

# Arboreal Folivores Limit Their Energetic Output, All the Way to Slothfulness

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**ABSTRACT:** By exploiting unutilized resources, organisms expand into novel niches, which can lead to adaptive radiation. However, some groups fail to diversify despite the apparent opportunity to do so. Although arising multiple times, arboreal folivores are rare and have not radiated, presumably because of energetic constraints. To explore this hypothesis, we quantified the field metabolic rate (FMR), movement, and body temperature for syntopic two- and three-toed sloths, extreme arboreal folivores that differ in their degree of specialization. Both species expended little energy, but three-toed sloths (162 kJ/day\*kg<sup>0.734</sup>) possessed the lowest FMR recorded for any mammal. Three-toed sloths were more heterothermic and moved less than two-toed sloths. We then compared FMRs and basal metabolic rates (BMRs) for 19 species of arboreal folivores along a spectrum of specialization. Overall, arboreal folivores had lower BMRs and FMRs than other mammals, and increasing specialization led to lower FMRs but not BMRs. Thus, reduced energetic expenditure in specialized species was the result of thermoregulatory and behavioral strategies, rather than simply a proportionate reduction in BMR. Altogether, our findings support the concept that arboreal folivores are tightly constrained by nutritional energetics and help to explain the lack of radiation among species exploiting a lifestyle in the trees.

**Keywords:** herbivore, metabolism, species diversity, tree sloths.

## Introduction

Adaptive radiation, the evolutionary divergence within a rapidly multiplying lineage into different forms, is one of the most important forces shaping biodiversity (Schluter 2000). Beyond the classic examples—lizards (*Anolis* spp.) on Caribbean islands (Losos 2009), cichlids (Cichlidae) in the East African Great Lakes (Seehausen 2006), or finches (*Geospiza* spp.) of the Galapagos (Grant and Grant 2008)—it is increasingly recognized that many animals and plants from both terrestrial and aquatic systems have arisen via ecological speciation and adaptive radiation (Schluter 2000). In

general, species radiation is precipitated by the emergence of an “ecological opportunity” and establishment of a “key innovation” that enables the exploitation of this new environmental condition (Losos 2010). However, some groups fail to radiate despite apparent opportunity. While attention has focused on the forces shaping adaptation within diversified groups, the constraints for groups that have failed to radiate after successful niche expansion are far less understood (Losos 2010; Yoder et al. 2010).

More than one-third of terrestrial Earth is forested (Ramanakutty and Foley 1999), yet remarkably few vertebrates have evolved to live in the canopy and subsist on tree leaves. Although arboreal folivory has arisen in several mammalian lineages (e.g., primates, tree sloths, marsupials), it is one of the rarest lifestyles, occurring in less than 0.2% of mammals (Eisenberg 1978). Moreover, radiation after expansion into this niche is exceedingly uncommon. The overall lack of diversification has been attributed to energetic constraints associated with a strategy dependent on an energetically and nutritionally poor food resource (Eisenberg 1978). Arboreal folivores exhibit remarkably little variation in body size (Cork and Foley 1991), and the convergence of size is viewed as an energetic optimization between being light enough to access forage in the canopy and possessing sufficient size to efficiently process plant matter. Arboreal folivores share other characteristics that appear to minimize energetic expenditure (McNab 1978): small litter sizes (Eisenberg 1978), anatomical specializations related to digestion (Cork and Foley 1991), forms of locomotion to minimize transportation costs (Emmons and Gentry 1983; Cliffe et al. 2014), reduced activity patterns (MacLennan 1984), and unique behaviors associated with resource acquisition (Pauli et al. 2014) and thermoregulation (Briscoe et al. 2014). Notably, arboreal folivores also exhibit reduced basal metabolic rates (McNab 1986), in some cases dramatically so. Collectively, these shared traits are viewed as innovations to manage a precarious energy balance (Foley 1987; Pauli et al. 2014).

