Low-cost thermoregulation of wild sloths revealed by heart rate and temperature loggers

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Abstract: Arboreal herbivores require large digestive tracts for leaf fermentation and detoxification; however, they must also have a low body mass that allows them to reach the foliage. The three-toed sloth, *Bradypus tridactylus*, experiences this trade-off, as leaves comprise 97.2% of its diet. Their calorie intake is extremely low owing to the low available caloric density of leaves and slow digestive processes related to leaf fibre fermentation and secondary compound detoxification. Sloths may require a high body temperature to assist fermentation; however, thermogenesis is energy-consuming. To investigate how sloths accomplish thermoregulation using marginal energy, we attached heart rate (HR) and temperature loggers to wild *B. tridactylus* individuals inhabiting the Amazon rainforest and recorded their HR and body surface temperature (T_{skin}). T_{skin} changed with ambient temperature (T_a) but was higher than T_a in 99.2% of cases. Increases in T_{skin} and HR did not coincide, suggesting that the increases were not caused by thermogenesis. Instead, they may passively increase T_{skin} by selecting warmer microhabitats and sunbathing. Consequently, 90.5% of T_{skin} were within 27.6–36.0 °C while the T_a fluctuated between 21.5–42.9 °C. This low-cost thermoregulation results in a low HR. In this study, the mean HR during observation was approximately 38.4% of the expected value based on the mammalian allometric relationship between body mass and HR. Thus, these properties may contribute to the low metabolic rates of sloths, alleviating their restricted energy intake.

Keywords: thermoregulation; energy saving; body temperature; heart rate; bio-logging; *Bradypus tridactylus*

1. Introduction

Tree leaves are an abundant food resource for animals (Cork and Foley, 1991); however, a relatively small proportion of mammals rely on leaves as their main dietary source (Eisenberg, 1978; McNab, 1978), possibly owing to trade-offs between their digestive capacity and tree-climbing ability. Leaves are characterised by low amounts of available energy and high indigestible fibre content; therefore, herbivorous organisms require a large food intake volume (McNab, 1986). Furthermore, plants are protected by toxic or anti-nutrient compounds, which can cause death or severe physiological impairment in herbivores (Cork and Foley, 1991; Freeland and Janzen, 1974). Consequently, herbivores have developed specialised digestive tracts, which breakdown fibre and detoxify secondary chemical compounds using bacteria (Cork and Foley, 1991; Foley et al., 1995; Heymann et al., 2011; Queiroz, 1995). In the case of sloths and other foregut-fermenting arboreal herbivores, their forestomach provides a site for fermentation and detoxification (Cork and Foley, 1991; Foley et al., 1995). The digestive capacity of herbivores is limited by their digestive tract, which is almost directly proportional to their body mass (Parra, 1978); therefore, herbivorous mammals tend to be larger and heavier than non-herbivorous mammals (Burness et al., 2001; Clutton-Brock and Harvey, 1977). However, arboreal animals do not have large body sizes owing to their ecology and the weight-bearing properties of trees (Cork and Foley, 1991; Eisenberg, 1978; Pauli et al., 2016). Moreover, smaller animals tend to require higher energy intake per mass unit (Hildwein and Goffart, 1975; Kleiber, 1932). Consequently, arboreal herbivores are uncommon — approximately 4% of all mammalian genera include arboreal herbivorous species (Eisenberg, 1978).

As arboreal herbivores, three-toed sloths (*Bradypus* spp.) depend heavily on foliage; approximately 94.4–100% of their diet is composed of tree or liana leaves

(Chiarello, 1998; Queiroz, 1995; Taube et al., 2001; Carmo, 2002; Urbani and Bosque, 2007). In *B. tridactylus*, leaves comprise 97.2% of their diet (Carmo, 2002). Their calorie intake is low owing to the low available caloric density of leaves and the slow digestive processes related to the bacterial breakdown of structural carbohydrates and the detoxification of secondary compounds in leaves (Foley et al., 1995). Therefore, sloths may need to increase their body temperature to facilitate fermentation by foregut microbes (Cliffe et al., 2015; King et al., 2011). However, thermogenesis is energy consuming (Cannon and Nedergaard, 2011; Tattersall et al., 2016) and relying on thermogenesis to increase body temperature may not be feasible for sloths. Altogether, three-toed sloths face a serious trade-off between body temperature and energy requirements; if they do not increase their body temperature, they cannot sufficiently digest their food to acquire necessary energy.

