A Buff *Bradypus* or an Elephantine Edentate? Physiological and Ecological Insights into Giant Ground Sloth Integument

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ABSTRACT

Remains of megatheres such as *Eremotherium spp*. and *Megatherium spp*. have been known since the 18th-century and were among the first megafaunal vertebrates to be studied. While several examples of preserved integument show a thick coverage of fur for smaller ground sloths living in cold climates (i.e., *Mylodon* and *Nothrotheriops*), comparatively very little is known about megathere skin. Assuming a typical placental mammal metabolism, it was previously hypothesized that megatheres would have had little-to-no fur as they achieved giant body size and were living in temperate-to-tropical paleoclimates. Critically, however, it is unclear if megatheres had low metabolic rates that are common to extant xenarthrans and if that physiology would impact the amount of fur insulation required to survive in the Pliocene/Pleistocene. Here the "hairless model of integument" is tested using geochemical analyses to estimate body temperature to generate novel models of ground sloth metabolism and paleoclimate with Niche Mapper software. The simulations yielded rates of metabolic activity akin to those of modern xenarthrans and suggest that sparse fur coverage would have resulted in cold stress across all latitudinal ranges inhabited by ground sloths. Overall, *Eremotherium* favored dense 10 mm fur with implications for seasonal changes of coat depth in northern latitudes; *Megatherium* favored dense 50 mm fur year-round in its exclusive range of cooler, drier climates; *Mylodon* and *Nothrotheriops* favored full body, dense 50 mm fur to approximate full thermal neutrality, matching the remains of both genera, and further implying use of behavioral thermoregulation during the coldest months of the year. With the evidence provided herein, the hairless model of integument hypothesis is rejected until a megathere specimen is found with the integument preserved.

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DEDICATION

I dedicate this thesis to my loving family, who have always instilled in me a love of nature; Dr. Mark Witton, whose art and blog posts partly inspired me to pursue this research; Scott McKenzie, who revived my interest in paleontology as an undergraduate student at Mercyhurst University.

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Introduction

The superorder Xenarthra (Cope, 1889) has a rich and diverse history preserved in the fossil record dating back 60 million years ago (MYA) to the Eocene Epoch. The Xenarthra consists of the orders Cingulata (Illiger, 1811), which contains living armadillos and the extinct pampatheres and glyptodonts, and the Pilosa (Flower, 1883) comprising the true anteaters and tree sloths. While the genera *Choloepus* (two-toed sloths) and *Bradypus* (three-toed sloths) are the only extant linages of sloths, numerous extinct genera of ground sloths once occupied various niches during the Oligocene and persisted until the Late Pleistocene. Ground sloths thrived throughout South America and dispersed to eventually colonize the southern boundaries of modern-day North America following the Great American Biotic Interchange nearly 2.5–3 MYA (Feldhamer et al., 2007). Several of the extinct ground sloths such as *Eremotherium* and *Megatherium* became the largest xenarthrans ever to walk the Earth, reaching sizes comparable to or exceeding that of modern African elephants.

To date, preserved integumentary structures that are definitively attributed to the largest ground sloths *Eremotherium* and *Megatherium* have yet to be found. The only specimen of *Megatherium* having a sample of skin was lost before it could be inventoried (Pujos and Salas, 2004). Nonetheless, both taxa have been historically reconstructed as having a thick coat of long, shaggy fur similar to that of smaller ground sloths (e.g., *Mylodon* and *Nothrotheriops*) and extant tree sloths. This appearance, however, was challenged by Fariña (2002, 2013) who argued for a largely hairless integument in the largest ground sloths. And while a hairless form was originally, albeit briefly, suggested for *Eremotherium* (McNab, 1985), Fariña (2002) was the first to test this hypothesis quantitatively. It was hypothesized that given their massive sizes and the relatively warm (temperate) paleoclimate of the Argentinian Pampas, a large-bodied ground sloth would not be thermally neutral in that habitat if it were covered in thick fur. For example, if the integument of *Megatherium* closely mirrored that of the largest extant terrestrial mammals (i.e., elephants, hippopotamuses, and rhinoceroses), then it would be in a thermal neutral zone even if the surrounding temperatures were approximately -17°C, which would be unlikely for the Argentinian pampas (Fariña, 2002, 2013).

The "hairless model of integument" was again hypothesized in a recent publication (Lindsey et al., 2020) regarding a mass assemblage of *Eremotherium* remains recovered from Tanque Loma in Ecuador. The cause of death of these animals was believed to be disease (or drought) from fecal matter contamination of the marsh. Lindsey et al. (2020) postulated that wallowing behavior would be advantageous if *E. laurillardi* had a hairless integument, as it would offer protection against the sun and tropical insects, and thus would be similar to a protective strategy used by the largest-bodied terrestrial mammals of the modern aspect.

Despite evidence in favor of a hairless (or nearly hairless) model of integument in the largest ground sloths that ever lived, there were critical assumptions applied to the previous methodologies that may not be tenable. First, Fariña (2002) did not accurately account for the basal metabolism of extant xenarthrans for calculations of heat flux. Instead, the basal metabolic rate (BMR) of a naked human was isometrically scaled up to the size of *Megatherium* assuming similar core body temperature and skin thickness to that of human primates (Fariña, 2002). Second, Fariña (2002) attempted to determine the BMR of *Megatherium americanum* by halving the estimated metabolic rate and concluded that it could still be naked and thermally neutral in environments with ambient temperatures of -10°C. Thermal neutrality values of -4°C and -28°C, have also been respectively calculated for a completely furless *Mylodon darwini* relative to a conspecific with a fur coat 4 cm long, but with each having an equivalent body mass of 2,000 kg (Fariña, 2002).

The fossil evidence known for *Mylodon*, however, suggests that it was extensively covered in fur, which was as long as 6.5 cm in some regions of its body (Collins, 1933), although some anecdotal data claim that it may have had fur is as long as 15–22 cm. The annual ambient temperature in the Andes mountains where *Mylodon* was known to inhabit was only -2.9°C by paleoclimate estimations (Kull et al., 2007). Moreover, the calculations of Fariña (2002) have yet to be tested on other megafauna that are known to have thick fur coats such as woolly mammoths and woolly rhinos, yet they may also produce results that are unlikely to be consistent with the available fossil integument and paleoclimate data. In addition, the relationship between body mass and body temperature in mammals is complex and mediated primarily through ecology (Clarke and Rothery, 2008). Last, there is no "generalized theory of integument," even among closely related taxa living in similar environments (Holtz, 2018).

The objective of this research is to further test the hairless model of integument for the largest ground sloths, *Eremotherium* and *Megatherium*. To rigorously test the model through quantitative means, numerous factors must be taken into account, including habitat preference, body mass, core body temperature, and ambient temperatures of the paleoclimate. Simultaneously, integrating these variables may more reasonably reconstruct the life appearance and behaviors of the largest ground sloths until skin and/or fur samples are discovered. In addition to physiological and ecological constraints on integument, a better understanding of the evolution of metabolic rate across various phylogenetic branches (living and extinct) of the suborder Folivora also can be achieved. It is hypothesized here that extinct ground sloths will represent an intermediate state between the metabolic rates of modern xenarthrans and those common for placental mammals. If correct, small ground sloths will have BMR closer to the extant xenarthran condition, whereas the largest ground sloths will have BMR closer to those of the typical placental mammal condition.

It is specifically predicted that the novel model data herein will support *Eremotherium* having a fur distribution that should vary depending on the geographical region that this species was known to inhabit (e.g., sparse fur coverage in more tropical environments and more dense fur coverage in temperate climates). In contrast, *Megatherium* will be modeled to have an integument consisting of a full body coverage of short fur to insulate it in the temperate environments it would have inhabited.

Materials and Methods

Fossil Specimens

Tooth and bone samples from *Eremotherium* (*N=4*), *Megatherium* (*N=3*), *Promegatherium* (*N=1*), and *Nothrotheriops* (*N=3*) were used in a series of geochemical analyses (Table 1). While no samples of *Mylodon* were obtained for this study, body temperature estimates for this genus were extrapolated from values obtained from *Promegatherium* given that both genera were similar in body size. The sampling strategy accounted for a wide geographic distribution of these taxa from the southernmost end of the range in Argentina to the northernmost end of the range in Florida. For the specimens that were collected from fossil localities in North America, enamel from mammoth (*Mammuthus*: *N*=1) teeth was also used as a control for assessment of diagenesis in the samples (Table 1). The enamel of a non-xenarthran mammal is more resilient to geochemical alteration during fossilization (MacFadden et al., 2010), and if relatively unaltered, would produce reliable body temperature estimates that are expected for a typical placental mammal (range: 37–38ºC). Any body temperature estimates deviating from those expected from *Mammuthus* enamel analysis would represent evidence for either the xenarthran condition or diagenetic alteration (see below).

Sample Preparation

The outer dentin of xenarthran teeth is not a reliable replacement for enamel due to its large uptake of rare earth elements (REE: MacFadden et al., 2010), thus the inner orthodentine was sampled instead, as recent studies using cathodoluminescence have revealed that this dental material is the most resistant tissue to diagenesis (Larmon et al., 2019). Approximately 300-400 mg of powderized internal orthodentine, and cortical bone and enamel (both from eutherian comparator fossils) were harvested with a power hand drill fit with a 0.7 mm diamond-tipped drill bit. To remove any organic contaminants, the samples were washed with 5.0±0.5 ml of 3% H_2O_2 for 3 hours in 15 ml conicals. The tubes remained open so that CO_2 could be released during preparation. The samples were then pelleted in a centrifuge at 10k rpm for 10 min. Specifically, all samples were centrifuged at a constant temperature of 25ºC, followed by 3 rinses in room temperature ddH_2O water. Any remaining liquid was decanted before drying overnight in an oven at 50ºC. Extra drying time in the oven was necessary for some of the samples to ensure complete desiccation.

Geochemical Alteration Analysis

To assess the amount of diagenesis present in the samples, REE analyses modeled after those of MacFadden et al. (2010) were performed on subsamples (5–10 mg) of prepared inner orthodentine (or enamel for *Mammuthus*) and cortical bone (the standard). These sample materials were first exposed to an acid digest using 3 ml of 1% nitric acid (HNO_3) and remaining residues in the conicals were rinsed with another 3 ml of 1% nitric acid. Both the samples and residues were then transferred to cuvettes and analyzed with an ICP mass spectrometer located at Youngstown State University. Briefly, three replicates were tested for each biomaterial sample type per species. Medium resolution was satisfactory for measurement and three blanks of 1% HNO_3 were used as controls, as well as Rhenium (Re) as an internal standard to obtain reliable measurement of values for REE present in parts per million (PPM). These standardization samples were prepared with five 1% nitric acid (HNO_3) washes in 25 ml volumetric flasks.

All measurements were additionally normalized using PAAS (Post-Archean Australian Shale) to compensate for the effects of the Oddo-Harkins even-odd abundance. Gravimetrically prepared REE and standard reference material (SRM) 1400 (bone ash) standards also were used to establish normal curves to precisely quantify and normalize all measurements. Once the masses of each element were obtained and normalized, the sum of all REE present in orthodentine/enamel were divided by the sum of all REE found in cortical bone and expressed as a ratio (REE_N sample/REE_N cortical bone). Ratios >1.0 indicate significant diagenetic alteration signifying that isotopic geochemical data should be treated with caution, whereas ratios <1.0 indicate reliable isotopic data.

Bioapatite Isotope Geochemistry and Body Temperature Estimates

The majority (by mass) of the harvested/purified samples of inner orthodentine were exposed to primary clumped isotope analysis performed at the University of California, Los Angeles using a Thermo-Finnigan MAT 253 gas source isotope ratio mass spectrometer. Previously, Eagle et al. (2010) demonstrated a relationship between the number of C^{13}–O^{18} bonds in the crystal lattice of bioapatite and body temperature (in ºC) in both extinct and extant mammalian taxa. To derive more accurate estimates of internal body temperature in large ground sloths, levels of C^{13}–O^{18} abundance were analyzed from their fossilized teeth as previously done for those of woolly mammoth (*Mammuthus primigenius*) and woolly rhinoceros (*Coelodonta antiquitatis*) taxa. Specifically, 2–3 replicates of each sample of fossilized teeth biomaterial were analyzed using established methods (Eagle et al., 2010). First, digestion of bioapatite samples in H_3PO_4 was carried out to extract CO_2 for mass spectrometry at 90ºC for 20 min. Hydrocarbon contaminants were removed via purification in liquid nitrogen, while Ag adsorbents were used to remove sulfurous gasses in the CO_2. Purified samples were then loaded into the isotope ratio mass spectrometer and clumped isotope measurements were taken with a stable 16-volt signal at atomic mass 44. Last, once Δ_{47} estimates had been made, they were input in the equation used by Ghosh et al. (2006) expressed as: $\Delta_{47} = (0.0592x10^6 \text{ x } T^{-2}) - 0.02$, to solve for T in ºC.

Modeling of Physiology and Paleoclimate

Body temperature estimates obtained from the literature for extant xenarthrans (e.g., McNab, 1985; Seitz and Puig, 2018; Cliffe et al., 2018) as well as those derived from clumped isotope paleothermometer analyses were input into a novel biophysiological model with simulations performed in Niche Mapper software (Lovelace et al., 2020). *A priori* body temperature estimates (in ºC) previously reported for extant xenarthrans were log-transformed and plotted against the log of body mass (kg) to predict body temperature for all initial simulations (Suppl. Fig. 1). Basal metabolic rate (BMR) was estimated using a published 'edentate' scaling relationship (63.9 $M^{0.66}$: Withers, 1992), where M is body mass in grams, and the resulting BMR (in kJ/hr) was converted into watts (W). An activity multiplier of 2 was used to estimate values of field metabolic rate (FMR). The scaling relationship (3.3 $M^{0.76}$: Fariña, 2002), where M is body mass in kg, was originally derived from Kleiber (1932) and it was used to compare metabolic rates derived from a mammal of similar body size with the typical placental metabolism.

To account for environmental conditions of the fossil localities during the Pleistocene, the Paleobiology Database (PBDB) was used to determine the northernmost and southernmost latitudinal species ranges, in addition to a mid-latitude species range to test a variety of climatic conditions for each taxon. Corresponding average yearly temperatures were obtained from the supplementary materials of Holden et al. (2018) and the factored difference from modern climate values from Niche Mapper's global climate extractor was used to determine monthly temperature values for these localities during the Pleistocene Epoch.

Determinations of how animal surface area is affected by environmental factors involved using three-dimensional models of both *Eremotherium* and *Mylodon* to estimate the rate of heat dissipation, and these data further served as proxies for the same expected parameters in models of *Megatherium* and *Nothrotheirops*, respectively. Mass estimates for *Eremotherium* (6,550 kg: Larmon et al., 2019), *Megatherium* (3,706 kg: Brassey and

Gardiner, 2015), *Mylodon* (1,986 kg: Christianson and Fariña, 2003), and *Nothrotheriops* (463 kg: McDonald, 2005) were obtained and input into these simulations. Models of both *full body* and *partial body* (i.e., fur on only dorsal portion of the body) fur coverage were tested at depths of 10 and 50 mm for all four taxa in addition to bare skin models for *Eremotherium*. Fur densities that were tested specifically consisted of *dense* fur of 2,000 hairs/cm^2 (element density previously tested by Lovelace et al., 2020) and 1,300 hairs/cm^2 (horse flank fur density: Tregear, 1965), in addition to *sparse* fur of 8.5 hairs/cm^2 (pig flank fur density: Tregear, 1965) and 0.07 hairs/cm^2 (maximum elephant fur density: Myhrvold et al., 2012).

Statistical Analysis

The physiological effects of temperature on the taxa of interest were assessed by a series of metabolic chamber simulations on both *full body* and *partial body* fur coverage models at predicted values of BMR for each taxon assuming no sunlight and a constant wind speed of 0.1 ms^{-1} (Suppl. Figs 2–5). Predictions of daily metabolic rate (in kJ day^{-1}) that were generated by the climate simulations of each integument model were plotted as a series of curves to determine which model best fit the estimated minimum and maximum metabolic rates for each taxon. Once the most thermally neutral integument models were established, estimates of maximum hours of metabolic activity were compared across the geographic distribution of each taxon along with those of extant mammals of similar size ranges. Wet mass (in kg) of forage consumed was additionally estimated and data were fit with second order polynomial regressions to statistically evaluate patterns of monthly food consumption in the respective predicted habitats of the sampled fossil taxa.

Results

Physiological Parameters of Ground Sloths

A wide range of ambient temperatures were modeled for the four genera of ground sloths (Fig. 1). *Eremotherium* was predicted to have experienced variable ambient temperatures (range: 1.89–30.1ºC) throughout its extensive geographic range, while *Nothrotheriops* was modeled to inhabit environments with similar maximum but colder minimum ambient temperatures (range: -3.2–25.4ºC). Both *Megatherium* and *Mylodon*, however, were predicted to primarily have inhabited cold-to-temperate environments (Fig. 1). With the exception of *Eremotherium*, which was calculated to have a maximum FMR of 1,119.2 W, the estimated range of metabolic activity did not exceed 1,000 W for the sampled ground sloth taxa (Fig. 2); all metabolic rate estimates were 70–77% less than those approximated by Fariña (2002). Moreover, beyond the previous core body temperature estimate of 34ºC for *Nothrotheriops* (Ho, 1967), the scaling of body mass and body temperature showed no relationship among extant xenarthrans (Suppl. Fig. 1).

The taxa *Eremotherium* and *Megatherium* were predicted to have variable degrees of thermal neutrality at different ambient temperature ranges at the specified fur depths and densities. Full body coverage models for *Eremotherium* showed the most extreme amount of variation in integument thermal neutrality with dense (2,000 and 1,300 hairs/cm^2) 50 mm fur being favorable at lower ambient temperatures; dense 10 mm fur being favorable at intermediate ambient temperatures; sparse (8.5 and 0.07 hairs/cm^2) fur being preferred at the upper limit of ambient temperatures (Suppl. Fig. 2A, C). The partial body coverage models at 10 mm fur depths of all density types as well as the bare skin models all converged along an ambient temperature gradient of 21–30°C, while partial body, dense 50 mm fur depths showed that more dense insulation is favorable at lower ambient temperatures (Suppl. Fig. 2B, D).

Sparse fur curves for *Megatherium* did not fall within the predicted range of metabolic activity regardless of full body or partial body coverage model estimations (Suppl. Fig. 3). While models having dense fur were shown to be thermally neutral for this genus; dense 50 mm, full body coverage in fur would have only been useful at lower ambient temperatures (range: 1–17ºC), and dense 10 mm full body and dense 50 mm partial body coverage models being equally thermally neutral at warmer ambient temperatures (range: 17–25ºC). Models for both *Mylodon* and *Nothrotheriops* produced similar results for both full body and partial body coverage models with the 10 mm fur depth curves being entirely outside of the range of their estimated metabolic activity, whereas full body, dense 50 mm fur was shown to be thermally neutral within the predicted range of metabolic activity and ambient temperature values. Partial body, dense 50 mm fur estimates for both taxa were only thermally neutral at uppermost ambient temperatures that they would have experienced (Suppl. Figs 4 and 5).

Paleoclimate of Ground Sloths

Consistent outcomes to those of metabolic chamber analyses were generally observed when multiple climatic variables (i.e., relative humidity, precipitation, wind speed, etc.) were considered. In some taxa, however, there were notable deviations from the output of the metabolic models. Namely, *Eremotherium* was estimated to be thermally neutral in all environments with dense 10 mm fur insulation (1,300–2,000 hairs/cm^2), but with prominent cold stress expected in northern latitudes and mild cold stress expected in the southernmost latitudes during the coldest months of the year in both localities sampled

(Fig. 3). Dense 50 mm fur insulation for this genus was shown to be mostly detrimental by resulting in overall heat stress, except for during the winter months in only the northern latitudes. Conversely, *Eremotherium* was shown to be moderately thermally neutral with sparse 50 mm fur insulation during the warmest months of the year in mid-latitudinal environments.