Tree sloths (*perezosos* [Spanish], *preguiças* [Portuguese]; i.e., “lazies”) are slow-moving Neotropical mammals (sub-

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order Folivora) that lie at the extreme end of specialization toward arboreal folivory (Cork and Foley 1991). The two phylogenetic groups, two-toed (*Choloepus* spp.) and three-toed (*Bradypus* spp.) sloths, both of which are foregut-fermenting arboreal mammals (Cork and Foley 1991), diverged more than 20 million years ago (Delsuc et al. 2004). Two-toed sloths possess comparatively large home ranges (up to 140 ha; Peery and Pauli 2012) and a relatively diverse diet that includes animal matter and fruits as well as leaves. In contrast, three-toed sloths possess constricted home-range sizes (<15 ha; Pauli and Peery 2012) and are resource specialists (Mendoza et al. 2015). Indeed, three-toed sloths are strict folivores, and a three-toed sloth will roost and consume leaves from only a few tree species and even a small number of individual trees (Montgomery and Sunquist 1978; Mendoza et al. 2015). Three-toed sloths also possess the slowest rate of digestion for any mammal (Foley et al. 1995) and an exceedingly low metabolic rate (McNab 1978).

Given its extreme specialization, it follows that the daily energy expenditure of a sloth should be low and a function of degree of arboreal folivory. Using doubly labeled water, Nagy and Montgomery (1980) found that the field metabolic rate (FMR, or daily energy expenditure by an animal in the wild) for three-toed sloths was 74% of the predicted basal metabolic rate (BMR, the energy expenditure of a normothermic animal at rest) for a mammal of its size; no one, however, has previously quantified the FMR for a two-toed sloth, and a direct comparison between these two related arboreal folivores is lacking. Further, although metabolic rates have been quantified for a number of arboreal folivores, how specialization toward arboreal folivory relates to metabolic rate and energetic expenditure has not been explored. If arboreal folivory is constrained by nutritional energetics, increasing specialization should be accompanied by reduced energetic needs. Here, we quantified the FMRs for two species of co-occurring tree sloths, representing the two phylogenetic groups, simultaneously. During our trials, we also monitored the daily movement patterns, habitat use, and thermal profile of the labeled sloths. We predicted that, regardless of habitat use, the more specialized three-toed sloth would move less and exhibit greater heterothermy and an overall reduced mass-specific FMR. Further, we predicted that, across species of mammalian arboreal folivores, increased specialization would be accompanied by reduced daily energetic expenditures.

### Methods

Our research took place in March 2014 within an agroecosystem of intact tropical forest, pastures, shade-grown cacao, and monocultures of banana and pineapple in northeastern Costa Rica (10.32°N, -83.59°W). Both brown-throated three-toed sloths (*Bradypus variegatus*) and Hoffmann's two-

toed sloths (*Choloepus hoffmanni*) are abundant across our study site. Fieldwork was conducted as stipulated and authorized by Institutional Animal Care and Use Committee protocol A01424 of the University of Wisconsin–Madison and adhered to the guidelines for the use of mammals in research set forth by the American Society of Mammalogists. Access was granted by the private landowner, and our project and sample collection were approved by the Ministerio de Ambiente, Energía y Telecomunicaciones, Sistema Nacional de Áreas de Conservación, Costa Rica. All samples were imported to the United States with CITES (Convention on International Trade in Endangered Species) and United States Fish and Wildlife Service approval.

We quantified FMR with the two-sample doubly labeled water method (i.e., measuring isotope levels in prerelease and post-recapture samples, each corrected for background; Speakman 1997). We captured 22 individual adult sloths (10 three-toed and 12 two-toed sloths) by hand from trees (Peery and Pauli 2014), weighed them ( $\pm 0.01$  kg), and then immobilized them with an intramuscular injection of 2.5 mg/kg ketamine and 0.02 mg/kg dexmedetomidine (Pauli et al. 2014). During immobilization, sloths were kept outdoors in a shaded location. We collected preinjection blood samples (2 mL) from the vena cava and immediately transferred them to vacutainers lined with EDTA (ethylenediaminetetraacetic acid). Mean baseline levels ( $\pm 1$  SE) of  $^{18}\text{O}$  and  $^2\text{H}$  were, respectively,  $5.10\text{‰} \pm 0.53\text{‰}$  and  $25.47\text{‰} \pm 0.88\text{‰}$  VSMOW (Vienna Standard Mean Ocean Water). We then injected a premixed dose of doubly labeled water intraperitoneally. The dose contained 0.17 g/kg body mass of a solution containing 96%  $\text{H}_2^{18}\text{O}$  (Sigma-Aldrich) and 0.10 g/kg 99%  $^2\text{H}_2\text{O}$  (Cambridge Isotope Laboratories, Andover, MA). We affixed temperature data loggers (iButtons Maxim DS1922L-F5; 3 g) under the fur on the dorsum of each sloth with prosthetic adhesive (Pros-Aide). To track environmental temperatures, we also deployed one temperature data logger to a shaded location in each of the three habitats that sloths utilize on the farm—(1) shade-grown cacao, (2) intact forest, and (3) pasture—to record the environmental temperature profile. All data loggers recorded hourly temperatures. We collected a second blood sample 3–4 hours after dosing, to allow for equilibration (Speakman 1997). We released each sloth at the site of capture and recaptured it 7–10.9 days later, when a third blood sample was taken and the temperature data logger removed with a solvent (Pros-Aide). All sloths sampled had previously been captured, marked with uniquely coded PIT (passive integrated transponder) tags (Biomark, Boise, ID) inserted subcutaneously between the shoulder blades, and fitted with radio collars (Mod-210, Telonics, Mesa, AZ). During this study, we located each sloth daily via radiotelemetry, using previously described radio-tagging procedures (Pauli and Peery 2012; Peery and Pauli 2012). We did not detect a change in body mass of sloths over the release-