The body temperature of three-toed sloths changes with ambient temperature (T_a). Montgomery and Sunquist (1978) investigated the rectum temperature of five free-ranging *B. variegatus* at 30 min intervals for 1 to 4 days in Panama, and showed that their rectum temperature varies between 29.4 °C (when T_a = 22.5 °C) and 37.8 °C (T_a = 31.9 °C), reaching a maximum at midday and a minimum between midnight and dawn. Pauli et al. (2016) investigated the body surface temperature (T_{skin}) of six *B. variegatus* at 1 h intervals for five days in agroecosystem of Costa Rica by affixing temperature loggers under the fur on the dorsum of each individual, and showed that the mean T_{skin} is 32.7 ± 0.15 [± standard deviation (SD)] °C within a range of 30.7–34.8 °C. Pauli et al. (2016) conclude that the T_{skin} measured by external attachment of loggers is comparable with the rectum temperature measured by Montgomery and Sunquist (1978); however, momentary T_{skin} may be higher during sunbathing and lower during raining than the rectum temperature. Measuring T_{skin} is easier than measuring the rectum or core body temperature under field conditions, and it is especially important when non-invasive methods are required.

In addition to T_a, radiation heat (from heat lamps or sunlight) may play an important role in increasing body temperature and conserving energy for thermoregulation (Geiser and Drury, 2003). In addition, *B. variegatus* tend to use trees with crowns exposed to sunlight, and maximum body temperatures are lower on days when it rains and is cloudy (Montgomery and Sunquist, 1978). During sunny periods, they frequently expose ventral body parts to solar radiation, which should increase their body temperature as well as enhance the action of symbiotic bacteria involved in the breaking down of fibre in the gut (Urbani and Bosque, 2007). Similarly, sunbathing behaviour is frequently observed in *B. tridactylus* in our study site.

To estimate the metabolic rate of wild animals under field conditions, using heart rate (HR) is an easy and non-invasive way. Since HR is correlated with oxygen consumption and hence the metabolic rate (Green, 2011), we can predict the relative metabolic rate of animals using HR loggers (Butler et al., 2004). Recently, HR loggers comprise optical sensors that measure the blood flow rate under the skin and estimate the HR without inserting electrodes into the animal bodies (Chu et al., 2016; Tamura et al., 2014). Therefore, using a temperature logger and an optical HR logger together, we can monitor the T_{skin} and HR of free-ranging wild animals without surgeries for implanting loggers or inserting electrodes.

Here, we applied the bio-logging approach to monitor HR and T_{skin} of wild pale-throated sloths (*B. tridactylus*) living in the Amazon rainforest. We attached temperature and HR loggers to the sloths to investigate thermoregulatory mechanisms with limited energy intake. We hypothesised that if they passively increase their body temperature, their T_{skin} would increase with T_a. Moreover, their T_{skin} would increase more rapidly than T_a if they utilise solar radiation to increase their body temperature. In both cases, the increases in T_{skin} would not coincide with increases in HR if they do not depend on thermogenesis to increase body temperature.

2. Material and methods

2.1. Study site

Fieldwork was conducted in an approximately 776 ha forest fragment around the Federal University of Amazonas, Brazil (03°04′34″ S, 59°57′30″ W) from July 2017 to June 2020. The density of our study species, the wild three-toed sloth (*B. tridactylus*), is approximately 2.2 individuals/ha in the study site (Carmo, 2002). The area is extensive and the vegetation is diverse for the study species to exhibit its natural behaviour.

2.2. Device preparation

(1) HR logger: Optical HR loggers were constructed using parts of the Fitbit Charge HR (Fitbit, San Francisco, CA, USA). The battery life was approximately 5 d. Each printed circuit board was coated with anti-humidity coating liquid (goot BS-C20B; Taiyo Electric Ind. Co., Ltd., Hiroshima, Japan), and the logger was waterproofed using a heat-shrink tube. The heat-shrink tube around the optical sensor and battery charging connector was removed, and the interface was adhered with cyanoacrylate adhesive to prevent water intrusion. The data from the HR logger were recorded every 5 min by averaging the data between 30 s before and after each 5 min interval.