Refined paleoclimate models showed that *Megatherium* would have been thermally neutral with full body, dense 50 mm fur insulation in all three of the simulated environments, whereas full body, sparse fur (both depths and densities) resulted in cold stress throughout the year (Fig. 4). That taxa *Mylodon* and *Nothrotheirops* were estimated to be largely thermally neutral with full body, 50 mm fur insulation (density: 1,300 hairs/cm^2) and expected to experience only mild cold stress, with the exception of *Mylodon* in only the southernmost extent of its geographic distribution (Figs. 5, 6).

Hourly Metabolic Expenditure of Ground Sloths

Estimates of daily hours of metabolic activity for the most thermally neutral integuments (by fur coverage, depth, and density) across the known geographic distributions of each taxon averaged approximately 15 h day^{-1} (Fig. 7). While the megatheres were modeled to have large metabolic expenditure in cold climates (northern geographic ranges of *Eremotherium*; mid-latitudinal and southern geographic ranges of *Megatherium*), the greatest number of hours of metabolic activity expended per day (17 h day^{-}1) were predicted in the southern latitudinal ranges of *Mylodon*. The taxon *Nothrotheriops* showed a consistent maximum metabolic activity value of 15 h day^{-1} throughout its geographic range (Fig. 7). Comparative data from the literature on daily energetic expenditures indicate that extant body size analogues of *Eremotherium*, *Megatherium*, and *Mylodon* (e.g., African elephant, Indian elephant, and Indian rhinoceros, respectively) all have values of 22 h day^{-1} (Deka and Sarma, 2015; Gravett et al., 2017), while that for the smaller *Nothrothierops*, a brown bear (*Ursus arctos*), was measured at 20 h day^{-1} (Stelmock and Dean, 1986). In sum, all ground sloth taxa were predicted to have 22.7–31.9% less of metabolic activity than modern placental mammalian analogues of similar body masses.

Monthly Dietary Intake of Ground Sloths

The estimated distributions of energy intake across all four genera indicated no statistically significant trends in monthly food consumption with a change in environment (Fig. 8). While a general increase in food consumption was demonstrated for large-bodied megatheres, *Eremotherium* was modeled to experience little-to-no increase in food consumption (R^2=0.039) throughout its wide geographic distribution. The genus *Megatherium* was modeled to experience a mild increase in monthly food intake in the southernmost latitudes (R^2=0.48), whereas the simulations of *Mylodon* predicted a similarly noticeable increase in food intake in southern latitudes, notably overlapping with those of *Megatherium* (R^2=0.31). Finally, the data trends for *Nothrotheirops* showed a moderately strong decrease in monthly food intake (R^2=0.66) in the southern latitudes during the summer months.

Discussion

Comparisons with Previous Analyses

The metabolic chamber and paleoclimate simulations yielded drastically different values of metabolic rates than those from the only previous study on ground sloth thermal energetics (Fariña, 2002). In addition to refined estimates of clade specific BMR for ground sloths, numerous other environmental factors beyond ambient temperatures were input and modeled across the geographic distributions of each genus to determine more exact boundaries of thermal neutrality. The BMR estimates derived from the 'edentate' scaling equation (Withers, 1992) produced metabolic rates representing only 21–28% of those for mammals with typical placental metabolism as determined by Kleiber's relationship (Kleiber, 1932; Fariña, 2002). Substantially lower BMR as predicted in the present study, thusly produced markedly different results for thermal neutrality ranges across the various integument models tested compared with those previously reported. For example, Fariña (2002) proposed that a sparsely furred *Megatherium* with a body mass of 4,000 kg and metabolism that was 50% less than a typical placental mammal would be thermally neutral at ambient temperatures of 10°C versus the results from the present climate simulations, which suggest that *Megatherium* under similar conditions would have been cold stressed. While heat stress was modeled to be present in the tropical populations of *Eremotherium* having a full body fur coverage at a depth of 50 mm, dense 10 mm fur depths would allowed it to be thermally neutral year-round, even during the hottest months of the year throughout its entire geographic range. The results for *Mylodon* and novel data for *Notrotheriops*, both with dense 50 mm fur depths, suggest nearly complete yearly thermal neutrality in their respective environments, with mild cold stress for the three coldest months of the year (predicted temperatures: -3.26–0.9°C). These results contrast with the calculations of Fariña (2002) who estimated that thermal neutrality for *Mylodon* having a BMR half of the typical placental metabolism and fur 40 mm deep would be thermally neutral at an unrealistic ambient temperature of -28°C.

Megathere Thermal Neutrality and Geographic Distribution

The data from the metabolic chamber analyses revealed critical insight into the thermoregulatory thresholds of ground sloths and how these would have impacted their life appearance. In particular, the results for *Eremotherium* suggested that a wide range of integument models could be plausible depending on ambient temperatures of their past environments. Given that *Eremotherium* had a geographic distribution spanning as far North as Florida and Virginia in North America and as far South as Bolivia in South America, it is plausible that this genus had varying degrees of fur coverage in life appearance throughout its geographic range. Sparse, full body fur coverage would have been beneficial only during the warmest months of the year at mid-latitudes. Changes in fur depth would also have been beneficial during warmer months for *Eremotherium*, although there is no evidence of coat shedding in extant xenarthrans. Nonetheless, dense 10 mm fur could have provided thermally neutral at average ambient temperature ranges of 15.4–30.1°C that *Eremotherium* was expected to have experienced.

However, if *Eremotherium* could have shed fur seasonally, then it is even more unlikely for sparse, 50 mm deep fur to be useful at mid-latitudes. Moreover, because *Eremotherium* crossed the isthmus of Panama into North America but subsequently retreated to South America during the last glacial maximum (McDonald et al., 2009), it is possible for it to have undergone seasonal migrations during times of extreme seasonality. Due to the modeled presence of mild cold stress with dense 10 mm fur and no thermal neutrality with a 50 mm fur depth in the southernmost latitudes, it is therefore suggested that *Eremotherium* had a intermediate fur depth or was well-adapted to the tropical conditions expected to be prevalent in its southern latitudes (see Fig. 9). The latter hypothesis notably agrees with the absence of *Eremotherium* in North America during the last glacial maximum.

Despite being similar in body size to *Eremotherium*, the genus *Megatherium* was modeled to have not been thermally neutral with sparse, full body fur coverage throughout its geographic range. This can be explained by *Megatherium* being known to have inhabited cooler, dry environments in the pampas of Argentina and Chile. Using similar modeling approaches to physiology as presented here, the sensitivity analyses conducted by Lovelace et al. (2020) revealed that ambient temperature and wind speed values were the two climatic factors that most strongly influence predicted values of BMR, while the variables of relative humidity and cloud coverage had little effect on simulated metabolism. Thus, dense fur for *Megatherium* might have been needed to counteract greater exposure to the elements (e.g., wind, rain, or snow) in more open environments. This form of life appearance is reflected in the present climate simulation results which suggest that with a full body coverage of fur at depths of 10 mm, *Megatherium* would have been constantly cold-stressed regardless of fur density, but it would have complete thermal neutrality in all latitudinal distributions with dense (1,300–2,000 hairs/cm^2) 50 mm deep fur (see Fig. 4). Moreover, considering that fur depths of 50 mm resulted in predicted heat stress for similarly-sized *Eremotherium* (with the exception of the coldest months at northern latitudes), it is reasonable to speculate that tropical conditions may have acted as a thermal gradient restricting *Megatherium* to southern latitudes and occupation of the westernmost regions of Peru and Ecuador (see Fig. 9) that experienced alpine glaciation in the Andes Mountain range 21,000 years ago.

Thermoregulation in Mylodon and Nothrotheriops

Both *Mylodon* and *Nothrotheriops* were modeled to favor dense 50 mm fur depths across their respective ranges of predicted ambient temperature exposure, which is directly observed in the preserved pelts from both genera (Ridgewood, 1901, Hausman, 1929). Nevertheless, given that *Mylodon* was known to inhabit the Andes Mountains in South America, and *Nothrotheriops* would have experienced paleoclimate temperatures as low as -3.3°C, behavioral thermoregulation is expected in cold climates in addition to having thick fur coverage. One hypothesis is that thermal neutrality could have been maintained by taking shelter in caves, for which fossil remains of both taxa have been found. A second hypothesis is that both taxa may have underwent periods of torpor and/or hibernation as a behavioral means of cold tolerance.

Isotopic and taphonomic studies on the extinct Patagonian 'panther' (*Panthera onca mesembrina*) revealed that bite marks attributed to this former predator have been found on the skull of *Mylodon* in Cueva del Milodón (Prevosti and Martin, 2013; Martin, 2018). While *Mylodon* was smaller than the megatheres, an adult individual was still much larger than a jaguar, which implies that individuals found with bite marks in caves were preyed upon in deep sleep when they would have been most vulnerable to attack. Additional support for the hypotheses proposed herein can also be linked to the behavioral thermoregulation strategies observed in modern armadillos. For example, the nine-banded armadillo (*Dasypus novemcinctus*) is known to seek shelter during periods of extreme cold and employ a combination of torpor with episodic foraging (McBee and Baker, 1982; Knight et al., 2020). Regular torpor has also been documented in the pichi armadillo (*Zaedyus pichiy*) (Superina and Boily, 2007; Superina and Abba, 2014) and it is the only known extant xenarthran to undergo true hibernation.

It is also possible that *Mylodon* and *Nothrotheriops* may have had higher activity levels than those estimated in the present analysis. However, higher metabolic demands in the smaller ground sloths would only be useful in temperatures well below the range of ambient temperatures predicted for both taxa. Thus, another potential explanation for their thermal energetics involves having a diet more rich in energy than their megathere conspecifics. Tejada et al. (2021) suggested that the diet of *Mylodon* could have consisted of animal protein due to the nitrogen signatures found in their fossilized bone material. Though the exact timings of nitrogen signatures indicative of omnivory could not be determined, animal protein consumption would have had thermoregulatory benefits for *Mylodon*. A protein-rich diet provides some flexibility to thermal neutrality in cold climates and it is possible that *Mylodon* consumed animal matter sporadically during the coldest winter months. Conversely, nitrogen isotopes recovered from *Nothrotheriops* fossil remains definitively did not show evidence for an omnivorous diet, and instead, this genus was eating carbohydrate-rich desert plants such as globemallow and casava root (Poinar et al., 1998).

Life Appearance and Comparative Behaviors

Ground sloths have historically been reconstructed as being densely furred taxa and the novel data provided by the Niche Mapper simulations do little to challenge this life appearance. In contrast, the modeling results disagree with more sparsely furred, elephant-like reconstructions of *Eremotherium* and *Megatherium* (*sensu* Fariña, 2002, 2013). Despite the obvious discrepancies between studies on thermal neutrality and its effects on ground sloth integument, several critical behavioral and ecological preferences can now be inferred. For example, recent isotopic analyses propose a completely herbivorous diet for *Eremotherium* and *Megatherium* (Green et al., 2015; Dantas et al., 2021) despite previous speculation that they were possibly omnivorous (Fariña and Blanco, 1996). Indeed, the diets of *Eremotherium* and *Megatherium* would have primarily consisted of leaves and other high-growing vegetation (Bargo et al., 2006; Green and Kalthoff, 2015; Saarinen and Karme, 2017; Olivera et al., 2020), which overlap with those of their closest extant relatives *Bradypus spp*. (Chiarello, 1998; Urbani and Bosque, 2007; Cliffe et al., 2015). Leaves are poor in nutritional value correlating with the extremely low metabolic rates observed in *Bradypus variegatus* (Pauli et al., 2016; Cliffe et al., 2018) and may be a primary factor for why megatheres would have had low metabolic rates for mammals of their massive body size.

One of the main outcomes of the present study is that megatheres are predicted to have a BMR more similar to modern xenarthrans that other placental mammals. Yet, they also could have had a number of behaviors similar to large extant mammals with the typical placental metabolism. Notably, Lindsey et al. (2020) described a bone bed of *Eremotherium* at Tanque Loma in southwest Ecuador consisting of multiple individuals that died in a stagnant marsh or swamp. The assemblage was interpreted as evidence of herding behavior in megatheres. It was further suggested that *Eremotherium* engaged in wallowing behavior for thermoregulatory purposes akin to that observed in a modern hippopotamus (Stears et al., 2018). The modeled variation in integument appearance (i.e., density and depth of fur) across the geographic range of *Eremotherium* is arguably more broadly correlated with a thermoregulatory strategy. Large migratory ungulates such as the American bison (*Bison bison*) shed their dense winter coat to a lighter, patchy coat that coincides with wallowing behavior (McMillian et al., 2000). *Megatherium* also could have engaged in wallowing, but would not have required shedding due to its year-round thermal neutrality when having a dense, deep 50 mm fur coat (see Fig. 4).

Social behavior dynamics of megatheres and large mylodonts such as *Lestodon* are further suggested to be consistent with those observed in large placental mammals of the modern aspect (Tomassini et al., 2020; Lindsey et al., 2020), but differ greatly from the solitary lifestyles of extant tree sloths (Taube et al., 1999). One advantage to more complex social behavior could have been shared parental care (also inferred from the bonebed of *Eremotherium* at Tonque Loma: Lindsey et al. 2020) with multiple adult protecting juveniles most susceptible to predation. Conversely, a sole female *Bradypus spp.* raises her single offspring, and if it falls from the tree during weaning, then she does not invest in the metabolic energy to retrieve it (Urbani and Bosque, 2007).

Again, the present findings predict densely furred integument for *Mylodon* and *Nothrotheriops* as demonstrated by their mummified pelts (Ridgewood, 1901, Hausman, 1929). Given their size-specific estimated low metabolic rates, in addition to a lack of fossil bone beds consisting of multiple individuals, it is suggested that both genera potentially lived solitary lifestyles similar to extant tree sloths and armadillos (Naples, 1990; Borreo and Martin, 2012). Solitary denning behavior as seen in modern brown bears (González-Bernardo et al., 2020), a body size analog of both smaller ground sloth taxa, additionally may have been typical of *Mylodon* and *Nothrotheriops* in cave dwellings. Also, an ecological preference that could have overlapped with ursids is diet. The modern species of two-toed sloth, *Choloepus hoffmanni* (a close phylogenetic relative to *Mylodon*: Delsuc et al., 2019), has been known to occasionally consume meat in captivity (Hayssen, 2011) and is more active compared to *Bradypus* (Sunquist and Montgomery, 1973; Urbani and Bosque, 2007), which specializes in leaves (Chiarello, 1998) akin to its megathere relatives.

Last, while it is tempting to focus on phylogenetic constraint as the singular reason for the predicted low BMR of ground sloths, it should be noted that traits can be secondarily lost or acquired throughout the evolutionary history of a clade. For example, Benton (2021) suggested that crocodilians secondarily acquired ectothermy as opposed to maintaining hypothesized moderate levels of endothermy that would have been ancestral to Archosauria, and higher levels of endothermy akin to other lineages such as pterosaurs, non-avian dinosaurs, and birds. A similar question of why might ground sloths not have secondarily acquired a typical placental metabolism when reaching giant sizes becomes important.

Prior to the Great American Biotic Interchange (GABI), the herbivore guild of South America was dominated by notoungulates that were mixed grazers and low browsers that went extinct by the end of the Miocene prior to the earliest occurrences of megatheres (Croft et al., 2020). The largest of the notoungulates were members of the families Toxodontidae, Astrapotheriidae, and Homalodotheriidae. While toxodonts lived alongside megatheres into the Pliocene/Pleistocene (and reached body masses of 1,000-1,200 kg), high-browsing astraoptheres and homalodotheres went extinct by the end of the Miocene. *Promegatherium*, an early relative of *Eremotherium* and *Megatherium* was no larger than *Mylodon*, and thus prior to reaching giant sizes, a lower metabolic rate would have reduced resource demands, thus limiting competition with the notoungulates.

This in turn could be understood as an “ecological steppingstone” towards occupying the vacant high-browser niche without requiring as many calories as a similarly-sized mammal with a typical placental metabolism. The trends in daily food intake in megatheres suggest little change in the amount of food consumed across their various geographic regions (see Fig. 8). This major ecological factor also could have limited intraspecific competition for resources in megatheres, but notably reduced the pressure of interspecific competition with herds of proboscideans (e.g., mammoths and mastodons) with much greater energetic demands that entered South America following GABI.

Limitations

The novel data generated herein suggest several intriguing implications for ground sloth integument, thermal energetics, ecology, and behavior. However, it is acknowledged that the results are not definitive. One issue that is persistent with studies like the present one is use of the available ‘edentate’ scaling equation from Withers (1992) to estimate daily BMR of xenarthrans. For instance, size-scaled predicted values for *B. variegatus* are nearly nine-fold higher than measured values (3,765.4 kJ day^{-1} vs. 432±155 kJ day^{-1}: Cliffe et al., 2018). However, overall metabolic rates are expected to have been absolutely higher in ground sloths due to their much larger body sizes than modern tree sloths (~4–8 kg). The modeling simulations presented here also assumed consistent fur depth and density across the entire body, whereas these parameters can vary about the body surface area and this factor should be taken into account when considering the full implications of the results. Other factors such as hair shaft thickness, underfur, and the presence/absence of hollow hair shafts should additionally be taken into account with future analyses.

Pliocene climates were excluded from this analysis due to Pleistocene climate variables being easier to use for extrapolation of reasonable monthly values from modern climate data. The inclusion of Pliocene Epoch climate data would give more insight into how integument could have varied in earlier populations of *Eremotherium* and *Megatherium*. Finally, the clumped isotope and REE analyses have yet to be completed. These future results have the potential to affect the current interpretations of the Niche Mapper simulations. Preliminary data on body temperature estimates for *Mammuthus* indicate inconsistent body temperature estimates between trial replicates (e.g., UF 147588: 31.5±3.4°C vs. 38.3±4.8°C). Two fossil teeth specimens of *Eremotherium* yielded extremely low temperatures (UF 312730: 0.6±5.6°C; CM 41277: 26.8±1.6°C) and are suspected to be diagenetically altered; however, one specimen each of *Eremotherium* (UF 95869: 34.2°C) and *Megatherium* (FMNH P13725; 33.1°C) yielded body temperature estimates within the range of extant xenarthrans. While the latter values are believed to represent accurate physiologic body temperatures and originate from orthodentine with little geochemical alteration, these results have yet to be standardized, and the degree of diagenesis cannot determined without calculation of REE indexes.

Conclusions

The “hairless model of integument” for *Megatherium* as proposed by Fariña (2002) is untenable when more accurate estimates of xenarthran basal metabolism are considered for this taxon and *Eremotherium*. Giant ground sloths likely had a variety of integument from dense, thinner fur coverage in the tropics to dense, thicker fur coverage in cold environments. Smaller ground sloths would have needed dense, thick fur supplemented with behavioral thermoregulation to endure cold climates throughout the year. The novel modeling data also point to surprising adaptability of xenarthran physiology in both largest and smaller ground sloths. Moreover, the predicted integument models for the largest taxa are believed to be accurate unless refuted by a future specimen with extensive preserved integument. Prospective models must examine other taxa (e.g., *Megalonyx*, *Thalassocnus*, *Lestodon*, etc.) and include histological studies to help determine how low the BMR of ground sloths could have been, thus providing further insight into the physiology of these and other fossil xenarthrans and how their metabolic rates impacted their life appearance, growth rates, ecology, and behavior.

References

Amidon, W. H., Fisher, G. B., Burbank, D. W., Ciccioli, P. L., Alonso, R. N., Gorin, A. L., Silverhart, P. H., Kylander-Clark A. R. C., and Christoffersen, M. S. (2017). Mio-Pliocene aridity in the south-central Andes associated with Southern Hemisphere cold periods. *Proc. Nat. Acad. Sci.* 114, 6474-6479.

Bakker, E. S., Gill, J. L., Johnson, C. N., Vera, F. W., Sandom, C. J., Asner, G. P., and Svenning, J. C. (2016). Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proc. Nat. Acad. Sci*. 113, 847-855.