recapture interval ( $\bar{x}_{\Delta\text{mass}} = 0.1 \pm 0.2$  kg;  $t_{21} = 0.66$ ,  $P = .52$ ).

Blood was stored in cryogenically stable tubes, refrigerated (for 0.5 months), and then frozen (5 months) until analysis by isotope ratio mass spectrometry. Water from blood samples was extracted by centrifugation (4°C, 45 min at 10,000 rpm) on regenerated cellulose filters (YM-50, Centricon, Bedford, MA). Deuterium isotopic enrichments in hydrogen gas were measured, after chromium reduction, with a Thermo Scientific (West Palm Beach, FL) DeltaPlus isotope ratio mass spectrometer (Thorsen et al. 2010). The  $^{18}\text{O}$  abundance (average precision 0.03%) was measured with a Thermo Scientific Delta IV equipped with a Gas Bench (Thermo Scientific; Thorsen et al. 2010). Rates of  $\text{CO}_2$  production were calculated with the single-pool equation, as recommended by Speakman (1997) for mammals lighter than 10 kg. Body pool size, required in the equation, was determined from dilution of both isotopes in a blood sample collected at least 3 h after injection; the intercept method for calculation of pool size was used (Speakman 1997). The average pool size, expressed as the percentage of mass that was water, was  $61.7\% \pm 1.9\%$  ( $n = 15$ ), which was within realistic limits (Speakman 1997). Four individual two-toed and three individual three-toed sloths appeared not to reach equilibration, which might be associated with slower metabolism (Speakman 1997), and their initial values were instead estimated on the basis of their measured doses, body masses, and the average pool size of the other sloths. The rate of  $\text{CO}_2$  production was converted to kilojoules per day (kJ/d) with the conversion factor of 21.7 kJ/L  $\text{CO}_2$  suggested for herbivores (Nagy et al. 1999).

We scaled our estimate of total daily energy expenditure to one based on body size (i.e., per  $\text{kg}^{0.734}$ ; Nagy 2005). We then compared differences in FMR by species (two- vs. three-toed sloth) and sex via a two-way ANOVA. We calculated the daily and cumulative distances moved for each sloth in ArcGIS (ESRI; Redlands, CA). We scaled daily distance moved to body mass ( $\text{m}/\text{day} \cdot \text{kg}^{1/4}$ ; Garland 1983) and compared between sloth species with a  $t$ -test. We fitted a generalized additive mixed model to ambient and sloth body temperatures (°C), using individuals as a random effect (Wood 2006), to visualize hourly temperature trajectories for both species in relation to ambient temperature in the R statistical platform.

