>Papio anubis</i> ⁹	Research station	8	adult	16.18	-	15.11	831.72	45
<i>Pan paniscus</i> ⁷	Sanctuary	4	17.5	37.95	35.4	13.0	1767	49
<i>Pan troglodytes</i> ⁷	Sanctuary & zoo	10	18.0	57.05	54.3	6.1	2386	49
<i>Homo sapiens</i> ⁶	Hadza population	30	37.0	46.63	38.9	17.7	2212	53
<i>Homo sapiens</i> ⁶	Westerners	195	41.7	72.24	49.3	32.3	2482	42
<i>Pongo pygmaeus</i> ⁵	Zoo	3	25.3	74.85	61.2	16.9	1984	33
<i>Gorilla gorilla</i> ⁷	Zoo	5	21.4	123.72	108.0	10.5	3160	35

Sources: ¹Blanc *et al.* 2003; ²Drack *et al.* 1999; ³Milton and Nagy 1978; ⁴New data; ⁵Pontzer *et al.* 2010; ⁶Pontzer *et al.* 2012; ⁷Pontzer *et al.* 2014; ⁸Rising *et al.* 2008; ⁹Rosetta *et al.* 2011; ¹⁰Schmid and Speakman 2000; ¹¹Simmen *et al.* 2010

RESULTS

As reported for other primates, capuchin TEE (mean = 342; standard deviation = 107.66) was 54% lower than expected for body size, compared with other non-primate eutherians (Figure 1). However, analysis of variance (ANOVA) showed that there is no significant difference between capuchin TEE and the other previously studied platyrrhines, including marmosets and howlers, from Pontzer *et al.* (2014) ($p = .05$; $r^2 = 4.33$). In multiple regression analysis, capuchin body mass and TEE significantly correlated ($p < .001$; $r^2 = 0.96$), and females tended to have lower body mass and lower TEE than males (Figure 2). ANOVA showed that the difference between TEE in capuchins and all other primates was not significant ($p = 0.45$; $r^2 = 0.60$; Figure 1).

Consistent with previous studies, there was no correlation between daily travel distance and residual TEE in capuchins ($p = 0.65$; $r^2 = -0.12$; Figure 3A) (Pontzer *et al.* 2014). There was, however, a potential connection between travel distance and body composition. Daily travel distance and percent body fat had a significant negative correlation ($p = 0.03$; $r^2 = 0.56$; one outlier removed Figure 3B). Individuals with lower body fat tended to travel longer distances, whereas individuals with higher body fat tended to travel shorter distances per day. Importantly, these analyses excluded one subject, Nicknack, who traveled over twice the distance of the others. With this individual included, travel distance and percent fat did not correlate ($p = 0.64$; $r^2 = -0.12$).