Billet, G., Germain, D., Ruf, I., de Muizon, C., and Hautier, L. (2013). The inner ear of Megatherium and the evolution of the vestibular system in sloths. *J. Anat.* 223, 557-567.

Bargo, M. S. (2001). The ground sloth *Megatherium americanum*: skull shape, bite forces, and diet. *Acta Paleo Pol.* 46, 173-192.

Bargo, M. S., De Iuliis, G., and Vizcaíno, S. F. (2006). Hypsodonty in Pleistocene ground sloths. *Acta Paleo Pol*. 51, 53-61.

Benton, M. J. (2021). The origin of endothermy in synapsids and archosaurs and arms races in the Triassic. *Gondwana Res*. 100, 261-289.

Bocherens, H., Cotte, M., Bonini, R. A., Straccia, P., Scian, D., Soibelzon, L., and Prevosti, F. J. (2017). Isotopic insight on paleodiet of extinct Pleistocene megafaunal Xenarthrans from Argentina. *Gondwana Res.* 48, 7-14.

Borrero, L. A., and Martin, F. M. (2012). Ground sloths and humans in southern Fuego-Patagonia: taphonomy and archaeology. *World Archaeol*. 44, 102-117.

Brassey, C. A., and Gardiner, J. D. (2015). An advanced shape-fitting algorithm applied to quadrupedal mammals: improving volumetric mass estimates. *Royal Soc. Open Sci.* 2, 150302.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* 85, 1771-1789.

Carretero, D. D., García, A., and Dacar, M. A. (2004). First data on differential use of the environment by Pleistocene megafauna species (San Juan, Argentina). *Curr. Res. Pleist.* 21, 91-92.

Chiarello, A. G. (1998). Activity budgets and ranging patterns of the Atlantic forest maned sloth *Bradypus torquatus* (Xenarthra: Bradypodidae). *J. Zool*. 246, 1-10.

Chiarello, A. G. (1998). Diet of the Atlantic forest maned sloth Bradypus torquatus (Xenarthra: Bradypodidae). *J. Zool*. 246, 11-19.

Christiansen, P., and Fariña, R. A. (2001). Mass estimation of two fossil ground sloths, *Mylodon darwini* and *Glossotherium gracilis*. *J. Morphol.* 248, 95-101.

Clack, A. A., MacPhee, R. D., and Poinar, H. N. (2012). Mylodon darwinii DNA sequences from ancient fecal hair shafts. *Ann. Anat.* 194, 26-30.

Clarke, A., and Rothery, P. (2008). Scaling of body temperature in mammals and birds. *Funct. Ecol.* 22, 58-67.

Cliffe, R. N., Haupt, R. J., Avey-Arroyo, J. A., and Wilson, R. P. (2015). Sloths like it hot: ambient temperature modulates food intake in the brown-throated sloth (Bradypus variegatus). *PeerJ* 3, e875.

Cliffe, R. N., Scantlebury, D. M., Kennedy, S. J., Avey-Arroyo, J., Mindich, D., and Wilson, R. P. (2018). The metabolic response of the Bradypus sloth to temperature. *PeerJ* 6, e5600.

Collins, R. L. (1933). Mylodont (ground sloth) dermal ossicles from Colombia, South America. *J. Wash. Acad. Sci.* 23, 426-429.

Cope, E. D. (1889). The edentata of North America. *Am. Nat.* 23, 657-664.

Croft, D. A. (2016). Horned armadillos and rafting monkeys: the fascinating fossil mammals of South America. *Indiana Univ. Press*.

Croft, D. A., Gelfo, J. N., and López, G. M. (2020). Splendid innovation: the extinct South American native ungulates. *Ann. Rev. Earth Planet. Sci.* 48, 259-290.

Dantas, M. A. T., Dutra, R. P., Cherkinsky, A., Fortier, D. C., Kamino, L. H. Y., Cozzuol, M. A., and Vieira, F. S. (2013). Paleoecology and radiocarbon dating of the Pleistocene megafauna of the Brazilian Intertropical Region. *Quat. Res.* 79, 61-65.

Dantas, M. A. T., Omena, É. C., da Silva, J. L. L., and Sial, A. (2021). Could Eremotherium laurillardi (Lund, 1842) (Megatheriidae, Xenarthra) be an Omnivore Species? *Anuário do Instituto de Geociências* 44, 1-5.

de Fátima Rossetti, D., de Toledo, P. M., Moraes-Santos, H. M., and de Araújo Santos Jr, A. E. (2004). Reconstructing habitats in central Amazonia using megafauna, sedimentology, radiocarbon, and isotope analyses. *Quaternary Res.* 61, 289-300.

Deka, R. J., and Sarma, N. K. (2015). Studies on feeding behaviour and daily activities of *Rhinoceros unicornis* in natural and captive condition of Assam. *Indiana J. Anim. Res.* 49, 542-545.

Delsuc, F., Kuch, M., Gibb, G. C., Karpinski, E., Hackenberger, D., Szpak, P., and Billet, G. (2019). Ancient mitogenomes reveal the evolutionary history and biogeography of sloths. *Curr. Biol*. 29, 2031-2042.

de Stefani Munaó Diniz, L., and Oliveira, P. M. (1999). Clinical problems of sloths (*Bradypus sp*. and *Choloepus sp*.) in captivity. *J. Zoo Wildlife Med.* 30, 76-80.

De Vivo, M., and Carmignotto, A. P. (2004). Holocene vegetation change and the mammal faunas of South America and Africa. *J. Biogeography* 31, 943-957.

Dodds, P. S., Rothman, D. H., and Weitz, J. S. (2001). Re-examination of the “3/4-law” of metabolism. *J. Theor. Biol.* 209, 9-27.

Doughty, C. E., Faurby, S., and Svenning, J. C. (2016). The impact of the megafauna extinctions on savanna woody cover in South America. *Ecography*, 39, 213-222.

Dowsett, H. J., Chandler, M. A., and Robinson, M. M. (2009). Surface temperatures of the Mid-Pliocene North Atlantic Ocean: implications for future climate. *Phil. Trans. Royal Soc. A: Math., Phys. Eng. Sci.* 367, 69-84.

Eagle, R. A., Schauble, E. A., Tripati, A. K., Tütken, T., Hulbert, R. C., and Eiler, J. M. (2010). Body temperatures of modern and extinct vertebrates from 13C-18O bond abundances in bioapatite. *Proc. Nat. Acad. Sci.* 107, 10377-10382.

Fariña, R. A., and Blanco, R. E. (1996). Megatherium, the stabber. *Proc. Royal Soc.* 263, 1725-1729.

Fariña, R. A. (2002). Megatherium, the hairless: appearance of the great Quaternary sloths (Mammalia; Xenarthra). *Ameghiniana* 39, 241-244.

Fariña, R. A., Vizcaíno, S. F., and De Iuliis, G. (2012). Megafauna: giant beasts of Pleistocene South America. Indiana University Press, Bloomington.

Feldhamer, G. A., Drickamer, L. C., Vessey, S. H., Merritt, J. F., and Krajewski, C. (2007). Mammalogy: adaptation, diversity, and ecology. John Hopkins University Press, Baltimore.

Flower, W. H. (1883). An Introduction to the Osteology of the Mammalia. Macmillan and Company, London.

Foley, W. J., Engelhardt, W. V., and Charles-Dominique, P. (1995). The passage of digesta, particle size, and in vitro fermentation rate in the three toed sloth Bradypus tridactylus (Edentata: Bradypodidae). *J. Zool.* 236, 681-696.

Gallo, V., Avilla, L. S., Pereira, R. C., and Absolon, B. A. (2013). Distributional patterns of herbivore megamammals during the Late Pleistocene of South America. *Anais da Academia Brasileira de Ciências* 85, 533-546.

Gaudin, T. J. (2004). Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence. *Zool. J. Linnean Soc.* 140, 255-305.

Gaudin, T. J., and Nyakatura, J. A. (2018). Epaxial musculature in armadillos, sloths, and opossums: functional significance and implications for the evolution of back muscles in the Xenarthra. *J. Mammal. Evol.* 25, 565-572.

Ghosh, P., Adkins, J., Affek, H., Balta, B., Guo, W., Schauble, E. A., Schrag, D., and Eiler, J. M. (2006). ^{13}C–^{18}O bonds in carbonate minerals: a new kind of paleothermometer. *Geochimica et Cosmochimica Acta* 70, 1439-1456.

Giné, G. A. F., Cassano, C. R., de Almeida, S. S., and Faria, D. (2015). Activity budget, pattern and rhythm of maned sloths (*Bradypus torquatus*): responses to variations in ambient temperature. *Mammal. Biol.* 80, 459-467.

Goffart, M., Holmes, O., and Bacq, Z. M. (1962). Some mechanical properties of skeletal muscle in the sloth. *Archives Internationales de Physiologie et de Biochimie*, 70, 103-106.

González-Bernardo, E., Russo, L. F., Valderrábano, E., Fernández, Á., and Penteriani, V. (2020). Denning in brown bears. *Ecol. Evol.* 10, 6844-6862.

Gorvet, M. A., Wakeling, J. M., Morgan, D. M., Segura, D. H., Avey-Arroyo, J., and Butcher, M. T. (2020). Keep calm and hang on: EMG activation in the forelimb musculature of three-toed sloths (*Bradypus variegatus*). *J. Exp. Biol.* 223, jeb218370.

Grand, T. I. (1978). Adaptations of tissue and limb segments to facilitate moving and feeding in arboreal folivores. In The Ecology of Arboreal Folivores (ed. G. G. Montgomery), pp. 231-241. Smithsonian Institution Press, Washington, DC.

Gravett, N., Bhagwandin, A., Sutcliffe, R., Landen, K., Chase, M. J., Lyamin, O. I., and Manger, P. R. (2017). Inactivity/sleep in two wild free-roaming African elephant matriarchs–Does large body size make elephants the shortest mammalian sleepers? *PLoS One* 12, e0171903.

Green, J. L., and Kalthoff, D. C. (2015). Xenarthran dental microstructure and dental microwear analyses, with new data for Megatherium americanum (Megatheriidae). *J. Mammal.* 96, 645-657.

Greenwood, A. D., Castresana, J., Feldmaier-Fuchs, G., and Pääbo, S. (2001). A molecular phylogeny of two extinct sloths. *Mol. Phylogen. Evol.* 18, 94-103.

Hausman, L. A. (1929). The ovate bodies of the hair of Nothrotherium shastense. *Am. J. Sci.* 106, 331-333.

Hausman, L. A. (1936). Further studies of the hair of the fossil ground sloth (*Nothrotherium shastense*) and of its problematical" ovate bodies". *Am. J. Sci*. 183, 223-228.

Hayssen, V. (2011). *Choloepus hoffmanni* (Pilosa: Megalonychidae). *Mammal. Spec.* 43, 37-55.

Hinojosa, L. F., and Villagrán, C. (1997). History of the southern South American forests. 1. Paleobotanical, geological and climatical background on Tertiary of southern South America. *Revista Chilena de Historia Natural* 70, 225-239.

Ho, T. Y. (1967). Relationship between imino acid contents of mammalian bone collagen and body temperature as a basis for estimation of body temperature of prehistoric mammals. *Comp. Biochem. Physiol*. 22, 113-119.

Hofreiter, M., Betancourt, J. L., Sbriller, A. P., Markgraf, V., and McDonald, H. G. (2003). Phylogeny, diet, and habitat of an extinct ground sloth from Cuchillo Cura, Neuquen Province, southwest Argentina. *Quat. Res.* 59, 364-378.

Holden, P. B., Edwards, N. R., Rangel, T. F., Pereira, E. B., Tran, G. T., and Wilkinson, R. D. (2019). PALEO-PGEM v1. 0: a statistical emulator of Pliocene–Pleistocene climate. *Geosci. Model Dev.* 12, 5137-5155.

Holtz, T. R., Jr. (2018). Integumentary Status: It's Complicated: Phylogenetic, Sedimentary and Biological Impediments to Resolving the Ancestral Integument of Mesozoic Dinosauria [Conference Poster]. *Soc. Vert. Paleo* 2018, Albuquerque, NM, United States.

Höss, M., Dilling, A., Currant, A., and Pääbo, S. (1996). Molecular phylogeny of the extinct ground sloth *Mylodon darwinii*. *Proc. Nat. Acad. Sci.* 93, 181-185.

Hutchinson, J. R., Schwerda, D., Famini, D. J., Dale, R. H., Fischer, M. S., and Kram, R. (2006). The locomotor kinematics of Asian and African elephants: changes with speed and size. *J. Exp. Biol.* 209, 3812-3827.

Illiger, C. (1811). Prodromus systematis mammalium et avium additis terminus zoographicis utriusque classis. *C. Salfedl, Berolini*,

Kleiber, M. (1932). Body size and metabolism. *Hilgardia* 6, 315-353.

Knight, F., Connor, C., Venkataramanan, R., and Asher, R. (2020). Body temperatures, life history, and skeletal morphology in the nine-banded armadillo (*Dasypus novemcinctus*). *PCI-Ecol*. https://doi.org/10.17863/CAM.50971

Kull, C., Imhof, S., Grosjean, M., Zech, R., and Veit, H. (2008). Late Pleistocene glaciation in the Central Andes: temperature versus humidity control—a case study from the eastern Bolivian Andes (17 S) and regional synthesis. *Glob. Planetary Change* 60, 148-164.

Larmon, J. T., McDonald, H. G., Ambrose, S., DeSantis, L. R., and Lucero, L. J. (2019). A year in the life of a giant ground sloth during the Last Glacial Maximum in Belize. *Sci. Adv.* 5, 1-9.

Lindsey, E. L., Reyes, E. X. L., Matzke, G. E., Rice, K. A., and McDonald, H. G. (2020). A monodominant late-Pleistocene megafauna locality from Santa Elena, Ecuador: Insight on the biology and behavior of giant ground sloths. *Paleogeo.* 544, 109599.

Lovelace, D. M., Hartman, S. A., Mathewson, P. D., Linzmeier, B. J., and Porter, W. P. (2020). Modeling Dragons: Using linked mechanistic physiological and microclimate models to explore environmental, physiological, and morphological constraints on the early evolution of dinosaurs. *PloS one* 15, e0223872.

Martin, F. M. (2018). Cueva del Milodón. The hunting grounds of the Patagonian panther. *Quat Internat.* 466, 212-222.

McBee, K., and Baker, R. J. (1982). *Dasypus novemcinctus*. *Mammal. Spec.* 162, 1-9.

MacFadden, B. J., DeSantis, L. R., Hochstein, J. L., and Kamenov, G. D. (2010). Physical properties, geochemistry, and diagenesis of xenarthran teeth: prospects for interpreting the paleoecology of extinct species. *Paleogeo.* 291, 180-189.

McDonald, H. G., Harington, C. R., and De Iuliis, G. (2000). The ground sloth Megalonyx from Pleistocene deposits of the Old Crow Basin, Yukon, Canada. *Arctic* 53, 213-220.

McDonald, H. G. (2005). Paleoecology of extinct xenarthrans and the Great American Biotic Interchange. *Bull. Florida Mus. Nat. Hist.* 45, 313-333.

McDonald, H. G., and Jefferson, G. T. (2008). Distribution of Pleistocene Nothrotheriops (Xenarthra, Nothrotheriidae) in North America. *Nat. Hist. Mus. Los Angeles County Sci. Series* 41, 313-331.

McDonald, H. G., and Lundelius Jr, E. L. (2009). The giant ground sloth Eremotherium laurillardi (Xenarthra. Megatheriidae) in Texas. *Mus. of N. AZ, Papers on Geol., Vert. Paleo. Biostrat. in Honor of Michael O. Woodburne Bull.* 65, 407-421.

McDonald, H. G., Dundas, R. G., and Chatters, J. C. (2013). Taxonomy, paleoecology and taphonomy of ground sloths (Xenarthra) from the Fairmead Landfill locality (Pleistocene: Irvingtonian) of Madera County, California. *Quat. Res.* 79, 215-227.

McMahon TA. (1975). Using body size to understand the structural design of animals: quadrupedal locomotion. *J. Appl. Physiol.* 39, 619-627.

McMillan, B. R., Cottam, M. R., and Kaufman, D. W. (2000). Wallowing behavior of American bison (Bos bison) in tallgrass prairie: an examination of alternate explanations. *Am. Mid. Nat*. 144, 159-167.

McNab, B. K. (1985). Energetics, population biology, and distribution of xenarthrans, living and extinct. In The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas (ed. G. G. Montgomery), pp. 219-232. Smithsonian Institution Press, Washington, DC.

McNab, B. K. (2008). An analysis of the factors that influence the level and scaling of mammalian BMR. *Comp. Biochem. Physiol. A, Mol. Int. Physiol.* 151, 5-28.

McNab, B. K. (2012). Extreme measures: the ecological energetics of birds and mammals. University of Chicago Press, Chicago.

McNab, B. K. (2019). What determines the basal rate of metabolism? *J. Exp. Biol.* 222, jeb205591.

Montgomery, G. G., and Sunquist, M. E. (1978). Habitat selection and use by two-toed and three-toed sloths. In The Ecology of Arboreal Folivores, pp. 329-359. Smithsonian Press, Washington, DC.

Merriam, J. C. (1906). Recent discoveries of Quaternary mammals in Southern California. *Science* 24, 248-250.

Morgan, G. S. (2005). The great American biotic interchange in Florida. *Bull. Flor. Mus.Nat. Hist.* 45, 271-311.

Muchlinski, M.N., Snodgrass, J.J. and Terranova, C.J. (2012). Muscle mass scaling in primates: An energetic and ecological perspective. *Am. J. Primatol*. 74, 395-407.

Myhrvold, C. L., Stone, H. A., and Bou-Zeid, E. (2012). What is the use of elephant hair? *PLoS One* 7, e47018.

Naples, V. L. (1990). Morphological changes in the facial region and a model of dental growth and wear pattern development in *Nothrotheriops shastensis*. *J. Vert. Paleontol.* 10, 372-389.

Naples, V. L., and McAfee, R. K. (2012). Reconstruction of the cranial musculature and masticatory function of the Pleistocene panamerican ground sloth Eremotherium laurillardi (Mammalia, Xenarthra, Megatheriidae). *Hist. Biol.* 24, 187-206.

Oliveira, J. F., Asevedo, L., Cherkinsky, A., and Dantas, M. A. T. (2020). Radiocarbon dating and integrative paleoecology (δ13C, stereomicrowear) of Eremotherium laurillardi (LUND, 1842) from midwest region of the Brazilian intertropical region. *J. South Am. Earth Sci.* 102, 1-9.

Pant, S. R., Goswami, A., and Finarelli, J. A. (2014). Complex body size trends in the evolution of sloths (Xenarthra: Pilosa). *Evol. Biol.* 14, 1-8.

Pauli, J. N., Peery, M. Z., Fountain, E. D., and Karasov, W. H. (2016). Arboreal folivores limit their energetic output, all the way to slothfulness. *Am. Nat.* 188, 196-204.

Poinar, H. N., Hofreiter, M., Spaulding, W. G., Martin, P. S., Stankiewicz, B. A., Bland, H., Evershed, R. P., Possnert, G., and Pääbo, S. (1998). Molecular coproscopy: dung and diet of the extinct ground sloth *Nothrotheriops shastensis*. *Science* 28, 402-406.

Presslee, S., Slater, G. J., Pujos, F., Forasiepi, A. M., Fischer, R., Molloy, K., Mackie, M., Olsen, J. V., Kramarz, A., Tagiloretti, M., Scaglia, F., Maximilano L., Lanta, J. L., Southon, J., Feranec, R., Bloch, J., Hajduk, A., Martin, F. M., Gismondi, R. S., Reguero, M., de Muizon, C., Greenwood, A., Chait, B. T., Penkman, K., Collins, M., and MacPhee, R. D. E. (2019). Palaeoproteomics resolves sloth relationships. *Nature Ecol. Evol.* 3, 1121-1130.

Prevosti, F. J., and Martin, F. M. (2013). Paleoecology of the mammalian predator guild of Southern Patagonia during the latest Pleistocene: ecomorphology, stable isotopes, and taphonomy. *Quat. Internat.* 305, 74-84.