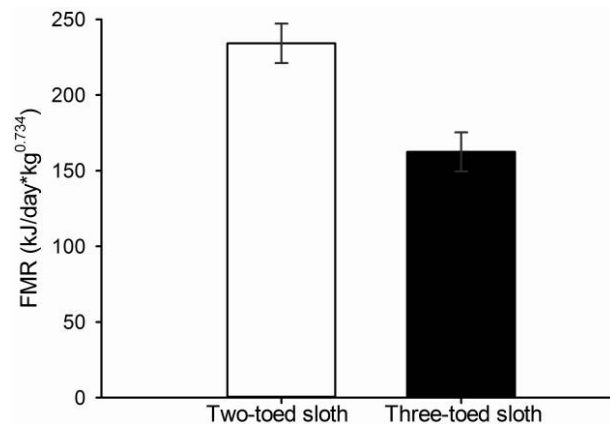
We then explored the influence of body temperature on metabolic rates as

$$I_c = aM^b 10^{((T_c - T_b)(\log Q_{10})/10)}, \quad (1)$$

where  $I_c$  is an overall temperature-corrected metabolic rate (either BMR or FMR) for the species,  $a$  is the allometric coefficient (BMR = 4.12, FMR = 4.82),  $b$  is the allometric mass exponent (BMR = 0.734, FMR = 0.69),  $T_c$  is the

temperature to which  $I_c$  is to be corrected,  $T_b$  is the mammal's body temperature, and  $Q_{10}$  is the rate change for a 10°C change in temperature (White and Seymour 2003, 2005). We chose this approach over a presumed universal temperature dependence of biological processes (Gillooly et al. 2001) because of the availability of values for mammals ( $Q_{10} = 2.8$ ;  $T_b = 36.2^\circ\text{C}$ ; White and Seymour 2005), and both approaches yield rather similar conclusions (White and Seymour 2003).

To compare our estimates of energy expenditure in sloths to those previously collected for other arboreal folivores, we searched peer-reviewed literature for the 52 genera of mammals identified as specialized arboreal folivores (Eisenberg 1978) and recorded BMRs and FMRs (see app. A for details; apps. A, B available online). We compared the measured BMR and FMR (kJ/day) of each mammal to the value predicted for it from body mass, using allometric equations for BMR (White and Seymour 2003) and FMR (Nagy 2005). We also regressed the normalized estimates of BMR ( $\text{kJ}/\text{day} \cdot \text{kg}^{0.69}$ ) and FMR ( $\text{kJ}/\text{day} \cdot \text{kg}^{0.734}$ ) against the degree of arboreal folivory (a value ranking from 0.0 to 1.0; see app. A for details). As arboreal folivores represent a diverse group of mammals with varying degree of relatedness, we also conducted our regression analysis with phylogenetic independent contrasts (Rezende and Diniz-Filho 2012). Specifically, we assembled a phylogenetic supertree (Creevey and McInerney 2005) and estimated branch lengths from previously published nuclear and mitochondrial sequences (see app. B for details). We then calculated phylogenetic independent contrasts for FMR, BMR, and ranking of arboreal folivory with COMPARE 4.6b (Martins 2004). We fitted the resultant independent contrasts with a linear regression forced through the origin (Rezende and Diniz-Filho 2012). Because