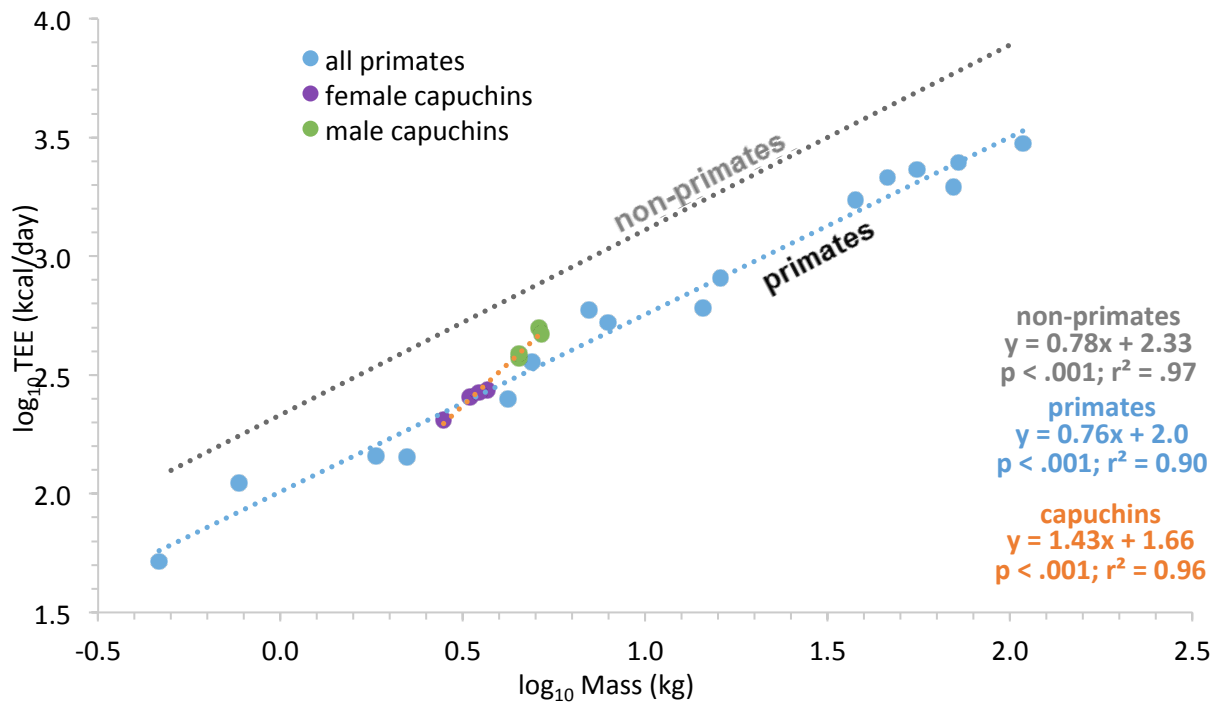


Figure 1. \log_{10} Body Mass: \log_{10} Total Energy Expenditure for Primates & Non-primate Eutherians. *Microcebus murinus* was removed from the analysis, as per Pontzer et al. 2014.