Pujos, F., and Salas, R. (2004). A systematic reassessment and paleogeographic review of fossil Xenarthra from Peru. *Bulletin de l'Institut Français d'études Andines* 33, 331-377.

Pujos, F. (2008). Paleogeographic distribution and anatomical adaptations in Peruvian megatheriine ground sloths (Xenarthra: Megatherioidea). In The Biology of the Xenarthra, pp. 56-63. University Press of Florida, Gainesville.

Rancy, A.(2000). Paleoecologia da Amazônia: megafauna do Pleistoceno. Universidade Federal de Santa Catarina. *Editoria da UFSC*.

Ridewood, W. G. (1901). Memoirs: On the Structure of the Haris of *Mylodon listai* and other South Amercian Edentata. *J. Cell Sci.* 2, 393-411.

Seitz, V. P., and Puig, S. (2018). Aboveground activity, reproduction, body temperature and weight of armadillos (Xenarthra, Chlamyphoridae) according to atmospheric conditions in the central Monte (Argentina). *Mammal. Biol.* 88, 43-51.

Sinclair, W. J. (1910). Dermal bones of *Paramylodon* from the asphaltum deposits of Rancho La Brea, near Los Angeles, California. *Am. Phil. Soc.* 49, 191-195.

Stears, K., McCauley, D. J., Finlay, J. C., Mpemba, J., Warrington, I. T., Mutayoba, B. M., Power, M. E., Dawson, T. E., and Brashares, J. S. (2018). Effects of the hippopotamus on the chemistry and ecology of a changing watershed. *Proc. Nat. Acad. Sci.* 115, E5028-E5037.

Stelmock, J., and Dean, F. C. (1986). Brown bear activity and habitat use, Denali National Park–1980. *Int. Conf. Bear Res. Manag*. 6, 155-167.

Sunquist, M. E., and Montgomery, G. G. (1973). Activity patterns and rates of movement of two-toed and three-toed sloths (*Choloepus hoffmanni* and *Bradypus infuscatus*). *J. Mammal.* 54, 946-954.

Superina, M., and Boily, P. (2007). Hibernation and daily torpor in an armadillo, the pichi (*Zaedyus pichiy*). *Comp. Biochem. Physiol. A, Mol. Int. Physiol.* 148, 893-898.

Superina, M., and Jahn, G. A. (2013). Effect of low-quality diet on torpor frequency and depth in the pichi, *Zaedyus pichiy* (Xenarthra, Dasypodidae), a South American armadillo. *J. Therm. Biol.* 38, 280-285.

Superina, M., and Abba, A. M. (2014). *Zaedyus pichiy* (Cingulata: Dasypodidae). *Mammal. Spec.* 46, 1-10.

Taube, E., Vié, J. C., Fournier, P., Genty, C., and Duplantier, J. M. (1999). Distribution of Two Sympatric Species of Sloths (*Choloepus didactylus* and *Bradypus tridactylus*) along the Sinnamary River, French Guiana 1. *Biotropica* 31, 686-691.

Tejada, J. V., Flynn, J. J., MacPhee, R., O'Connell, T. C., Cerling, T. E., Bermudez, L., and Popp, B. N. (2021). Isotope data from amino acids indicate Darwin's ground sloth was not an herbivore. *Sci. Reports* 11, 1-10.

Tito, G. (2008). New remains of *Eremotherium laurillardi* (Lund, 1842) (Megatheriidae, Xenarthra) from the coastal region of Ecuador. *J. South Am. Earth Sci.* 26, 424-434.

Toledo, N., Bargo, M. S., Vizcaíno, S. F., De Iuliis, G., and Pujos, F. (2017). Evolution of body size in anteaters and sloths (Xenarthra, Pilosa): phylogeny, metabolism, diet and substrate preferences. *Earth Environ. Sci. Trans. R. Soc. Edinburgh.* 106, 289-301.

Tomassini, R. L., Montalvo, C. I., Garrone, M. C., Domingo, L., Ferigolo, J., Cruz, L. E., Sanz-Pérez, D., Fernández-Jalvo, Y., and Cerda, I. A. (2020). Gregariousness in the giant sloth Lestodon (Xenarthra): multi-proxy approach of a bonebed from the Last Maximum Glacial of Argentine Pampas. *Sci. Reports* 10, 1-16.

Tregear, R. T. (1965). Hair density, wind speed, and heat loss in mammals. *J. Appl. Physiol.* 20, 796-801.

Urbani, B., and Bosque, C. (2007). Feeding ecology and postural behaviour of the three-toed sloth (Bradyp*us variegatus flaccidus*) in northern Venezuela. *Mammal. Biol.* 72, 321-329.

van der Hammen, T. (1974). The Pleistocene changes of vegetation and climate in tropical South America. *J. Biogeo*. 1, 3-26.

Vizcaíno, S. F., Bargo, M. S., and Cassini, G. H. (2006). Dental occlusal surface area in relation to body mass, food habits and other biological features in fossil xenarthrans. *Ameghiniana* 43, 11-26.

Wang, Z., O'Connor, T. P., Heshka, S., and Heymsfield, S. B. (2001). The reconstruction of Kleiber's law at the organ-tissue level. *J. Nutrit*. 131, 2967-2970.

Webb, S.D., and A. Rancy. 1996. Late Cenozoic evolution of the neotropical mammal fauna, In Evolution and environment in tropical America (eds. J. B. C. Jackson, A. F. Budd, A. G. Coates), pp. 335-358. University of Chicago Press, Chicago.

West, G. B., Brown, J. H., and Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology." *Science* 276, 122-126.

Withers, P. C. (1992). Animal energetics. In Comparative Animal Physiology, pp. 82-121. Saunders College Publishing, Philadelphia.

Table 1. Fossil samples that were used in geochemical analyses. N^D = number of dentine samples; N^B = number of bone samples; N^E = number of enamel samples.

Specimen Number	**Genus**	**Sample Size**	**Locality**	**Institution**
CM 41277	*Eremotherium*	$N^D = 5$ $N^B = 1$	Talra Tar Pit, Peru	Carnegie Museum of Natural History
FMNH P13653	*Megatherium*	$N^D = 5$ $N^B = 1$	Tarija Valley, Argentina	Field Museum of Natural History
FMNH P15130	*Megatherium*	$N^D = 5$	Tarija Valley, Argentina	Field Museum of Natural History
FMNH P13725	*Megatherium*	$N^D = 5$	Tarija Valley, Argentina	Field Museum of Natural History
FMNH P14511/14401	*Promegatherium*	$N^D = 5$ $N^B = 1$	Puerta de Corral Quemado, Argentina	Field Museum of Natural History
UF 312728	*Eremotherium*	$N^B = 1$	Halie 7C, Alachua County, Florida, USA	University of Florida Museum of Natural History
UF 312730	*Eremotherium*	$N^D = 5$	Halie 7C, Alachua County, Florida, USA	University of Florida Museum of Natural History
UF 95869	*Eremotherium*	$N^D = 5$	Inglis 1A, Citrus County, Florida, USA	University of Florida Museum of Natural History
UF Uncat.	Proboscidea indet.	$N^B = 1$	Inglis 1A, Citrus County, Florida, USA	University of Florida Museum of Natural History
UF Uncat.	Mammalia indet.	$N^B = 1$	Leisey 1A, Hillsborough County, Florida, USA	University of Florida Museum of Natural History
UF 87131	*Nothrotheriops*	$N^D = 3$	Leisey 1A, Hillsborough County, Florida, USA	University of Florida Museum of Natural History
UF 87133	*Nothrotheriops*	$N^D = 1$	Leisey 1A, Hillsborough County, Florida, USA	University of Florida Museum of Natural History
UF 87139	*Nothrotheriops*	$N^D = 1$	Leisey 1A, Hillsborough County, Florida, USA	University of Florida Museum of Natural History
UF 145778	*Mammuthus*	$N^E = 5$	Leisey 1A, Hillsborough County, Florida, USA	University of Florida Museum of Natural History

Figure 1. Box and whisker plot of ambient temperature estimates for the environments inhabited by the four ground sloth taxa sampled.

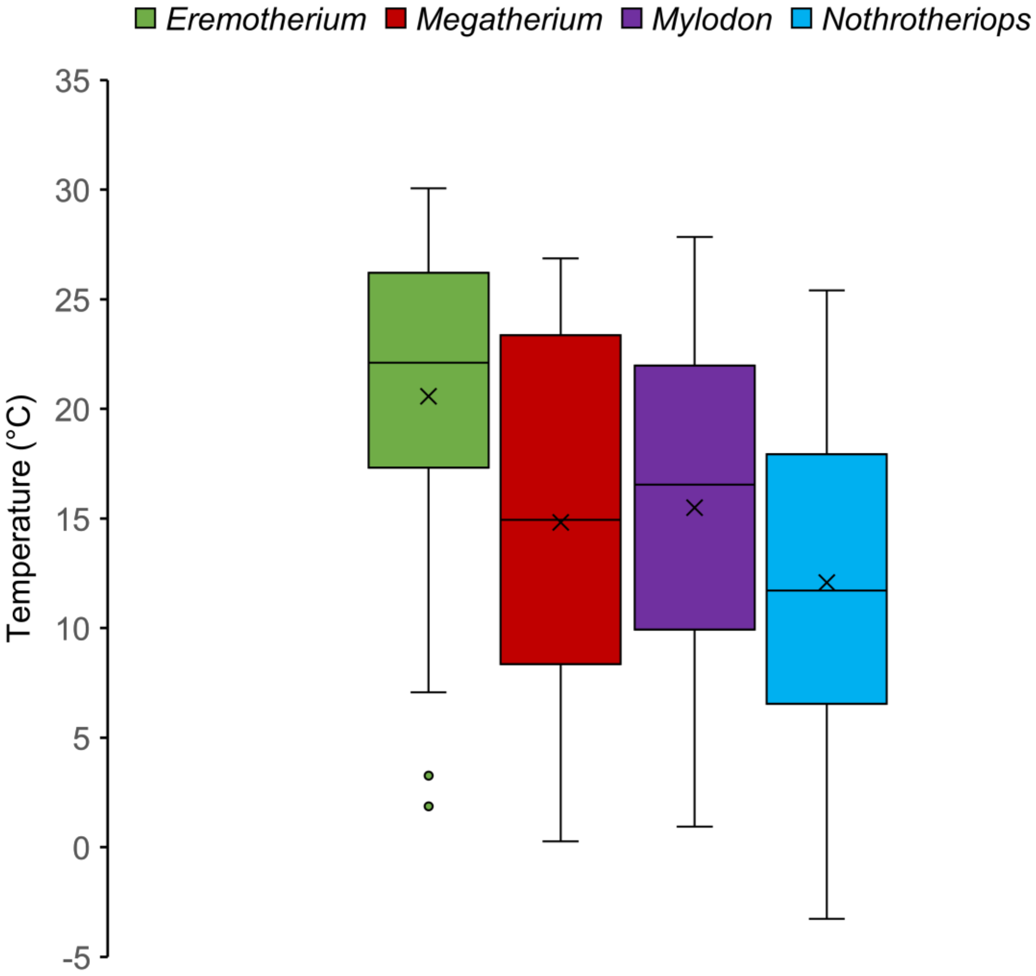

Eremotherium
Megatherium
Mylodon
Nothrotheriops
Temperature (°C)
35
30
25
20
15
10
5
0
-5

Figure 2. Bar chart of estimated basal metabolic rate (BMR) in ground sloths. Values (left) calculated from the ‘edentate’ scaling equation of Withers (1992) are compared to those (right) based on a ‘typical placental’ metabolism calculated by Fariña (2002). Overall metabolic rate increased with body mass, but the amount of metabolic heat production only exceeded 1,000 W in *Eremotherium*.

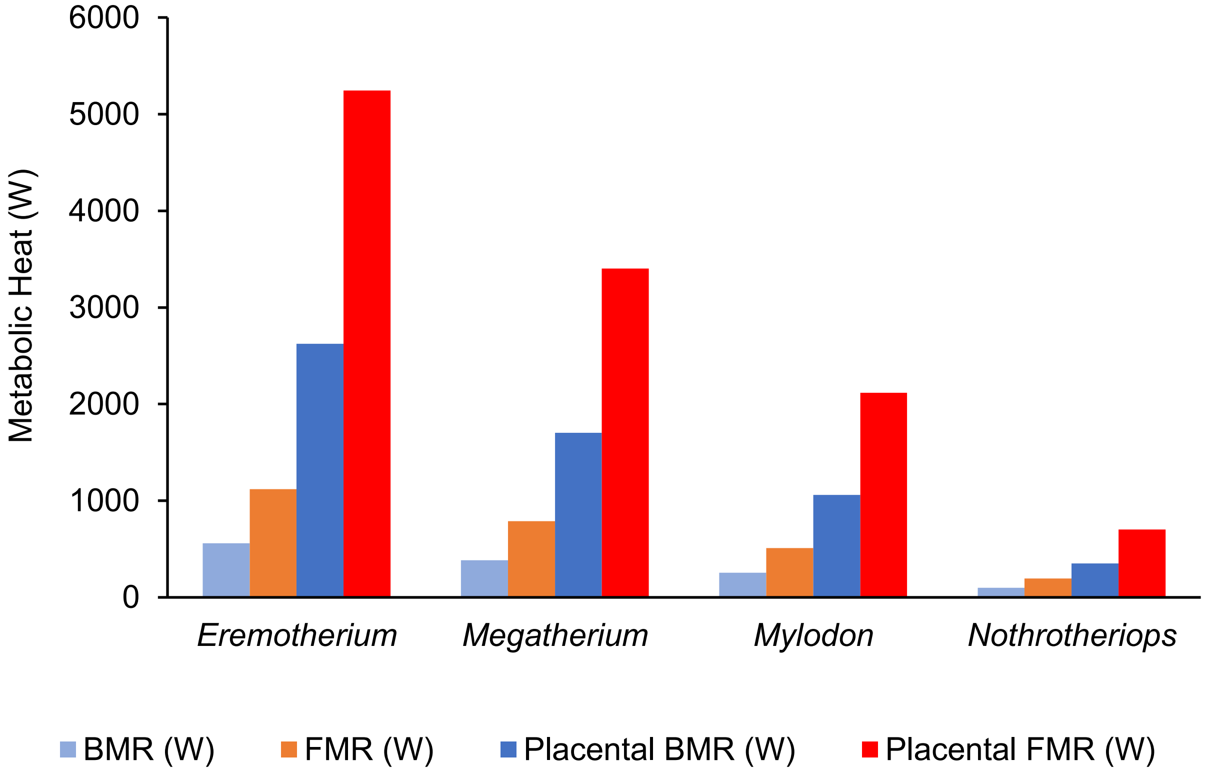

6000
5000
4000
3000
2000
1000
0
Metabolic Heat (W)
Eremotherium
Megatherium
Mylodon
Nothrotheriops
BMR (W)
FMR (W)
Placental BMR (W)
Placental FMR (W)

Figure 3. Modeled trends of thermal neutrality for *Eremotherium*. Daily metabolic activity (kJ day^{-1}) in response to climatic factors over the course of a year. Full body integument curves consist of 2,000 hairs/cm^2 (blue), 1,300 hairs/cm^2 (red), 8.5 hairs/cm^2 (green), and 0.07 hairs/cm^2 (yellow). Color-coded zones represent metabolic states such as heat stress (orange), cold stress (blue), and thermally neutral (green).

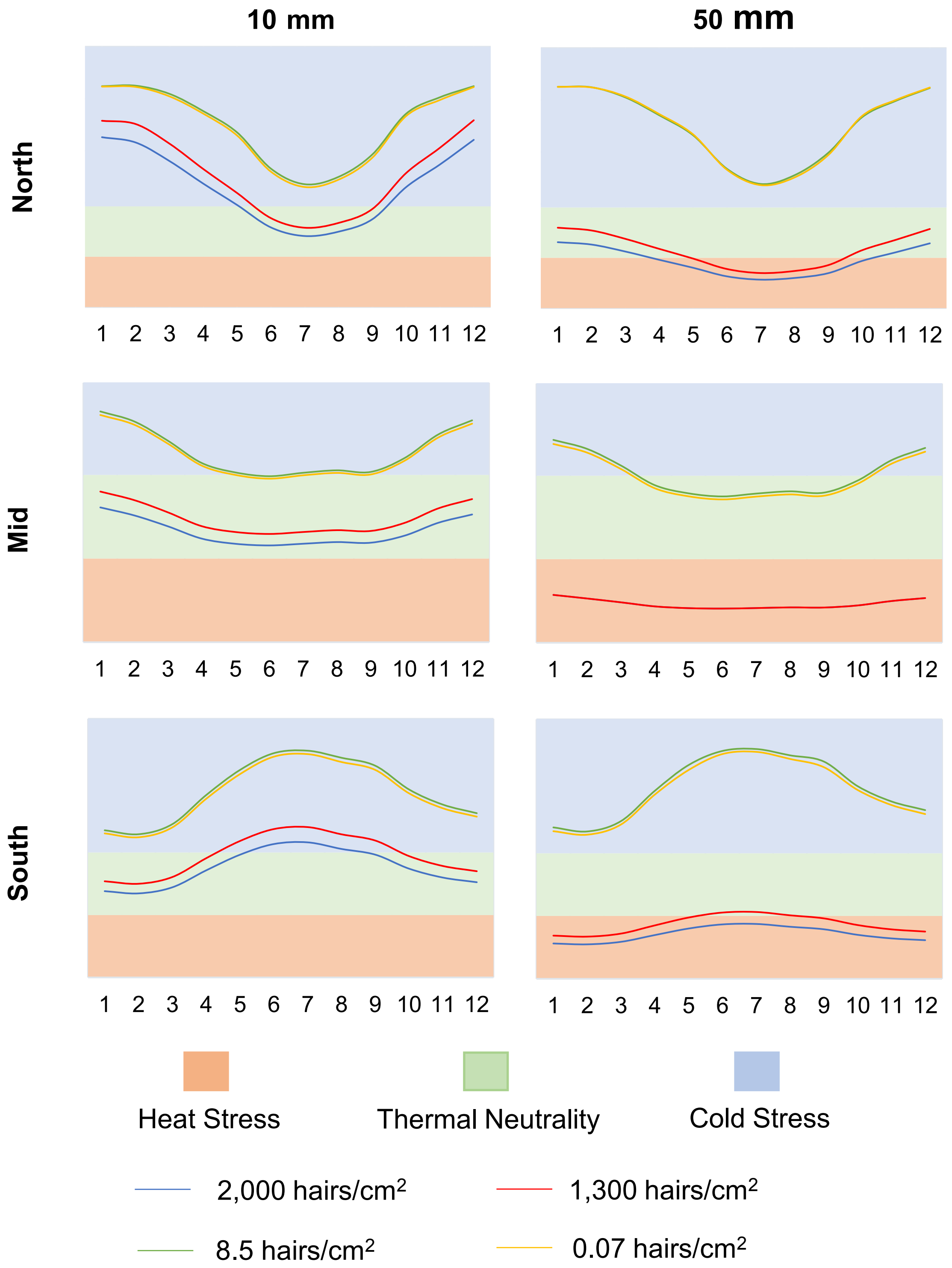

10 mm
50 mm
North
Mid
South
1 2 3 4 5 6 7 8 9 10 11 12
Heat Stress
Thermal Neutrality
Cold Stress
2,000 hairs/cm^2
1,300 hairs/cm^2
8.5 hairs/cm^2
0.07 hairs/cm^2

Figure 4. Modeled trends of thermal neutrality for *Megatherium*. Daily metabolic activity (kJ day^{-1}) in response to climatic factors over the course of a year. Full body integument curves consist of 2,000 hairs/cm^2 (blue), 1,300 hairs/cm^2 (red), 8.5 hairs/cm^2 (green), and 0.07 hairs/cm^2 (yellow). Color-coded zones represent metabolic states such as heat stress (orange), cold stress (blue), and thermally neutral (green).