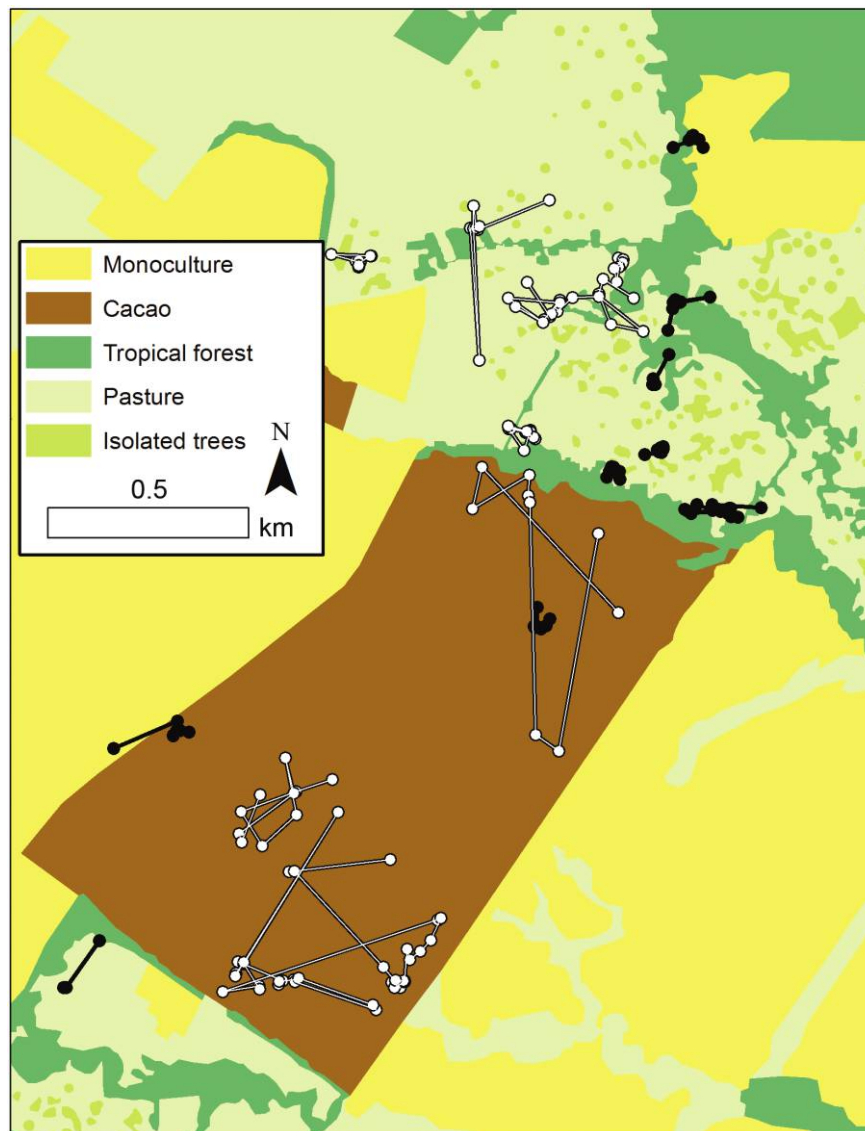
**Figure 1:** Total daily energy expenditure (FMR [field metabolic rate];  $\text{kJ}/\text{day} \cdot \text{kg}^{0.734}$ ;  $\pm 1$  SE) was lower (two-way ANOVA;  $P < .001$ ; see text for details) for three-toed sloths ( $n = 10$ ) than for two-toed sloths ( $n = 12$ ) in Costa Rica, 2014.

of the limited number of FMR estimates for arboreal folivores and the resultant low statistical power, as well as our a priori prediction of declining metabolism with arboreal folivory, we evaluated the significance of our phylogenetic contrasts with a one-tailed test.

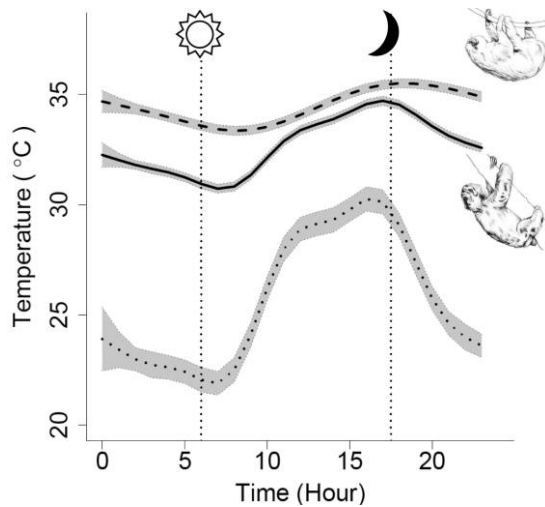
### Results

The FMR ( $\text{kJ/day} \cdot \text{kg}^{0.734}$ ) was, on average, 31% lower ( $F_{1,21} = 16.5$ ,  $P < .001$ ) for three-toed sloths ( $\bar{x} = 162 \pm 12.9$ ,  $n = 10$ ) than for two-toed sloths ( $\bar{x} = 234 \pm 13.0$ ,  $n = 12$ ; fig. 1). We detected a marginal difference in FMR between the sexes ( $F_{1,21} = 3.82$ ,  $P = .07$ ) but no interac-

tion between sex and species ( $F_{1,21} = 0.21$ ,  $P = .65$ ). As predicted, daily distance moved was numerically greater in the two-toed sloth ( $147.3 \pm 71.5$  m [ $\pm 95\%$  confidence interval]; fig. 2) than in the three-toed sloth ( $49.3 \pm 16.2$  m); this difference was statistically confirmed after body mass differences were accounted for ( $t_{20} = 1.72$ ,  $P = .019$ ). Body temperatures of two- ( $34.5^\circ \pm 0.16^\circ\text{C}$ ,  $\pm 1$  SE) and three-toed ( $32.7^\circ \pm 0.15^\circ\text{C}$ ) sloths exhibited consistent daily rhythms (fig. 3). Three-toed sloths, compared with two-toed sloths, possessed a lower maximum temperature ( $34.8^\circ$  vs.  $35.7^\circ\text{C}$ ) and minimum temperature ( $30.7^\circ$  vs.  $33.2^\circ\text{C}$ ) and a larger overall temperature range ( $4.1^\circ$  vs.  $2.5^\circ\text{C}$ ). The energetic impact (eq. [1]) of hour-by-hour differences in average body