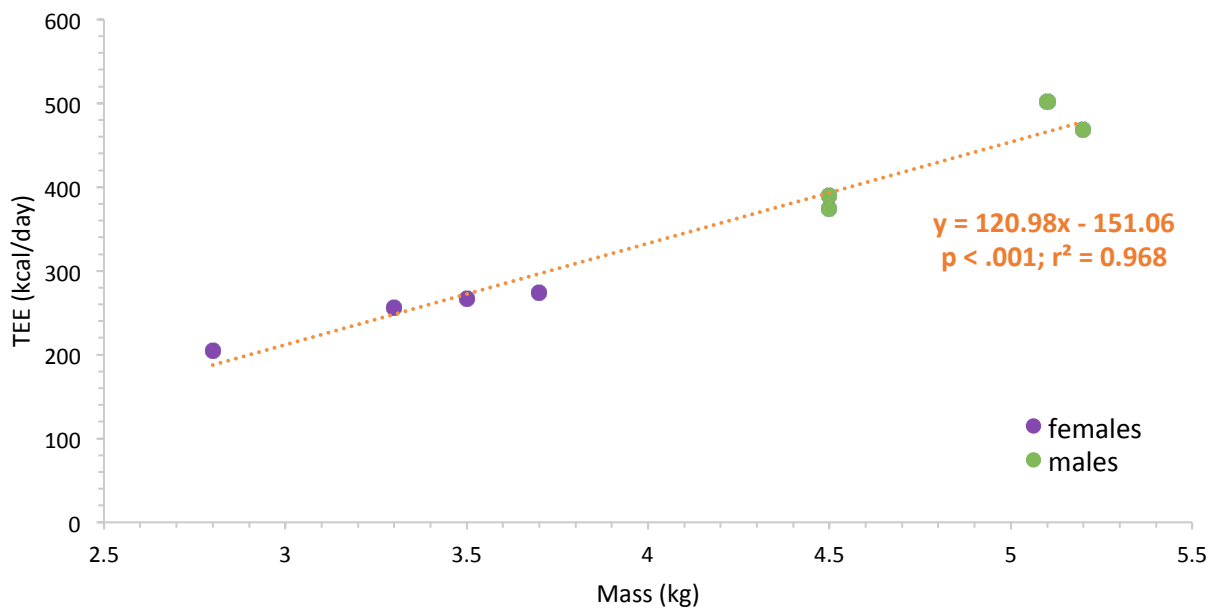


Figure 2. Body Mass:Total Energy Expenditure for capuchins

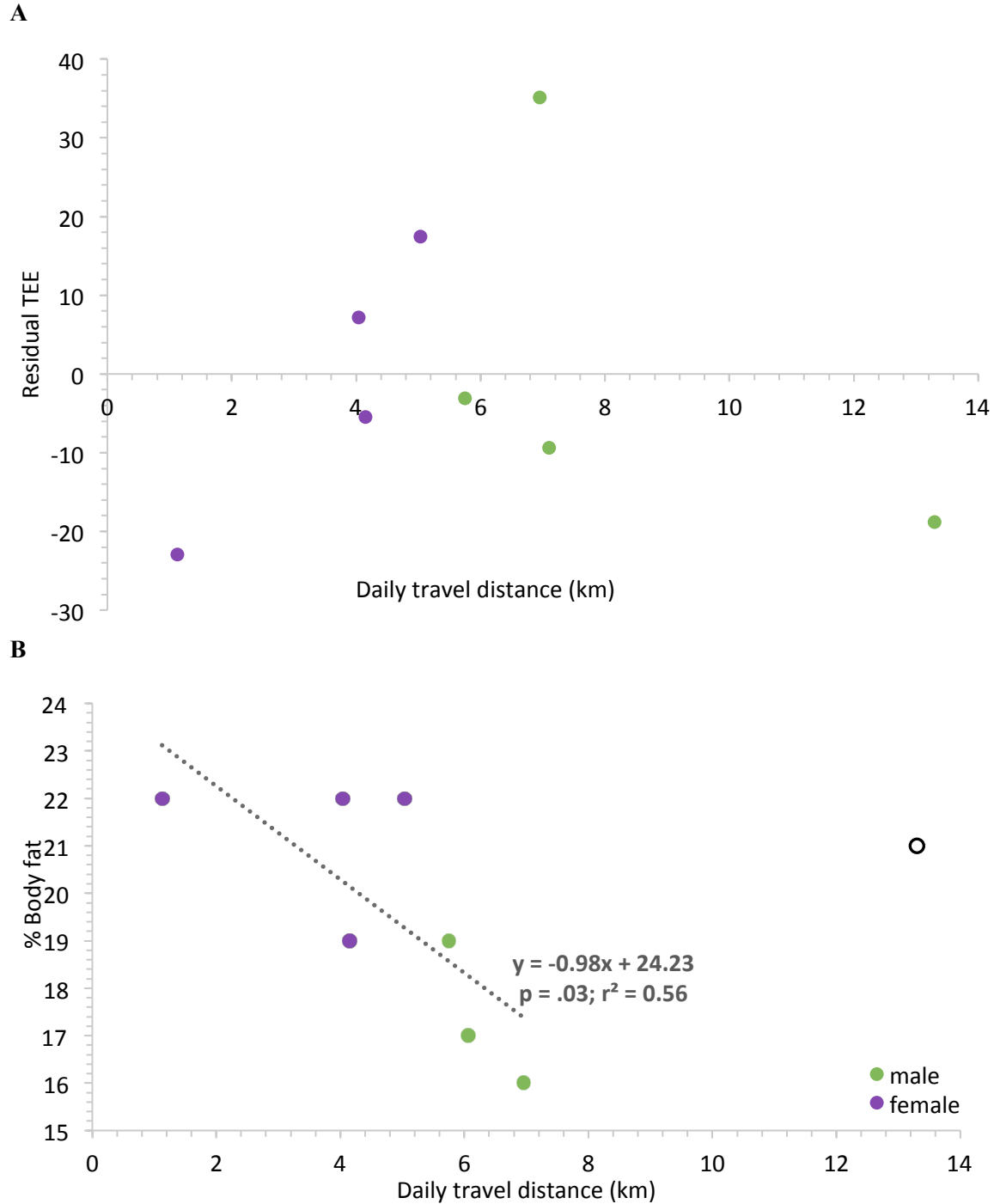


Figure 3. (A) Residual TEE, controlling for body mass does not correlate with travel distance for capuchins. (B) Daily travel distance correlates with percent body fat in capuchins. One subject, Nicknack was removed as an extreme outlier, and is indicated as the open black circle in the figure.