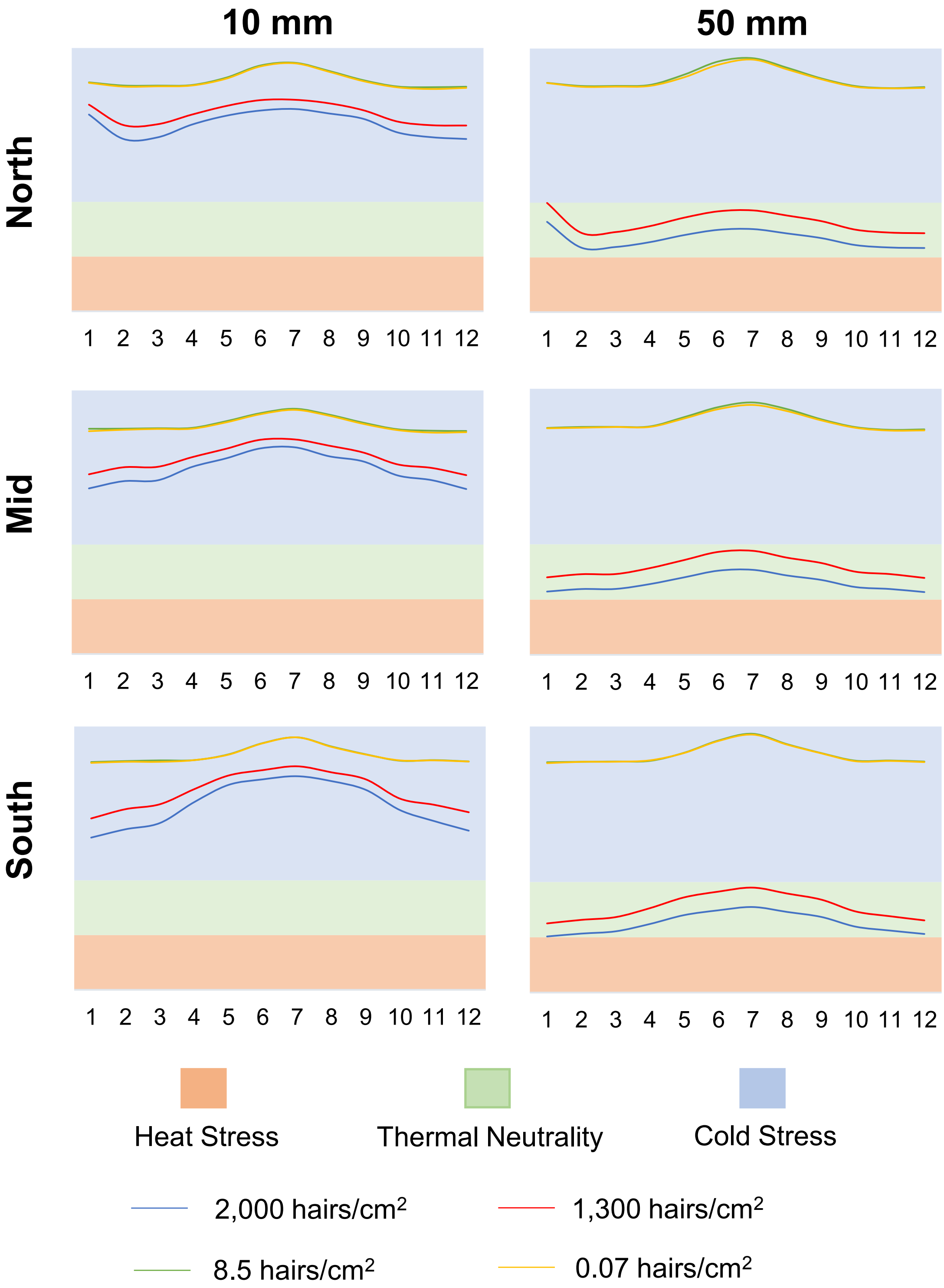

10 mm
50 mm
North
Mid
South
1 2 3 4 5 6 7 8 9 10 11 12
Heat Stress
Thermal Neutrality
Cold Stress
2,000 hairs/cm^2
1,300 hairs/cm^2
8.5 hairs/cm^2
0.07 hairs/cm^2

Figure 5. Modeled trends of thermal neutrality for *Mylodon*. Daily metabolic activity (kJ day^{-1}) in response to climatic factors over the course of a year. Full body integument curves consist of 2,000 hairs/cm^2 (blue), 1,300 hairs/cm^2 (red), 8.5 hairs/cm^2 (green), and 0.07 hairs/cm^2 (yellow). Color-coded zones represent metabolic states such as heat stress (orange), cold stress (blue), and thermally neutral (green).

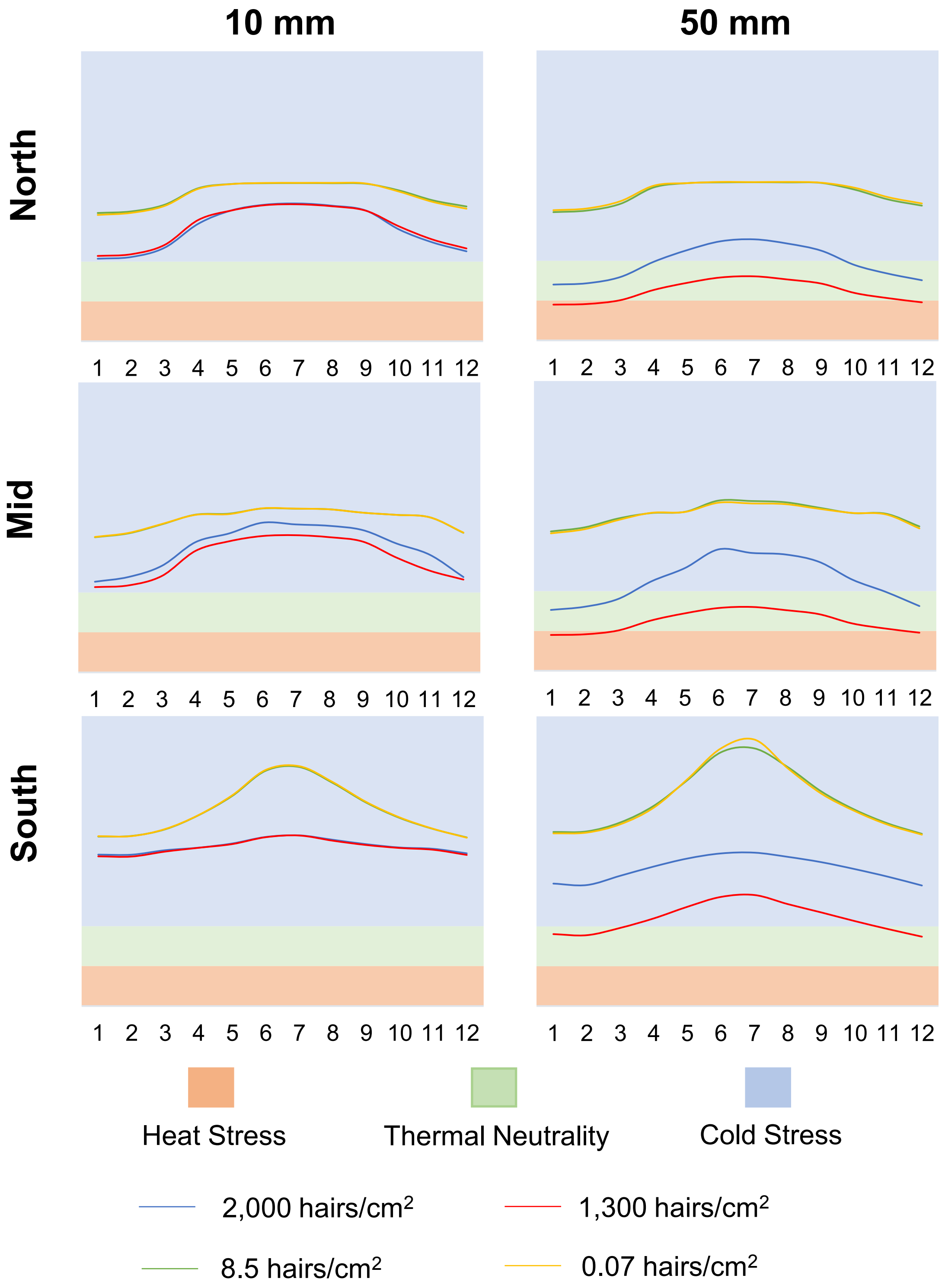
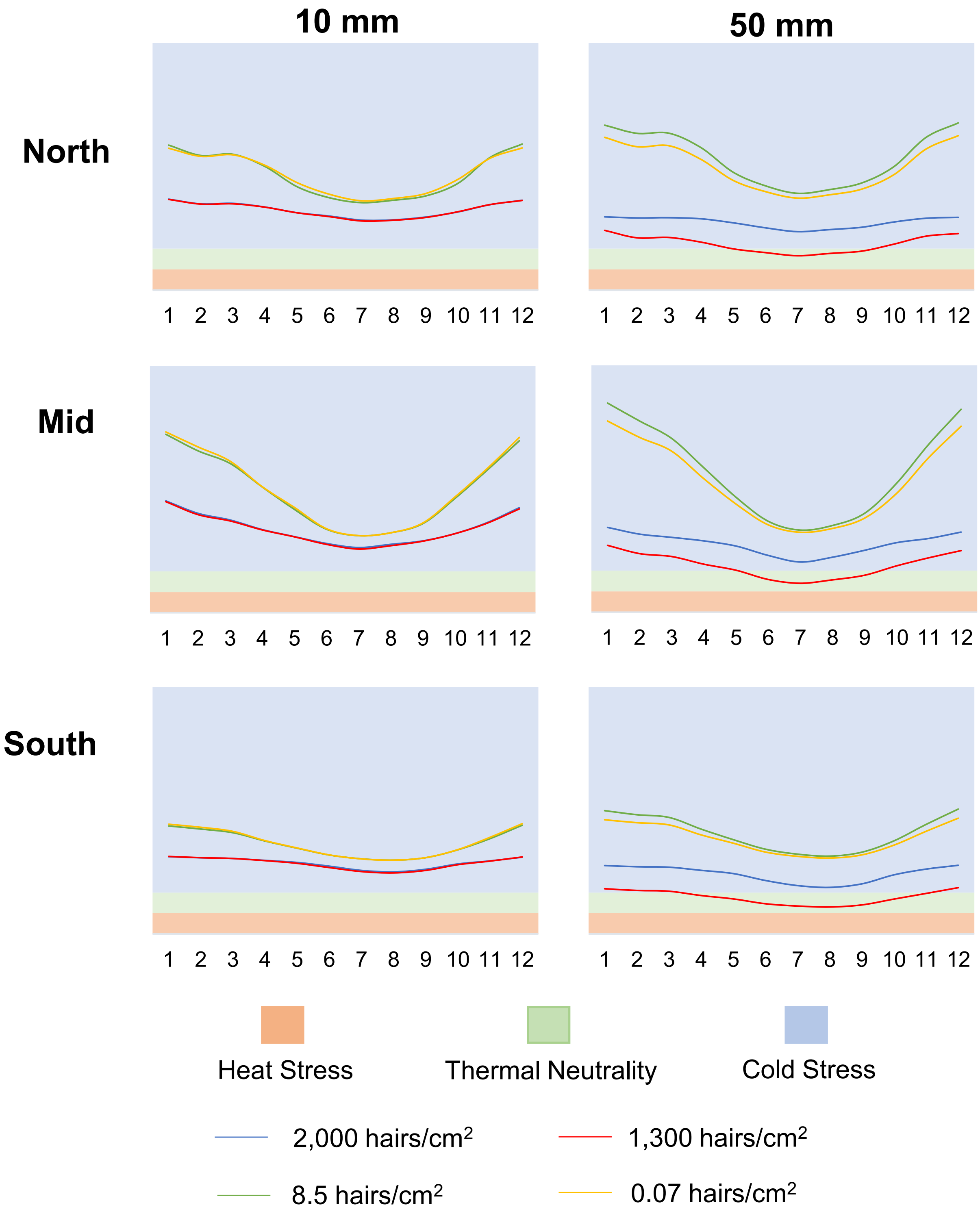
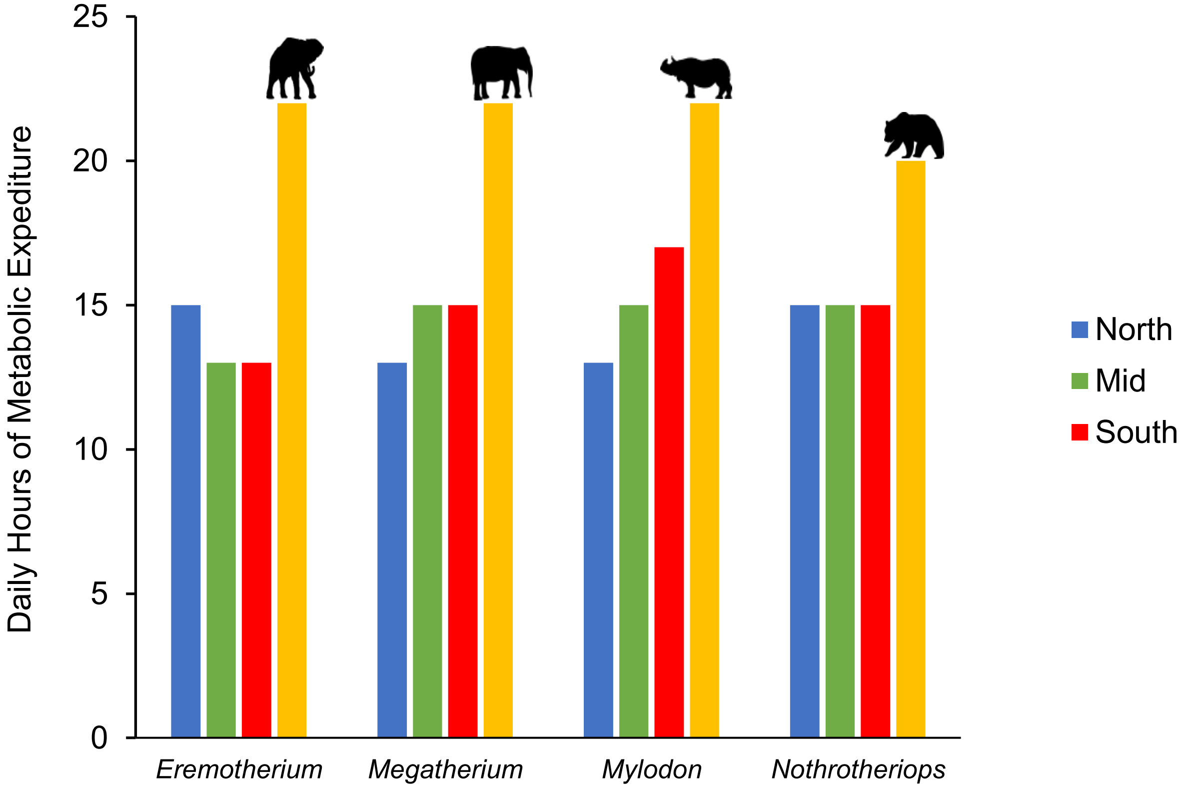

10 mm
50 mm
North
Mid
South
1 2 3 4 5 6 7 8 9 10 11 12
Heat Stress
Thermal Neutrality
Cold Stress
2,000 hairs/cm²
1,300 hairs/cm²
8.5 hairs/cm²
0.07 hairs/cm²

Figure 6. Modeled trends of thermal neutrality for *Nothrotheriops*. Daily metabolic activity (kJ day^{-1}) in response to climatic factors over the course of a year. Full body integument curves consist of 2,000 hairs/cm^2 (blue), 1,300 hairs/cm^2 (red), 8.5 hairs/cm^2 (green), and 0.07 hairs/cm^2 (yellow). Color-coded zones represent metabolic states such as heat stress (orange), cold stress (blue), and thermally neutral (green).



10 mm
50 mm
North
Mid
South
1 2 3 4 5 6 7 8 9 10 11 12
Heat Stress
Thermal Neutrality
Cold Stress
2,000 hairs/cm²
1,300 hairs/cm²
8.5 hairs/cm²
0.07 hairs/cm²

Figure 7. Bar chart of maximum daily hours of metabolic expenditure for each ground sloth genera throughout its geographic distribution compared to extant placental mammals of similar body sizes. Shown as silhouettes are the body size analogues in order left-to-right: African bush elephant (*Loxodonta africana*) for *Eremotherium*; Asian elephant (*Elephas maximus*) for *Megatherium*; Indian rhinoceros (*Rhinoceros unicornis*) for *Mylodon*; brown bear (*Ursus arctos*) for *Nothrotheirops*. Total hours of activity for extant analogues were based on daily hours of sleep reported in the literature (Stelmock and Dean, 1986; Deka and Sarma, 2015; Gravett et al., 2017).



25
20
15
10
5
0
Daily Hours of Metabolic Expediture
Eremotherium
Megatherium
Mylodon
Nothrotheriops
North
Mid
South

Figure 8. Scatter plot of kilograms of wet food mass consumed per day throughout the year for each thermally neutral integument model for northern latitudes (blue), mid-latitudes (green), and southern latitudes (red). Data for each genus of ground sloth are fit with second order polynomial regressions. *Eremotherium* ($y = -0.5992x2 + 8.169x + 163.42$, $R^2 = 0.0399$); *Megatherium* ($y = -1.0121x2 + 13.029x + 95.619$, $R^2 = 0.4803$); *Mylodon* ($y = -1.4442x2 + 19.584x + 35.527$, $R^2 = 0.3153$); *Nothrotheriops* ($y = 0.7511x2 - 10.349x + 68.348$, $R^2 = 0.666$).