**Figure 2:** Movement and habitat use for three-toed sloths (black points and paths;  $n = 10$ ) and two-toed sloths (white points and paths;  $n = 12$ ) in Costa Rica, 2014.



**Figure 3:** Average ( $\pm 95\%$  confidence intervals) sloth body temperature (6 three-toed sloths [solid line] and 1 two-toed sloth [dashed line]) and ambient temperature (3 habitats [dotted line]) logged every hour for 5 days, fitted with a generalized additive mixed model, Costa Rica, March 18–23, 2014. Both species of sloths exhibited consistent temperature rhythms, but daily body temperature was consistently more variable and lower among three-toed sloths.

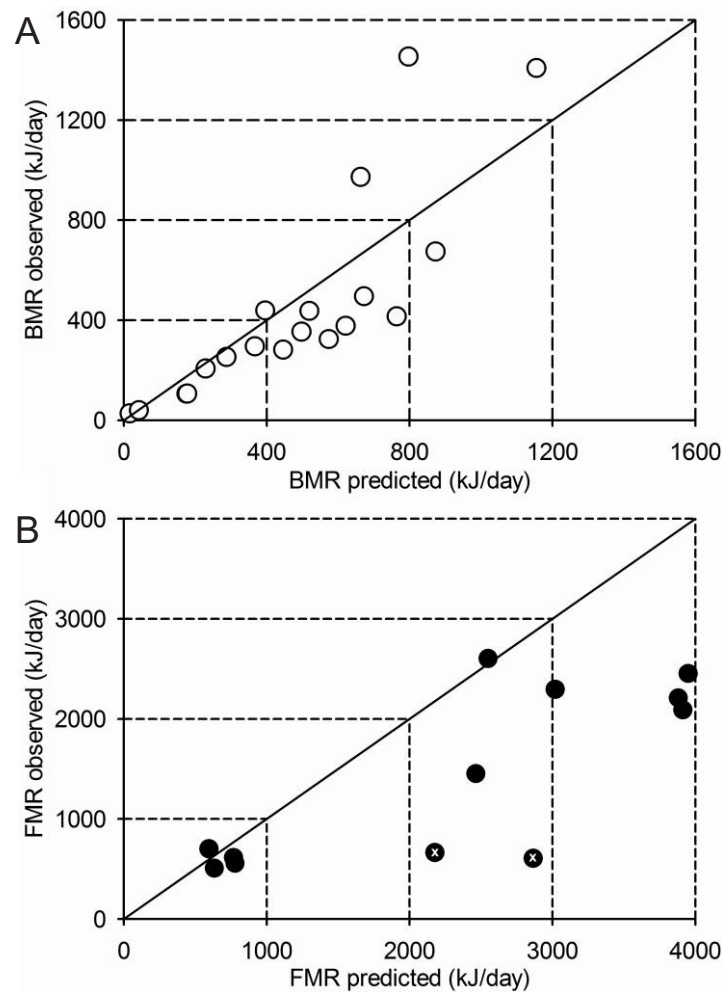
temperatures between the two- and three-toed sloths accounts for the majority of the difference in FMR between them (i.e., 17 percentage points of the 31% observed). The average body temperatures accounted for a considerable amount of the observed difference in FMR between sloths and other mammalian homeotherms: three-toed sloths possessed an FMR 79% less than that predicted for a mammal of the same mass, 30 percentage points of which was attributable to lower average body temperature; two-toed sloths possessed an FMR 69% less than that predicted, with body temperature accounting for 16 percentage points (see app. A for details).