DISCUSSION & CONCLUSION

Consistent with previous analyses of primate TEE (Pontzer *et al.* 2014), I found that the platyrrhine *Sapajus apella* expended on average 54% less energy than non-primate eutherians of similar body mass. I hypothesized that capuchins would have greater TEE for their body size than other platyrrhines because of their higher degree of encephalization. This is not the case. Controlling for body mass, capuchins expended a similar amount of energy than the other previously studied less encephalized platyrrhine species (Figure 1).

As in Pontzer *et al.* (2014), capuchin TEE showed no significant correlation to travel distance, when controlling for body mass (Figure 3A). There was, however, a correlation between body composition and travel distance. Individuals with higher body fat percentage had shorter daily travel distances, while individuals with lower body fat percentages had longer daily travel distances (Table 1; Figure 3B). After removing one outlier, Nicknack, a low-ranking male with slightly higher than average percent body fat and who traveled over 2 times the distance that the other individuals traveled, the correlation is significant. Males tended to have lower percent body fat and longer daily travel distances and also tended to have higher TEE. However, more research remains to be done to explain these differences.

Previous studies have proposed that body size and life history are related (Sibly *et al.* 2007). Specifically, primates' low TEE for their body size may be related to their remarkably slow life history patterns, as suggested by the fact that orangutans have the lowest TEE for their body size and very slow life history patterns (Pontzer *et al.* 2010). Further, according to Pontzer *et al.* (2014), growth, reproduction, and senescence correlate with TEE, after controlling for body mass and phylogenetic relatedness. Because shifts in life history show a related shift in TEE, they argue that variation in TEE between species may be caused by differences in percentage of

TEE allocated to production (Pontzer *et al.* 2014). This may serve to explain not only why the primate Order, in general, shows lower energy throughput than non-primate eutherians, but that capuchins, despite their large brains, do not have higher TEE for their body size (Fragaszy and Bard 1997; Gibson 1986; Pontzer *et al.* 2014). Although more work needs to be done to better understand how interspecific differences in life history and general ecology influence energy throughput, these differences may be explained by changes in energy allocation.

It has been argued that the lower TEE exhibited in primates reflects an evolved energy-saving strategy related to primates' slow life history patterns (Pontzer *et al.* 2010, 2014). Though capuchins are highly encephalized primates, which tends to manifest a higher BMR as a percentage of TEE (Pontzer *et al.* 2014), they retain low TEE for their body size, similar to other smaller-brained platyrrhines. The interspecific variation in terms of percent expected TEE for body mass (Table 2) though not significantly different, may also reflect changes in energy allocation on a different scale. The addition of capuchins to the ever-growing body of energy expenditure data serves to underscore the fact that primates are a highly variable Order, and that the underlying mechanisms driving this energetic interspecific variation remain to be explained. These data demonstrate further evidence supporting the hypothesis that changes in energy expenditure may have been influential in the evolution of the primate Order.

LIMITATIONS & FUTURE DIRECTIONS

This study was limited by its low sample size of only 8 capuchins. Performing this study on a larger group could serve to clarify the relationships between primate TEE and life history, and the evolutionary significance of energy throughput. Increasing the sample size may also help clarify the relationship between body composition and travel distance in capuchins. In the future,

it would be beneficial to collect BMR data for capuchins to determine how it compares with BMR in other platyrrhines and primates.

ETHICS STATEMENT

Institutional Animal Care and Use Committee (IACUC) approvals (Hunter College – City University of New York, and Franklin and Marshall College) were obtained prior to data collection and analysis.

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