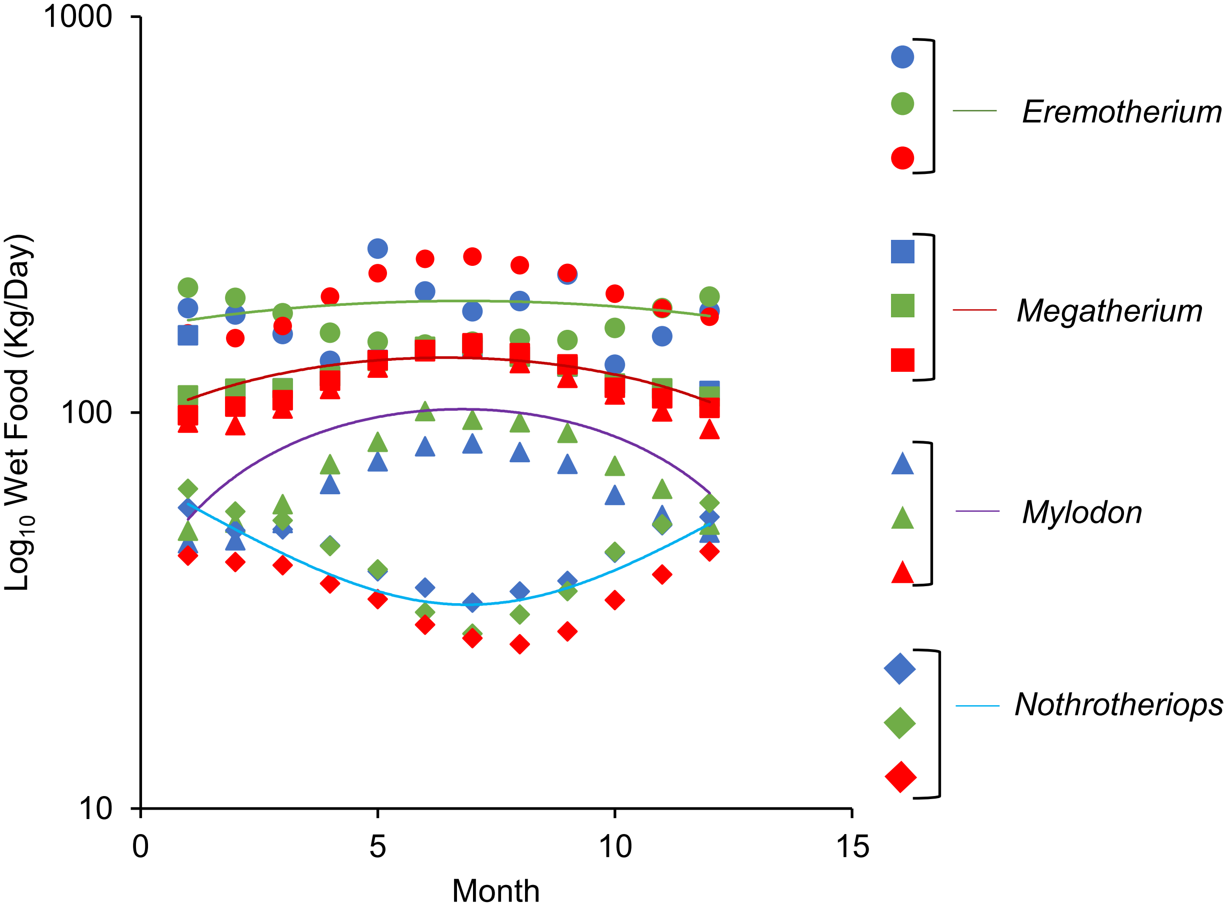
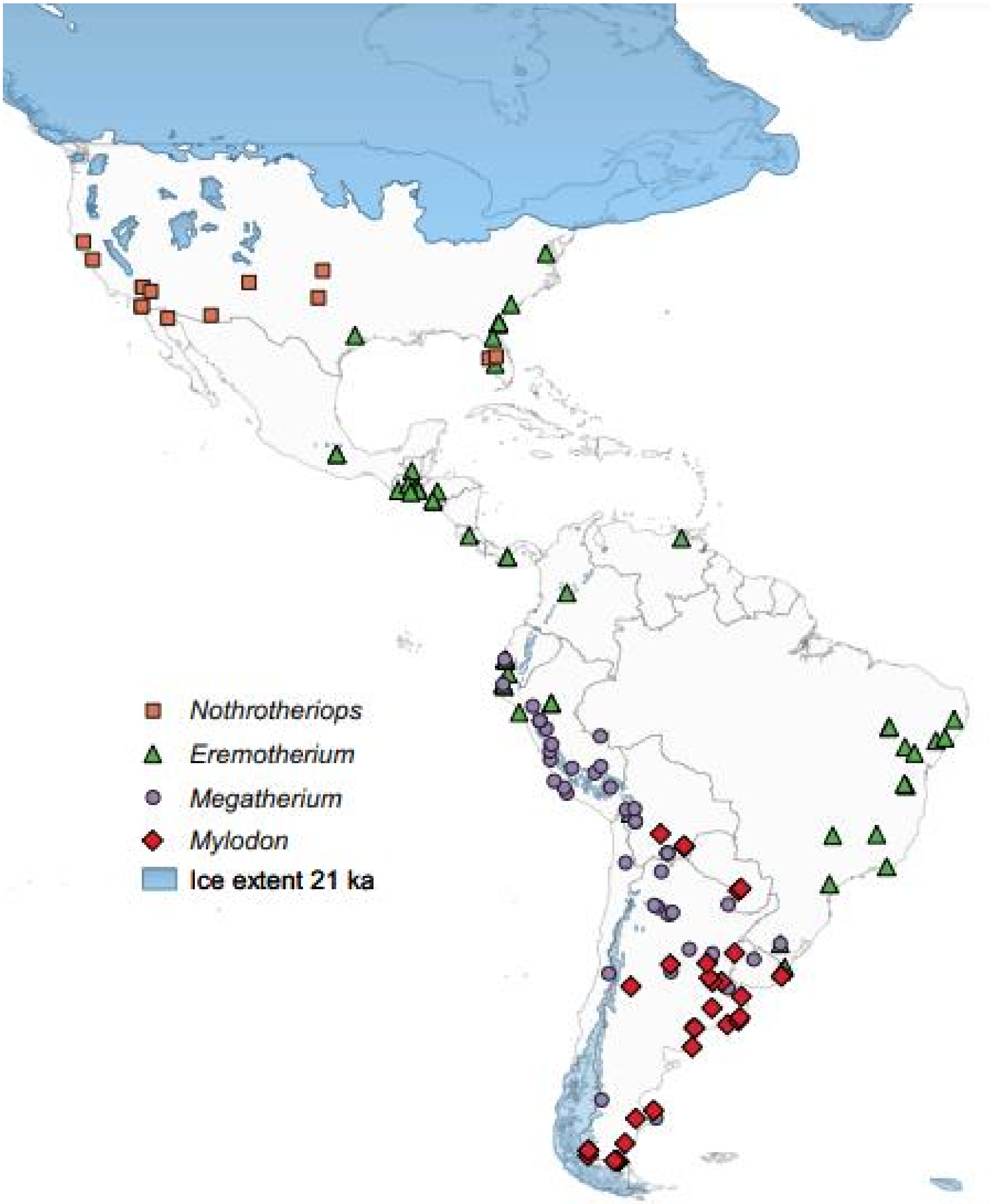

1000
100
10
0
5
10
15
Month
Log10 Wet Food (Kg/Day)
Eremotherium
Megatherium
Mylodon
Nothrotheriops

Figure 9. Map of geographic distribution for sites of fossil remains of ground sloths *Eremotherium*, *Megatherium*, *Mylodon*, and *Nothrotheriops*. Areas shaded blue represent the extent of glaciers during the last glacial maximum (LGM) 21,000 years ago.


Nothrotheriops
Eremotherium
Megatherium
Mylodon
Ice extent 21 ka

APPENDIX

Current Sloth Phylogeny

The superorder Xenarthra has a rich and diverse history preserved in the fossil record dating back 60 million years ago (MYA) to the Eocene Epoch. The Xenarthra consists of the orders Cingulata, which contains living armadillos and pampatheres and glyptodonts (both extinct), and the Pilosa comprising the true anteaters and tree sloths. While the genera *Choloepus* (two-toed sloths) and *Bradypus* (three-toed sloths) are the only extant linages, numerous genera of extinct ground sloths once occupied various niches during the Oligocene and persisted up until the Late Pleistocene. Ground sloths thrived throughout South America and dispersed to eventually colonize the southern boundaries of modern-day North America following the Great American Biotic Interchange nearly 2.5-3 MYA. Several of these ground sloths such as *Megatherium* and *Eremotherium* became the largest xenarthrans ever to walk the Earth reaching sizes comparable to or exceeding that of extant elephants. The family Megatheriidae that includes both of these genera exhibited an increase in body size by 129 kg/MY (Pant et al., 2014), which was most likely due to the climatic changes occurring since the Miocene (Toledo et al., 2017). Since their extinction 12 thousand years ago (KYA), numerous fossil specimens have been collected revealing information regarding the phylogenetic placement (Guadin, 2004; Delsuc et al., 2019; Presslee et al., 2019), diet (Bargo, 2001; Fariña and Blanco, 1996; Hofreiter et al., 2003), and paleoecology (Martin et al., 1961; McDonald et al., 2005, 2013) of these massive herbivores.

There are approximately eight recognized families of the suborder Folivora (i.e., leaf eating taxa) consisting of extinct ground sloths and the two extant genera of tree sloths. The families Bradypodidae and Choloepodidae (recently erected by Delsuc et al., 2019) contain the four species of the genus *Bradypus* and the two species of the genus *Choloepus*, respectively. The family Megalocnidae contains species of the genera *Megaloncus*, *Parocnus*, and various other Caribbean ground sloths. The family Megalonychidae contains two subfamilies with taxa such as *Megalonyx* and *Diablotherium*, both placed within Megalonychinae, and Ortotheriinae comprised of genera such as *Pilomorphus* and *Psudotherium*. The family Mylodontidae contains multiple tribes of ground sloth containing the genera *Mylodon*, *Lestodon*, *Glossotherium*, and formerly members of Scelidotheridae before the revival of its family status by Presslee et al. (2019). Last, the family Nothrotheriidae consists of the North American *Nothrotherium*, as well as the coastal, aquatic sloth *Thalossocnus*, and was once considered to be monophyletic with the family Megatheriidae, which contains the largest ground sloths *Megatherium* and *Eremotherium*.

Earlier phylogenetic analyses based on morphological characters (consisting of 201 osteological characters of the skull, dentary, dentition, and hyoid apparatus in total) originally placed *Choloepus* within the family Megalonychidae that contains the ground sloths *Megalonyx* and *Diablotherium* (Gaudin, 2004). In the same study, the Caribbean ground sloths, including *Parocnus*, *Megalocnus*, and *Acratocnus* were recovered to be the sister taxa to the clade which contains living *Choloepus*, whereas the family Bradypodidae, which consists of all species of the genus *Bradypus*, was recovered as a monophyletic family that is the sister group to all other sloths (Gaudin, 2004). It should also be noted that an alternative hypothesis placing *Bradypus* closer to Megatheriidae and

Choloepus closer to Mylodontidae based on early molecular studies was not ruled out entirely by previous studies (Hoss et al., 1996; Greenwood et al., 2001).

Recently, ten mitogens of extinct ground sloth DNA were sequenced to formulate a new interpretation of sloth phylogeny and evolution (Delsuc et al., 2019). The resulting phylogenetic tree contradicted the previous interpretations that were based on morphology by *Choloepus* having closer affinities to *Mylodon* as opposed to being more closely grouped with the Caribbean ground sloths. This molecular-based analysis (Delsuc et al., 2019) also revealed that eight newly recognized sloth families emerged ~25-36 MYA, with Caribbean ground sloths diverging nearly 35 MYA. These current findings support the hypothesis that there was a biogeographic connection between the Northern tip of South America and the Greater Antilles as related to the early divergence of Caribbean ground sloths. In addition, Bradypodidae was instead revealed to be the sister group to clades containing *Nothrotheriops*, *Megalonyx*, and *Megatherium* (Delsuc et al., 2019) rather than being the sister group to all other sloths. Last, the family Megalonychidae was found to be polyphyletic with independent origins for the Caribbean ground sloths, *Megalonyx*, and extant *Choloepus* (now placed within the family Choloepodidae).

Despite 20 unique synapomorphies revealed previously in the Megalonychidae (Gaudin, 2004), the characteristics of the trenchant caniniforms (i.e., teeth) made up a majority of them. The results of the morphological analyses mainly relied on the assumption that the dental characteristics of *Bradypus* represent the ancestral character state. While the craniodental characteristics that *Choloepus* shares with Mylodontidae evolved through convergence (Gaudin, 2004), the results of Delsuc et al., (2019) show that these characteristics (e.g., leveled position of the mandibular condyle to the tooth row and the mandible possessing a straight, ventral edge) are synapomorphies between the two groups. The molecular analysis also revealed that sloths rapidly diversified once the three main clades appeared ~35 MYA. The eight lineages of sloth diverged 31-28 MYA, which corresponds to the formation of the Antarctic ice sheets and drier, and more open habitats forming in South America during the Oligocene. The divergence of *Bradypus* from the linages leading to *Nothrotheriops* and *Megalonyx* is now estimated to occur nearly 29 MYA as opposed to the earlier proposed age of divergence of 40 MYA (Gaudin, 2004). Interestingly, Delsuc et al., (2019) calculated the divergence of *Choloepus* from the family Mylodontidae to also have occurred 29 MYA.

A similar study based on proteomic analysis of mitochondrial DNA taken from collagen fiber samples (Presslee et al., 2019) also arrived at similar conclusions to those of Delsuc et. al., (2019). Specifically, Presslee et al. (2019) demonstrated that *Choloepus* groups within Mylodontidae and that both *Bradypus* and *Megalonyx* are nested within the superfamily Megatheroidea, in addition to providing strong support for the Caribbean ground sloths being monophyletic. These novel findings are the most consistent with radiation events evidenced in the fossil record by the presence of sloths in the West Indies by the mid-Cenozoic, as well as the radiation of South American sloths during the Early Miocene. These data additionally show that 'experimentation' in arboreal adaptations probably evolved early and multiple times in sloths, though the authors (Presslee et al., 2019) acknowledge that fossil tree sloths must be found to confirm this hypothesis.

Environmental Temperatures and Climate of Megatheriid Ground Sloth Habitats

Both *Megatherium* and *Eremotherium* appeared in the fossil record of South America during the Early Pliocene and went extinct in the Late Pleistocene. The beginning of the Pliocene saw global temperature fluctuations with South America becoming more arid, which is associated with global cooling (Amidon et al., 2017). The rise of the Andes Mountains would also create a rain shadow effect that aided in the adaptation of taxa to arid environments by fragmenting the regions once inhabited by tropical paleoflora (Hinojosa and Villagrán, 1997). Many organisms that were adapted to tropical conditions had to adapt to living in open grasslands. A warm period then occurred during the mid-Pliocene in which there was global warming with temperatures averaging nearly 2-3°C higher than modern times (Dowsett and Chandler, 2009). After this warm period, the paleoclimate would cool down once more as polar ice caps started to form at the poles marking the beginning of last ice age that began in the Pleistocene.

The climate during the Pleistocene Epoch continued the trend of global cooling as sea levels fell and massive glaciers formed in northern latitudes as well as in the Andes mountains. These glaciers would advance and retreat throughout the Pleistocene with various flora and fauna thriving during the interglacial periods between glacial maximums. In present day South America, the climate became drier with grasslands replacing tropical forests as the tree line descended to an altitude of about 2000 meters (Van Der Hammen, 1974). The types of vegetation that grew in these environments were responsible for the distribution patterns of megafaunal mammalian herbivores (De Vivo and Carmignotto, 2004) and there is evidence suggesting that the megafaunal herbivores were also responsible for shaping the arid grasslands that dominated the South America continent at this time, with a reduction in these habitats coinciding with their extinction

(Bakker et al., 2016; Doughty et al., 2016). However, it should be noted that many herbivorous megafauna taxa avoided arid, open grasslands and instead favored environments that were a mix of grassland and steppe or grassland and open forests (Gallo et al., 2013).

Habitat Preferences and Biogeographic Range of Megatheriid Ground Sloths

The habitat preferences of *Megatherium* and *Eremotherium* differ in that the former likely lived in more upland, temperate grasslands, while the latter would have likely lived in tropical conditions (Croft, 2016). Thus, *Eremotherium* was able to disperse as far North as the present day Southern United States following the Great American Biotic Interchange during the Pleistocene, but it was unable to disperse further into North America due to a possible intolerance to colder climates (Morgan, 2005; McDonald et al., 2009; Croft, 2016). According to Pujos (2008), remains assigned to the genus *Megatherium* have been recovered in southern South America in present day Argentina, Uruguay, Paraguay, Bolivia, and Chile, with the genus *Eremotherium* being found in Brazil, Venezuela, Columbia, Central America, and the Southern United States. Remains of both *Megatherium* and *Eremotherium* overlap in Ecuador and Peru with the former having a higher taxonomic diversity in the Andes of Peru, while the latter has lower taxonomic diversity and is restricted to the northern coast of Peru in latitudes below 8°S (individuals of *Eremotherium* also found from the coast of Ecuador: Tito, 2008). It has also hypothesized that species under the genus *Megatherium* and the subgenus *Pseudomegatherium* used the Andes as a migration route to the North as numerous fossil species have been recovered from Ecuadorian coasts near large rivers and oases (Pujos, 2008).

In contrast to the various Andean species of the genus *Megatherium*, the species *M. americanum* favored more open grasslands of the pampas of Argentina and the Bolivian Altiplano as opposed to forest edges (Pujos and Salas, 2004). Radioisotopic studies on the bones of Amazonian megafauna such as *Eremotherium* in the Itaituba locality show that there were high amounts of C3 plants (e.g., trees, shrubs, and non-grass herbs), but those did not necessarily correlate with a heavily forested environment (Rossetti et al., 2004). Given its extensive range, *Eremotherium* may have inhabited a wide range of habitats, but preferred more open habitats as opposed to closed forests, and instead favored open savanna, dry scrubland, and the edges of forests and open woodlands (Webb and Ranzi, 1996; Ranzi, 2000; Rossetti et al., 2004; Larmon et al., 2019). *Megatherium* also seemed to have a preference towards open habitats that were semiarid-to-arid as evidenced by a higher amount of grit in its dental microwear patterns seen in fossilized teeth (Bargo, 2001; Green and Kalthoff, 2015). The microwear patterns also contrasts to the microwear patterns of sloths living in more humid, densely forested environments (i.e., *Megalonyx* and extant tree sloths), which have greater scratch widths that are not as frequently seen in the teeth of sloths that live in more open environments.

Giant Ground Sloth Diet

For enormous herbivores that spend a large portion of their daily time budget consuming low energy leaves, a great amount of heat will be produced via digestive fermentation. In the case of the species *Eremotherium laurillardi*, which had a wide geographic distribution, the amount of C^{13} isotopes present in their fossilized bones and teeth suggest that it was a grazer in open habitats and a mixed browser in more closed habitats (Dantas et al., 2013). Moreover, Oliveria et al. (2020) revealed that populations of *E. laurillardi* that once inhabited mid-western Brazil consumed more foliage from trees and shrubs, while those in northeastern Brazil fed on C4 plants (i.e., grasses adapted to tropical and arid environments). This study also examined the microwear of the teeth, which had numerous scratches to and coarseness of the orthodentine surface indicative of a large consumption of grasses and foraging close to the ground.

In contrast, the diet of *Megatherium americanum* is proposed to have consisted primarily of leaves and woody plants as evident from microwear analyses (Bargo et al., 2006; Green and Kalthoff, 2015; Saarinen and Karme, 2017) and from putative coprolite samples attributed to this species (Carretero et al., 2004). The hypsodont pattern and estimated jaw mechanics of *M. americanum* also suggest that it had a strong bite, and that their hypsodont (i.e., high-crowned teeth designed for processing fiber-rich foods) and bilophodont (i.e., molar teeth with two transverse ridges) tooth structure was well-suited for shearing tough plant material, in addition to grinding moderate-to-soft plant material (Bargo, 2001; Bargo et al., 2006). The species *E. laurillardi* also possessed similar adaptations for oral food processing (Naples and McAfee, 2011) by examination of their cranial morphology, which suggests that both species of megatheriids had a low digestive efficiency. The higher degree of hypsodonty in *M. americanum* further implies that was adapted to more open, temperate ecosystems as opposed to *E. laurillardi*, which likely preferred more closed environments (Bargo et al., 2006). Collectively, these previous findings would also lead to the hypothesis that *M. americanum* had a lower fermentation capacity and possibly may have had a higher basal metabolic rate due to the adaptations for efficient mastication that is observed in the genus (Vizcanio et al., 2006). Fariña and Blanco (1996) have even made the assertion that the forelimb mechanics allowed for

Megatherium to deliver swift blows to smaller carnivores to seize control of a carcass as a part time scavenger. However, Carbon isotope analyses of *Megatherium* teeth reveal that the C^{13} composition matches that of other herbivores of similar sizes and thus no evidence for an omnivorous diet (Bocherens et al., 2017).

The Metabolism of Extant and Extinct Sloths

The amount of energy expended in the field (field metabolic rate or FMR) of an organism plays a fundamental role in shaping ecological and evolutionary processes as it impacts behavior, distribution, and reproductive rates (Brown et al., 2004, McNab, 2012). For an organism to survive, it must obtain energy from resources so that it reaches reproductive maturity and passes on its genes to the next generation. However, basal metabolic rate (BMR) reflects the limitations of an ecological niche and opportunities in a specific geographic range, while the environment and behavior reflect adjustments in muscle mass and activity levels (McNab, 2019). Thus, body size is a major factor for the BMR of endotherms as larger animals must obtain larger quantities of food to be at a caloric equilibrium with their body temperature and levels of activity (Feldhamer et al., 2007).