The BMRs and FMRs had previously been estimated for 19 and 12 species of arboreal folivores, respectively (app. A). The majority of arboreal folivores possessed BMRs (13/19) and FMRs (10/12) lower than those predicted for a mammal from body size (fig. 4); overall, this difference was 4 times as great for FMRs, which averaged  $32\% \pm 8\%$  less than expected, as for BMRs ( $8\% \pm 9\%$  less than expected). Measures of FMR exhibited a significant ( $F_{1,11} = 5.66$ ,  $P = .039$ ;  $r^2 = 0.361$ ) and negative relationship with degree of arboreal folivory (fig. 5); in contrast, we found no relationship ( $F_{1,18} = 0.12$ ,  $P = .73$ ) between the BMR and the ranking of a species' arboreal folivory (fig. 5). Both of these findings were confirmed by our analysis of phylogenetic independent contrasts: FMR exhibited a negative (FMR =  $-1.9x$ ) trend with arboreal folivory ( $F_{1,10} = 2.32$ ,  $P = .080$ ), whereas BMR exhibited no relationship ( $F_{1,17} = 0.20$ ,  $P = 0.33$ ).

## Discussion

Both species of sloth expend extremely little energy daily. Indeed, our estimate of FMR for three-toed sloths is the lowest recorded for any nonhibernating mammal. Nagy and Montgomery (1980) previously estimated the FMR for three-toed sloths in Panama at  $204 \text{ kJ/day} \cdot \text{kg}^{0.75}$ , which is about 20% greater than our estimate and more comparable to what we found among two-toed sloths. We think that the explanation for the difference between studies is primarily a technical one. Our assumed fractionation of evaporative water loss (Speakman 1997) differed from that of Nagy and Montgomery (1980), which alone accounts for 6%–7% of the difference in the FMR estimates. Nagy and Montgomery (1980) estimated body water by using a tritium dilution 20–25 h after administration; the use of tritium and a prolonged equilibration period can overestimate the body water dilution space (Speakman 1997). Consequently, the dilution space was estimated as 71% of body mass (Nagy and Montgomery 1980), higher than our estimate (61.7%). Inflated dilution space propagates into higher estimates of FMR because  $\text{CO}_2$  production is proportional to the product of dilution space and the difference in the elimination rate constants for the two isotopes (Speakman 1997). It is also possible, however, that the lower FMR for three-toed sloths that we observed could be reinforced by important differences in habitat between the two field sites. In particular, our study took place in an agroecosystem consisting mostly of shade-grown cacao and pastures with scattered trees, whereas the previous study (Nagy and Montgomery 1980) was conducted in a tropical reserve. Given that the trees are stunted in agricultural patches and that ascending and descending tall trees can represent a significant component of a sloth's daily energy budget (Pauli et al. 2014), a lower canopy could contribute to reduced energetic costs.

Although low in both species of sloth, FMR was nearly one-third lower in the three-toed sloth. This observation might be partly explained by smaller movement distances and less time engaged in energetically costly activities by three-toed sloths. Two- and three-toed sloths did not utilize different habitats during our work (fig. 2) but did exhibit pronounced differences in movement distances. As inherent measurement error in FMR makes individual-level analyses unreliable (Butler et al. 2004), we did not explicitly explore a relationship between individual movement and FMR. Although activity expenditures likely contributed to observed differences in FMR, we believe that the species-level difference was primarily driven by regulation of body temperature. Endothermy is costly, requiring up to 30 times as much fuel as ectothermy (Nagy 2005), and considerable energetic savings can be attained by reducing homeothermy (Geiser 2004). Our estimates of body temperature for both species of sloth, determined via external attachment of a

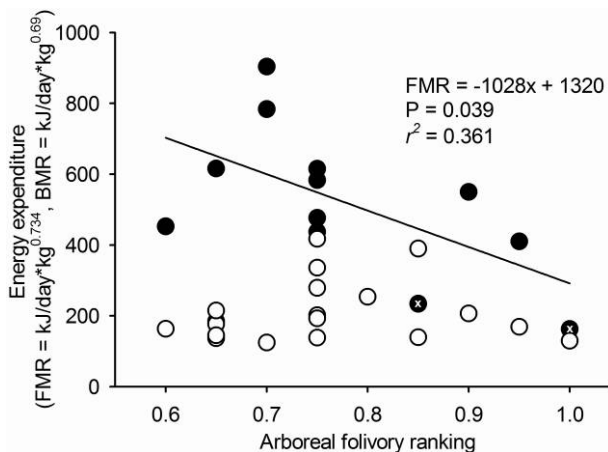


**Figure 4:** Predicted versus observed basal metabolic rate (BMR; *A*) and field metabolic rate (FMR; *B*) for species of arboreal folivores (the FMRs of sloths are denoted with crosses). Observed values were obtained from previous studies (app. A, available online), whereas predicted values were calculated on the basis of allometry for mammalian BMRs (White and Seymour 2003) and FMRs (Nagy 2005).