The BMR of an animal typically scales to the 3/4 power of the body mass (slope or b = 0.75). This observation was first made by Kleiber (1932) and became known as Kleiber's rule. However, BMR was initially expected to scale with the 2/3 power of body mass because body heat produced is lost through surface area (area and body mass scale to the 2/3 power), but the larger 0.75 exponent arises due to efficiency in transporting nutrients throughout the body (West et al., 1997). Similar observations have been made at the organ-tissue level (Wang et al., 2001) and the rule generally applies to organisms ranging from mouse-sized to elephant-sized. While variations in BMR are primarily determined by mass, it can also vary with body temperature and the taxon in question (Clarke et al., 2010). Nevertheless, there remains a large amount in support of Kleiber's rule and no evidence that body surface area scales proportionally (i.e., isometric scaling) with BMR (Dodds et al., 2001).

The modern genera *Bradypus* and *Choloepus* are well-known for their extremely low metabolic rates and ability to undergo fluctuations in their core body temperature beyond what is ordinary for a placental mammal (Kredel, 1928; Giné et al., 2015; Cliffe et al., 2018). This is primarily due to their energy poor, folivorous diet (Chiarello, 1998; Cliffe et al., 2015), as well as notably reduced skeletal muscle mass (~24% body mass) compared to other arboreal mammals (~33% body mass) of similar sizes (Goffart et al., 1962; Grand 1978; Muchlinski et al., 2012; Gaudin and Nyakatura, 2018). Most of their metabolic energy is used for digestion/fermentation of leaves in the foregut (i.e., modified stomach with multiple chambers), the duration of which could last nearly a month (Foley et al., 1995). For this reason, some species in the genus *Bradypus* may prefer young leaves with a higher nutritional content over that in mature leaves (Chiarello, 1998; Urbani and Bosque, 2007).

Recently, FMR, movement patterns, and body temperatures of both *Bradypus* and *Choloepus* were studied and compared between genera (along with BMR), as well as to those of other arboreal folivores (e.g., primates) (Pauli et al., 2016). While arboreal folivores, overall, tended to have lower FMRs and BMRs compared to other mammalian taxa, both genera of tree sloth expended the least amount of energy and the species *Bradypus variegatus,* in particular, possessed the lowest FMR of any extant non-hibernating mammal (Pauli et al., 2016). This same study also revealed that *B. variegatus* showed smaller movement distances across the study site than *Choloepus hoffmanni* and the internal body temperatures of both species of tree sloth are comparable to previously reported data (Montgomery and Sunquist, 1978). However, larger temperature fluctuations were observed in *Bradypus* related to greater energy conservation as evidenced in its very low FMR. The daily body temperature fluctuations observed are interpreted as heterothermy and later findings suggest that the heterothermic nature of tree sloth physiology relies on additional factors such as food intake (Cliffe et al., 2015) and ambient temperatures (Giné et al., 2015; Cliffe et al., 2018). With regards to the latter, perhaps it is for this reason that tree sloths prefer neotropical rainforests that have relatively little fluctuation in daily high and low ambient temperatures year-round to conserve metabolic energy. Sloths also engage in numerous behavioral thermoregulatory behaviors, including sun basking for warmth and take the cover of shade when overheated. Thick sloth fur is also noted to reduce thermal conductance and acts as insulation against changes in ambient temperatures (McNab, 1978).

Other studies have examined the effects ambient temperature on food intake in the species *B. variegatus* (Cliffe et al., 2015). The amount of *Cecropia* leaves consumed in three female *B. variegatus* were measured for 158 days in enclosures that simulated their natural habitat in the wild. The results of this study suggest that food intake increases with an increase in ambient temperature, and thus an increased rate of fermentation. In contrast, other mammals experience a greater food intake in cold ambient temperatures to keep within a thermal neutral zone (i.e., the range of ambient temperatures where an endotherm can maintain their body temperature without having to expend vast amounts of energy). Importantly, it has been demonstrated that maintaining a core body temperature (over a limited range) that maximizes digestive efficiency is critical for *Bradypus* to maintain their energy requirements (Cliffe et al., 2015). Further investigations by these authors (Cliffe et al., 2018) focused on the effect of ambient temperature on sloth body temperature and overall BMR to test the hypothesis that an increase in ambient temperature would result in an increase in metabolic rate. In this study (Cliffe et al., 2018), the metabolic rates of eight captive *B. variegatus* were measured along with the ambient temperature by utilizing a thermocouple inserted in the rectum and manipulating the temperature of the individuals 'resting' in a metabolic chamber. The results showed that the lowest metabolic rates were recorded at the lowest temperatures, while sex and captivity status had no effect on the measured BMR. The results also show that *Bradypus* is the only mammal observed thus far to lower its body temperature in response to high ambient temperatures, as well as lowering its body temperature in response to low ambient temperatures.

Regardless of the interesting findings cited above, it should be noted that extant tree sloths are not an exact analogue to the physiology of extinct ground sloths. It has been addressed by Fariña (2002) that the largest ground sloths (e.g., *Megatherium*) would have had a muscle mass far greater than that of the living tree sloths *Bradypus* or *Choloepus*, which is evident by the large muscle scars and insertion points on their fossilized post-cranial skeletons. Despite the realistic possibility of not having a metabolism as extremely low as their extant relatives, there is evidence that suggests that giant ground sloths had a metabolic rate that was reasonably low for mammals of their enormous size. For example, estimates of the body temperature of *Nothrotheriops* (based off amino acids preserved in bone collagen) show that it had a range of body temperature values akin to extant xenarthrans (Ho, 1967). Similar estimates of the metabolic rates and thermal conductivity of both *Mylodon* and *Nothrotheriops* suggest that both had low BMR and relatively poor thermal conductivity compared to other mammals of similar size (McNab, 1985). Conversely, *Megalonyx* may have had a higher metabolic rate than other ground sloths as the remains of this taxon have been found as far North as the Yukon (McDonald et al., 2000; Bakker pers. comm.).

Ground sloths indeed may have had low metabolic rates for mammals of their large size; however, this tentative conclusion does not imply that they were as slow moving as living tree sloths. Data from a trackway (i.e., fossilized footprints) in Pehuén-Có attributed to *Megatherium* and discovered by Blanco and Czerwonogora (2003) suggest that the average velocity was approximately 1.21 m s^{-1} (i.e., >10 times faster than extant *Bradypus* with an average walking velocity of 0.07 m s^{-1}: Diniz et al., 1999, Gorvet et al., 2020). Speeds of nearly 0.8–2.2 m s^{-1} (which is still lower than the top velocity of 5–6 m/s measured for elephants: Hutchinson et al., 2006) also have been estimated for *Megatherium* (Billet et al., 2013). While the data from the fossil record is robust with regards to ground sloth evolution, biogeography, and paleoecology, very little work has been done with respect to locomotor capacities. Moreover, the physiological constraints on integument in larger taxa (i.e., *Megatherium* and *Eremotherium*) have yet to be thoroughly examined. The extent of integumentary insulation can provide insight into thermoregulation and the general life appearance of the largest ground sloths.

A Review of Ground Sloth Integument

In contrast to some large mammalian herbivores found in permafrost of Siberia, the integument and life appearances of numerous ground sloth genera remains largely unknown. The two genera of ground sloths that have known hair samples preserved are *Mylodon* from Patagonia, and *Northrotherium* from the present day Southwestern United States with dermal ossicles found with various genera. The integument of *Mylodon* and *Nothrotherium* was recovered from Cueva del Milodón and Gypsum Cave, respectively, and both samples date back to the Pleistocene Epoch (2.6 million to 11,000 years ago). The cave systems for which the source material was discovered sheltered these samples from decaying via exposure to the elements and they remained undisturbed by scavengers. These integument samples have also been found to be associated with ground sloth coprolites and both are excellent sources of ancient DNA.

Recent analyses were able to sequence amplicons of approximately 147–152 base pairs long from strands of fur found in coprolites attributed to *Mylodon darwinii* (Clack et al., 2012). It was concluded that the fur indeed belonged to this species as the DNA samples closely matched the samples previously described by Hoss et al. (1996). While Clack et al. (2012) acknowledged that coprolites can contain a heterogeneous mixture of organic materials, the removal of fur samples from fecal debris and access to the cells of the hairs themselves prevented the samples from being contaminated, thus making them viable for destructive DNA tests while sparing more precious bone and other tissue samples to the same type of testing to procure DNA. The methods employed in this study (Clack et al., 2012) could also be applied to fecal fur samples recovered from more temperate and arid caves in the Americas to further establish the genetic diversity of ground sloth populations.

One of the earliest in-depth descriptions of the structure of the fur of *Mylodon listai* was originally documented by Ridgewood (1901). The skin samples described were recovered from the Consuelo Cavern in Patagonia and the microstructures of the fur were compared to those of extant members of the Pilosa. The individual hairs of the fur were reported to be ~6 cm in length with a thick, scaly cuticle, absence of underfur, and lacking any medulla. This is unlike the spongy cuticle found in the fur of modern *Bradypus* and more like the fur structure seen in extant *Dasypus* (long-nosed armadillos) and *Tamandua* (semi-arboreal lesser anteaters). Given that the individual hairs of *Mylodon* lack an extra cortex, Ridgewood (1901) went as far as claiming that *Mylodon* was more closely related to armadillos and anteaters than it was to extant tree sloths. However, subsequent phylogenetic analyses would recover *Mylodon* as a member of the order Pilosa and not as a member of order Cingulata or Vermilingua (suborder of anteaters).

The fur structure of the North American Shasta ground sloth, *Nothrotherium shastense*, has been described by Hausman (1929). The fur sample was found near the pelvic region of the post cranial skeleton collected by the Peabody Museum of Natural History at Yale University and consists of only over-hair. The cuticular scales of the individual hairs were pristinely preserved and were not found to be different from those found in other extant mammals. In particular, when the hair shaft was observed at higher magnification (18x), Hausman (1929) described “ovate bodies” that were darkly colored. The identity of these structures were proposed to be the cells of algae similar to those found to inhabit the fur in extant tree sloths in the neotropical rainforests of the Americas (Hausman, 1929, 1936). Nevertheless, it was also observed that the fur of *N. shastense* was not grooved as in modern *Bradypus* and *Choloepus*, and the strands of hair exhibited a smoothly elliptical cross section.

To date, preserved integumentary structures that are definitively attributed to the largest ground sloths *Megatherium* and *Eremotherium* have yet to be found. The only specimen of *Megatherium* having sample of skin, with which the fur could possibly be preserved, was lost before it could be collected (Pujos and Salas, 2004). Nonetheless, both taxa notably have been historically reconstructed as having a thick coat of long, shaggy fur similar to that of smaller ground sloths (e.g., *Mylodon* and *Nothrotheriops*) and extant tree sloths. This form, however, has been challenged by Fariña (2002, 2013) who argues for largely hairless integument in the largest ground sloths. It specifically has been hypothesized that given their massive sizes and the relatively warm climate of the Brazilian Pampas that a large-bodied ground sloth would not be thermally neutral in such a habitat if it were covered in thick fur. For example, if the integument of *Megatherium* closely mirrored that of the largest extant terrestrial mammals (i.e., elephants, hippopotamuses, and rhinoceroses), then it would be in a thermal neutral zone if the surrounding temperatures were nearly -17°C, which is highly unlikely in the temperate paleoclimate of the Brazilian pampas (Fariña, 2002, 2013).

A "hairless integument model" has also been proposed with regards to *Eremotherium*, but it is acknowledged that no skin samples are known to confirm the lack of fur (McNab, 1985). This model was once again championed in a recent publication (Lindsey et al., 2020) regarding a mass assemblage of *Eremotherium* remains recovered from Tanque Loma in Ecuador. A bone bed was described that contained numerous individuals of *E. laurillardi*. This bone bed consisted of individuals of various sizes and ontogenetic stages inhabiting what was once a marsh during the late Pleistocene. The cause of death of the specimen was believed to be due to disease (or drought) stemming from fecal matter contamination of the marsh. Supporting this interpretation is the discovery of partially digested plant material found intermixed with the ground sloth remains. This discovery provided deeper insight into the behavior of *E. laurillardi* in that it may have engaged in wallowing behavior like extant hippopotamuses, which are also prone to diseases from fecal contamination during the dry season. The authors (Lindsey et al., 2020) additionally postulated that wallowing would be advantageous if *E. laurillardi* had a hairless integument as it would offer protection against the sun and tropical insects akin to the benefits of this behavior in many large-bodied terrestrial mammals of the modern aspect.

Despite the references cited above providing a reasonable amount of evidence in favor of a hairless (or nearly hairless) integument in the largest ground sloths, there are questionable assumptions applied to each of their methodologies. For example, Fariña (2002) did not properly take into account the basal metabolism of tree sloths and other xenarthrans in his calculations of heat flux. Instead, the BMR of a naked human was first scaled up to the size of *Megatherium americanum*; assuming similar core body temperature and skin thickness to that of human primates (Fariña, 2002). While the skin of ground sloths with preserved integument (e.g., *Mylodon*) are known from the fossil record, the skin thickness was never accurately documented due to the desiccated state of preserved specimens. Thus, there is no true representation the actual skin thickness for giant ground sloths when the animals were alive. Second, Fariña (2002) attempted to estimate the BMR of *Megatherium* by dividing the estimated metabolic rate in half and concluded that it could still be naked and thermally neutral in environments of with ambient temperatures of -10°C. Thermal neutrality values of -4°C and -28°C, respectively, have also been calculated for a completely naked individual of *Mylodon darwinii* versus an individual of *M. darwinii* with a fur coat 4 cm long, each weighing 2,000 kg (Fariña 2002).

The fossil evidence known for *Mylodon*, however, suggests that it was extensively covered in fur, which could have been as long as 6.5 cm in some regions of the body (Collins, 1933), whereas anecdotal evidence claims that its fur could be as long as 15–22 cm in some regions of the body. The annual ambient temperature in the Andes where *Mylodon* was known to inhabit was estimated to on average -2.9°C (Kull et al., 2007) and this value not correspond with the thermal neutrality values of a completely furry *Mylodon* calculated by Fariña (2002). This suggests a thermal neutrality threshold of -28°C. Moreover, his calculations have yet to be tested on other megafauna that are known to have thick fur coats such as woolly mammoths and woolly rhinos and may produce results that are likely to be inconsistent with data on the fossil integument and paleoclimate. It also must be noted that there is no significant correlation between body mass and body temperature in mammals because the relationship is more complex an one that is mediated through ecology (Clarke and Rothery, 2008). Last, there is currently no "generalized theory of integument" even among closely related taxa living in similar environments (Holtz, 2018). To confirm or falsify a hairless model of integument of the largest ground sloths, a more complete understanding of the Xenarthran metabolism is required along with more data on the geographic distribution of giant sloths, in addition to evidence on the paleoclimate and environments that they once inhabited.

Objectives and Hypothesis

The “hairless model integument model” described above is primarily based on estimates of body mass, core body temperature, and ambient paleoclimate temperatures. But, paleoecology, paleodiet, and behavior also play an equally crucial role towards understanding the thermal energetics in giant ground sloth taxa (and thus insight into the form of their integument). The current literature is lacking a definitive consensus as to whether the internal body temperature and BMR of the largest ground sloths were comparable to those of the largest extant terrestrial mammals. The absence of remains from *E. laurillardi* from the fossil record of North America during the last glacial maximum suggests that large ground sloths were susceptible to cold temperatures, while the trackway evidence and proportions of the appendicular skeleton of *M. americanum* suggest that they were generally not fast moving and not nearly as fast as extant large bodied terrestrial mammals. In addition, *M. americanum* would have occupied a more southern (i.e., temperate) geographic range than *E. laurillardi*.

The objective of this research is to test the “hairless model of integument” of Fariña (2002, 2013) for largest ground sloths ever in existence, *Megatherium* and *Eremotherium*. In order to more rigorously test the model, numerous factors must be taken into account including habitat preference, species distribution, daily calorie intake, body mass, internal core temperature, and ambient temperatures of the paleoclimate. To complete the model, other variables on ground sloth physiology such as diet, shelter, and body posture will also be included. The total assemblage of variables is expected to determine the most reasonable reconstruction of the life appearance of the largest ground sloths until skin and/or fur samples are eventually discovered. In addition to physiological and ecological constraints on integument, a better understanding of the evolution of metabolic rate across various branches (living and extinct) of the suborder Folivora can also be achieved. It is hypothesized that extinct ground sloths will represent an intermediate state between the metabolic rates of modern xenarthrans and those typical of placental mammals. Thus, smaller ground sloths will have BMR values closer to the extant xenarthran condition, while larger ground sloths will have BMR values closer to those of the typical placental mammal condition.

It is specifically predicted that *Megatherium*, which have estimates of core body temperature values that are not as high as most placental mammals, will be predicted to have an integument consisting of a full body covering of short fur to insulate it in the temperate environments that is believed to inhabit. In contrast, *Eremotherium* will be predicted to have a variable body fur distribution that will be dependent on the various geographic regions that it was known to inhabit. That is, *Eremotherium* will be modeled to have sparse fur coverage in more tropical environments and more dense fur coverage in temperate environments.