temperature logger, are comparable to those previously reported for free-ranging sloths, obtained internally (Montgomery and Sunquist 1978). Both species of sloths exhibited strong daily patterns in heterothermy, similar to other heterothermic nonhibernating mammals (Grigg et al. 2004). The three-toed sloth, in particular, exhibited large fluctuations in body temperature, which likely accounted for much of the observed energy savings in FMR. Three-toed sloths behaviorally adjust to ambient temperatures and can be observed in the mornings ascending to top of the canopy, presumably to warm in full light, and descending into shade as daytime temperatures increase; such movements are far less common among two-toed sloths. (Montgomery and Sunquist 1978; J. N. Pauli and M. Z. Peery, personal observation). In addition to behavioral adaptations for thermoregulation, the long, coarse, and dense pelage of sloths also is likely to

reduce thermal conductance and buffer against changes in ambient temperature (McNabb 1978). The fact that sloth hair, because of cracks in its shafts, also absorbs large quantities of water might be advantageous not only in culturing phoretic organisms like algae (Pauli et al. 2014) or fungi (Higginbotham et al. 2014) but also in raising the mass-specific heat of hair to further attenuate swings in body temperature.

Overall, we found that the BMRs and FMRs of arboreal folivores are less than those expected for mammals. Further, within this guild, we detected a strong negative relationship between increasing specialization to arboreal folivory and FMR. Surprisingly, we did not detect a similar relationship between BMR and increasing arboreal folivory. For mammals, the dominant component of a daily energy budget is the BMR (Karasov 1992). Our results, then, suggest that,



**Figure 5:** Basal metabolic rate (BMR; white circles) and field metabolic rate (FMR; black circles; the FMRs of sloths are denoted with crosses) versus degree of arboreal folivory (ranking from Eisenberg 1978). The FMR declined with increasing specialization to arboreal folivory, whereas the BMR did not.

although arboreal folivores possess lower BMRs in general, increasingly specialized species are also relying heavily on thermoregulatory and behavioral strategies to reduce their total daily energetic expenditure. Recently, the FMRs for captive and free-ranging giant pandas were found to be nearly as low as those for sloths (185 kJ/day\*kg<sup>0.734</sup>, Nie et al. 2015). The authors concluded that pandas, a folivorous mammal with an unusually simple digestive tract, are capable of minimizing energy expenditure through a combination of smaller vital organs, low thermal conductance, and a genetic mutation lowering thyroid activity, coupled with reduced activity, to survive on a nutritionally poor diet of bamboo (Nie et al. 2015). Primates, in general, also possess lower-than-expected FMRs, which were attributed to metabolic adaptations (Pontzer et al. 2014). It has been suggested that reduced FMRs among primates can ultimately be explained as an adaptation to reduce starvation risk in unpredictable environments (Pontzer et al. 2010); given that a number of primates are arboreal and folivorous, the degree of arboreal folivory might also be a contributing factor. Regardless of the ultimate mechanism, specialization toward arboreal folivory is accompanied by a substantive reduction in FMR, but this is not driven solely by reduced BMR. Rather, arboreal folivores reduce their energetic expenditure via relaxation of thermoregulatory control and reduced movement to negotiate an energetically poor landscape.

Arboreal folivores, and sloths in particular, possess unexpected, and even bizarre, characters that extend beyond metabolism or anatomy and physiology (Foley et al. 1995) and into aspects of their mating system (Pauli and Peery 2012; Peery and Pauli 2012), resource use (Mendoza et al.

2015), interspecific dependencies (Pauli et al. 2014), and life-history strategies (Peery and Pauli 2014). It has been postulated that these adaptations are a consequence of the energetic constraints associated with arboreal folivory. Our findings reveal extremely low energetic output among arboreal folivores and support the notion that a suite of adaptations, rather than a single key innovation, are necessary to support an organism exploiting a lifestyle in the trees. Ultimately, this stark energetic landscape and the consequent syndrome of extraordinary adaptations may explain the lack of species diversification among arboreal folivores.

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