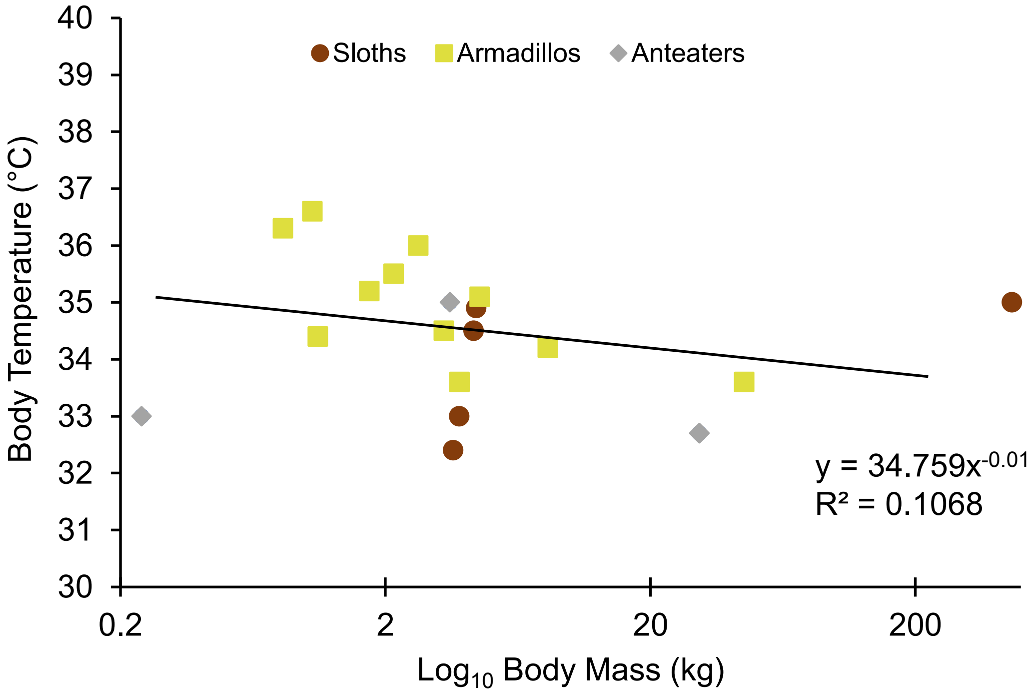
MATERIALS AND METHODS

Proposed Methods

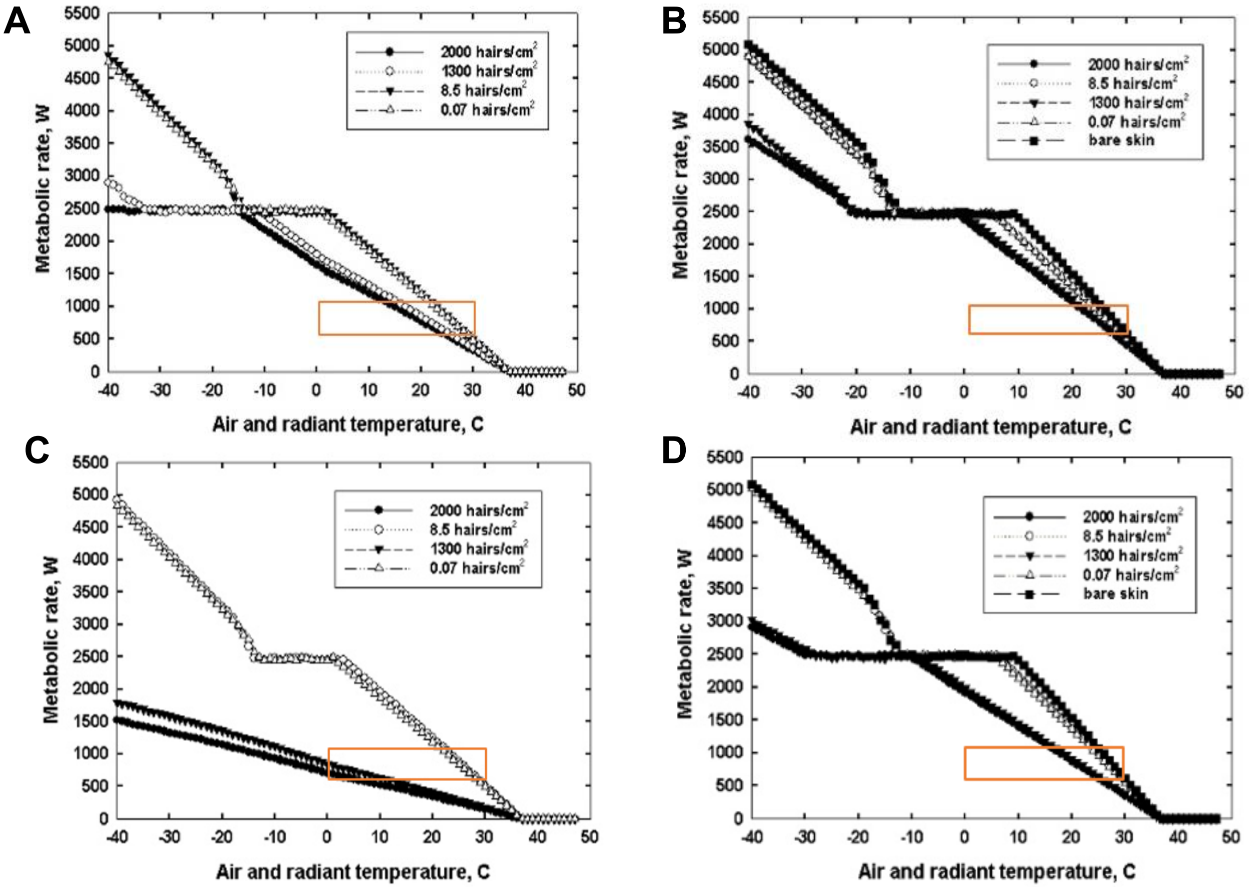
A more direct method of estimating internal body temperature in large ground sloths would include an analysis of C^{13}-O^{18} abundance in fossil bones and teeth as Eagle et. al. (2010) has done for the woolly mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*), and numerous extant species. Eagle et al. (2010) has demonstrated that there is a relationship between the number of C^{13}-O^{18} bonds in the crystal lattice in bioapatite and the body temperature in both extinct and extant taxa that is within one standard error of inorganic calcite. High and low body temperatures (in °C) correlate to low and high abundances of clumped C^{13}-O^{18} bonds respectfully. The primary challenge to overcome in terms of applying this methodology to extinct and extant sloths is the lack of enamel in sloth teeth (e.g. *Bradypus*). This caveat will prove to be rather difficult as the outer dentine layer that covers most xenarthran teeth is not a suitable replacement for enamel as it is prone to diagenetic alteration by minerals during fossilization (MacFadden et. al. 2010). However, recent geochemical analyses suggest the most diagenetically resistant layer (and thus the most reliable sampling spot to get geochemical data from) is the inner orthodentine (Larmon et al. 2019). I plan to sample the inner orthodentine from the teeth of *Megatherium*, *Eremotherium*, *Mylodon*, and *Nothrotheriops* to obtain body temperature values and thus make as little assumptions about their physiology as possible. These samples are to come from fossil specimens collected from localities with exceptional preservation so that diagenetic alteration can be kept to a minimum. Body temperature values obtained from fossil ground sloth teeth will also be compared to body mass and body temperature values for extant xenarthrans and large, terrestrial mammals as reported in the literature. These values will be plotted as a scatterplot and the data points will be logarithmically transformed to avoid data clumping. Preliminary data collected suggests that there is no relationship between body temperature and body mass in extant xenarthrans (see Figure 1).

Once these body temperature values are obtained, I am to utilize Niche Mapper, a software developed by the University of Wisconsin, to model paleoclimates and physiological constraints on the ground sloth taxa of interest. Niche Mapper can utilize 51 different variables for its climate models, and 270 parameters for its biophysiological model as well as predict survivorship based on the availability of resources and thermal constraints. Niche Mapper has had previously been utilized in determining the physiological constraints of the Triassic dinosaurs *Coelophysis* and *Plateosaurus* (Lovelace et al. 2020). The estimated body temperatures will give insight into the amount of metabolic heat (W) that will needed to be produced by providing a target temperature range. BMR will be determined over a broad spectrum of mammalian BMR that will be derived from equations developed by McMahon (1975) and McNab (2008) (also see Lovelace et al. 2020 Table S1). Ambient temperature and paleoclimate data will be obtained from the literature to further test their impact on ground sloth physiological constraints in addition to data on dietary intake. Given that the integument of *Megatherium* and *Eremotherium* is currently unknown, Niche Mapper will be useful in determining the fur density based on numerous other variables in addition to body temperature and ambient temperature data. Data from the largest ground sloth taxa will also reveal the maximum physiological threshold for integumentary structures in xenarthrans as a whole. More precise thermal neutrality data will also be complied for taxa that do preserve fur samples (i.e., *Mylodon* and *Nothrotheriops*) as an outgroup comparison.

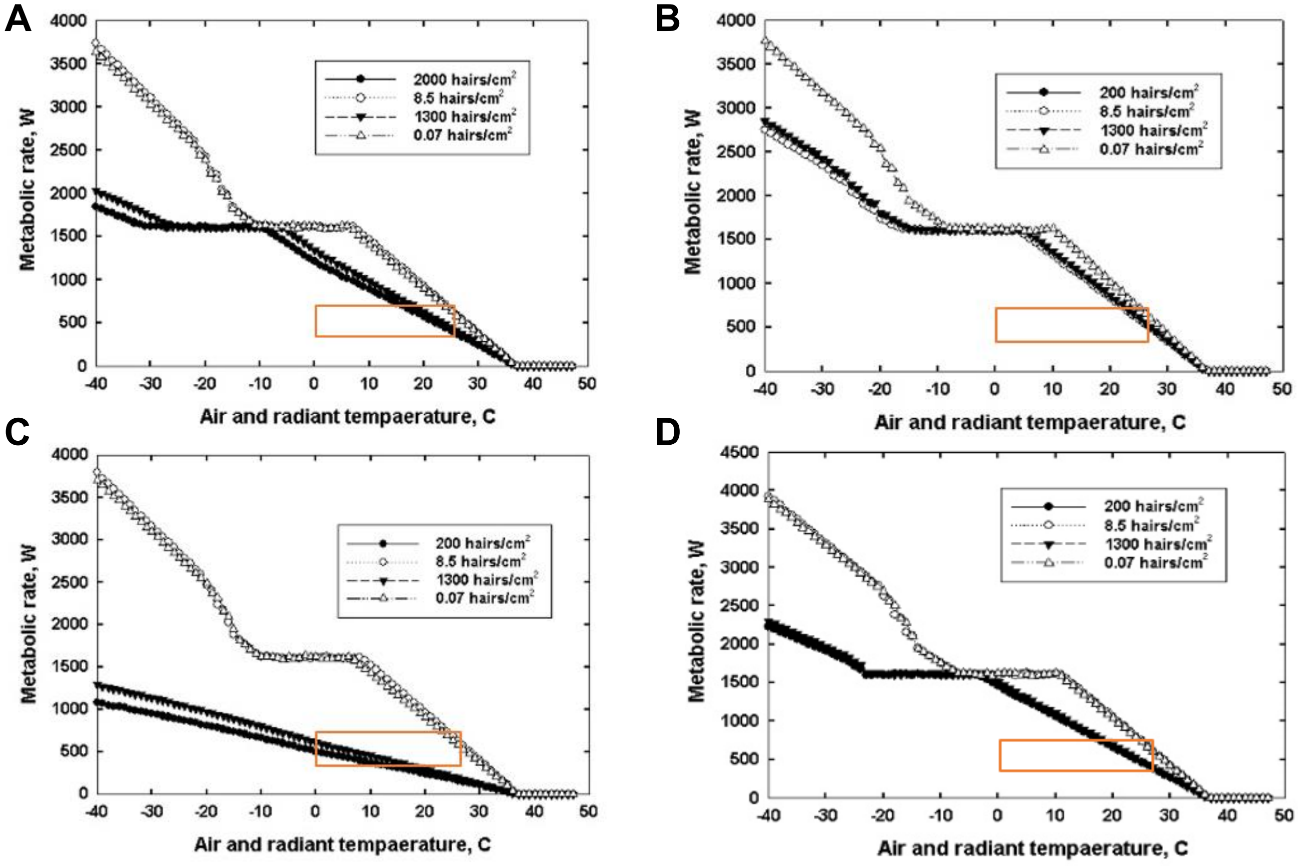
Supplemental Figure 1: Regression of xenarthran body mass against body temperature. The scaling exponent of -0.01 in the equation derived from power equation $y=aM^b$ indicates no relationship between body mass and body temperature in extant xenarthrans. The data are 3 sloth species (*N*=6), 8 armadillo species (*N*=11), and 3 anteater species (*N*=3) and were obtained from the literature (e.g., McNab, 1985; Seitz and Puig, 2018; Cliffe et al., 2018).


Sloths
Armadillos
Anteaters
Body Temperature (°C)
40
39
38
37
36
35
34
33
32
31
30
0.2
2
20
200
Log10 Body Mass (kg)
y = 34.759x-0.01
R² = 0.1068

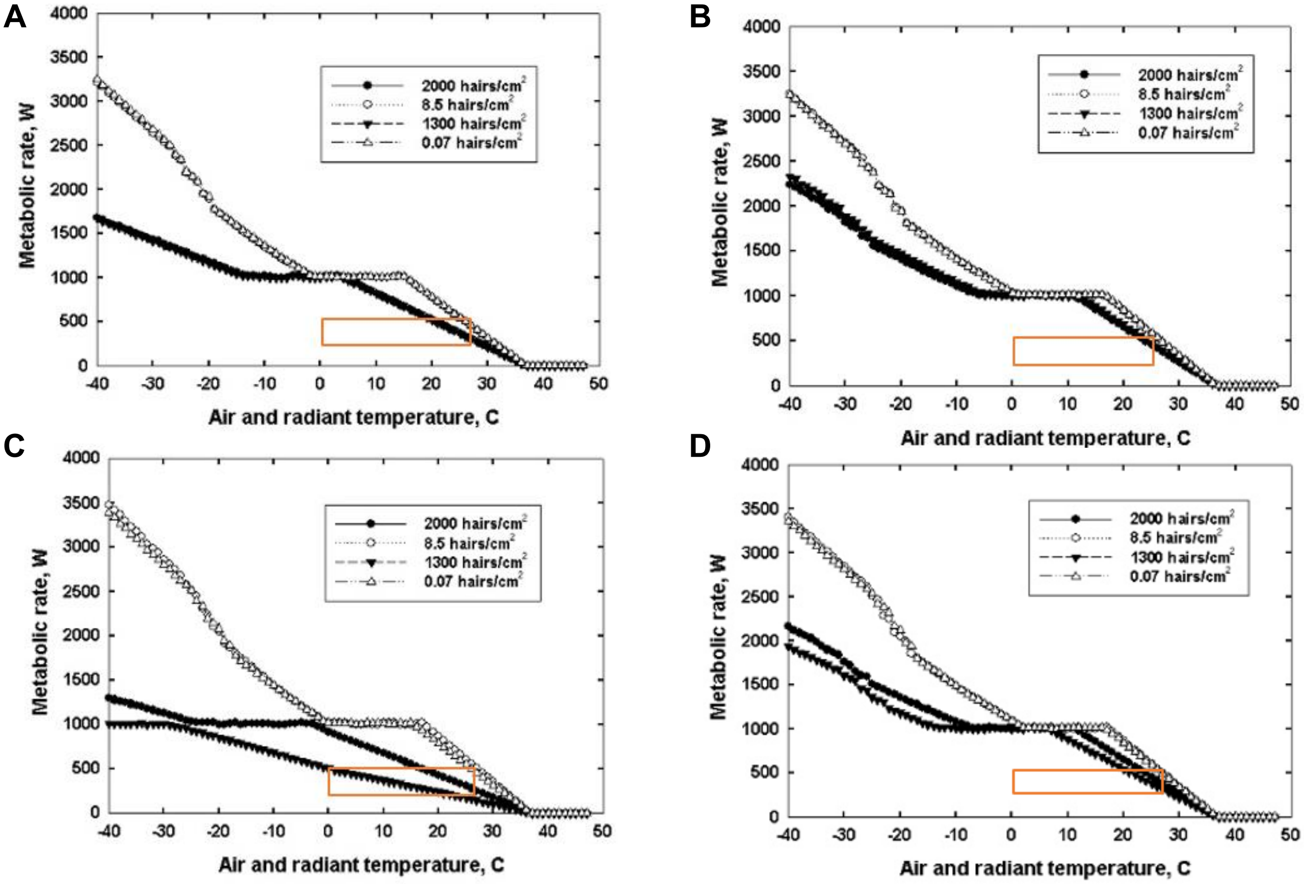
Supplemental Figure 2: Metabolic chamber curves for *Eremotherium*. The range of metabolic activity and ambient temperatures are represented by an orange box. (A) full body, 10 mm fur depths; (B) partial body, 10 mm fur depths and bare skin; (C) full body, 50 mm fur depths; (D) partial body, 50 mm fur depths and bare skin.


A
B
C
D
Metabolic rate, W
Air and radiant temperature, C
0
500
1000
1500
2000
2500
3000
3500
4000
4500
5000
5500
-40
-30
-20
-10
0
10
20
30
40
50
2000 hairs/cm^2
1300 hairs/cm^2
8.5 hairs/cm^2
0.07 hairs/cm^2
bare skin

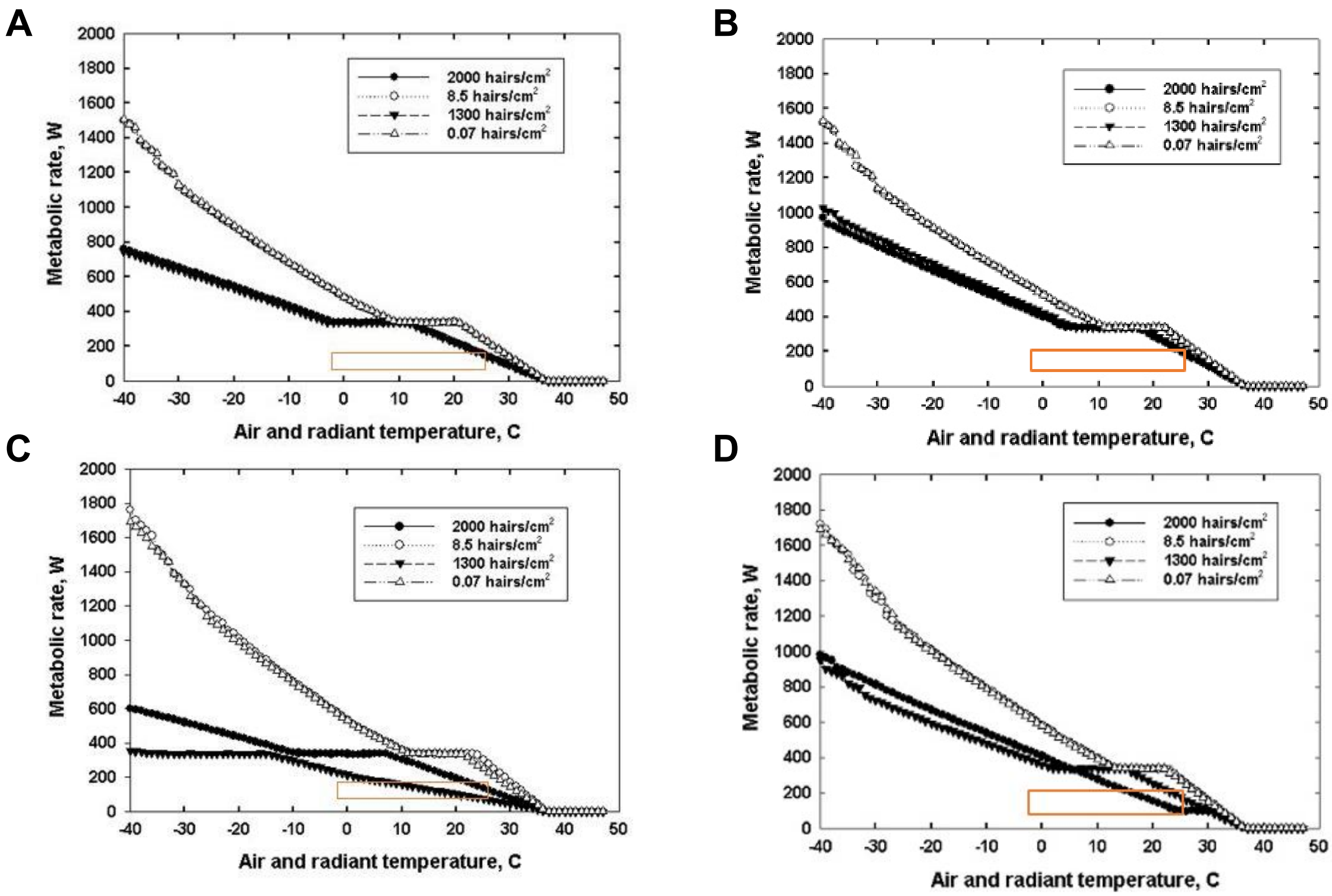
Supplemental Figure 3: Metabolic chamber curves for *Megatherium*. The range of metabolic activity and ambient temperatures are represented by an orange box. (A) full body, 10 mm fur depths; (B) partial body, 10 mm fur depths; (C) full body, 50 mm fur depths; (D) partial body, 50 mm fur depths.


A
B
C
D
2000 hairs/cm^2
200 hairs/cm^2
8.5 hairs/cm^2
1300 hairs/cm^2
0.07 hairs/cm^2
Metabolic rate, W
Air and radiant tempaerature, C
0
500
1000
1500
2000
2500
3000
3500
4000
4500
-40
-30
-20
-10
0
10
20
30
40
50

Supplmental Figure 4: Metabolic chamber curves for *Mylodon*. The range of metabolic activity and ambient temperatures are represented by an orange box. (A) full body, 10 mm fur depths; (B) partial body,10 mm fur depths; (C) full body, 50 mm fur depths; (D) partial body, 50 mm fur depths.


A
B
C
D
Metabolic rate, W
Air and radiant temperature, C
0
500
1000
1500
2000
2500
3000
3500
4000
-40
-30
-20
-10
0
10
20
30
40
50
2000 hairs/cm^2
8.5 hairs/cm^2
1300 hairs/cm^2
0.07 hairs/cm^2

Supplemental Figure 5: Metabolic chamber curves for *Nothrotheriops*. The range of metabolic activity and ambient temperatures are represented by an orange box. (A) full body, 10 mm fur depths; (B) partial body, 10 mm fur depths; (C) full body, 50 mm fur depths; (D) partial body, 50 mm fur depths.


A
B
C
D
Metabolic rate, W
Air and radiant temperature, C
2000 hairs/cm^2
8.5 hairs/cm^2
1300 hairs/cm^2
0.07 hairs/cm^2
0
200
400
600
800
1000
1200
1400
1600
1800
2000
-40
-30
-20
-10
0
10
20
30
40
50