(2) Temperature logger: Temperature loggers (Thermochron S1922L; KN Laboratories, Inc., Osaka, Japan) were used to record T_{skin} and T_a to an accuracy of 0.1 °C at intervals of 5 min. This device could record 4096 data points (i.e. for approximately 2 weeks). Each logger was coated with goot BS-C20B anti-humidity coating liquid.

(3) Very-high-frequency (VHF) transmitter and receiver: VHF transmitters (Holohil RI-2D; Ottawa, Canada), a VHF receiver (R410; Advanced Telemetry Systems, Isanti, MN, USA), and an antenna (Three Elements Folding Yagi; Advanced Telemetry Systems), which had a range of 164.000 to 165.999 MHz, were prepared.

(4) Harnesses and collars: Each time a sloth was captured, it was fitted with a custom-made collar and harness with 10 mm-wide webbings and plastic snapping buckles sewn together with cotton or nylon threads. HR and temperature loggers were attached to the collars with heat-shrink tubes (Fig. 1a). A VHF transmitter (Holohil RI-2D) and a global positioning system (GPS) logger (GiPSy-5 [TechnoSmArt, Rome, Italy] with a Saft LS17500 thionyl battery [Saft Groupe SAS, Levallois-Perret, France]; attached for separate studies) were attached to the harness with heat-shrink tubes (Fig. 1b). The mass of the collar (approximately 18 g) and harness (approximately 65 g) did not exceed 5% of the mass of each animal. GPS loggers or VHF transmitters were not attached to infants to avoid excess mass; instead, the signal from the VHF transmitter attached to the mother was used to locate them.

2.3. Animal capturing and device attachment

The study site was searched for *B. tridactylus*, and the search operation was sometimes conducted using the information provided by the local security staff. After a sloth was found, one of the authors or a field assistant climbed the tree using rock-climbing tools and captured the animal by hand. Individual sloths could be easily captured because they rarely tried to escape or exhibit aggressive behaviour. The captured sloths were placed in a thin nylon bag, lowered to the forest floor by rope, and brought to the laboratory at the study site. The body mass of each sloth was measured to the nearest 5 g using a digital scale. The sloths were sexed based on the presence of an orange spot (‘speculum’) on their backs, which is a male-specific secondary sexual trait (Hayssen, 2009). For young individuals that were difficult to sex (<1.5 kg), the sex was marked as ‘unknown’.

In the laboratory, the VHF transmitter and the HR, temperature, and GPS loggers were set up and attached to each individual using a collar and harness. Harnesses and collars were made of 10 mm-wide, 1.3 mm-thin polypropylene webbing, which was wide and soft to prevent damage to the animals. The HR logger was located on the dorsal surface of the neck at the flat part beside the vertebra, and the temperature logger was located on the ventral surface of the neck at the dimple beside the trachea. Prior to the experiment, the neck collar, HR logger, and temperature logger were tested on a human for 1 month to check for damage to the skin. Each time the animals were captured or observed, their condition, especially relating to the skin near the webbings and the optical sensor of the HR logger, was checked. The fur around the optical sensor of the HR logger (approximately 15 × 20 mm) was cut using a beard trimmer to expose the skin, and the HR logger and the hair of the sloths were bound with cotton strings to prevent misalignment. The hair around the neck was combed and tied to cover the collar and help obtain accurate T_{skin} measurements.

The captured sloths were released into the same trees from which they were found. Temperature loggers were also attached to the tree trunks at approximately 130 cm above the forest floor to record T_a at 5 min intervals. The time between the capture and release of each animal generally required 3–5 h. After more than one week, the same animals were located using the signal from the VHF transmitter. Whenever possible, the sloths were recaptured, and data were extracted from the data loggers.

2.4. Data compiling and statistical analysis

Obtained data were compiled on a sample basis: each sample (a single set of continuous data obtained from one successful release and recapture) contained the sample ID, individual ID, sex, body mass, HR data (approximately 5 d owing to the battery life of the HR logger), and T_a and T_{skin} data (up to 2 weeks owing to the memory limit of the temperature loggers); however, some data were missing owing to mechanical issues with the loggers. In some cases, more than two samples were taken from a single individual (see https://doi.org/10.17632/jy3ghfm37h.3 for details). The data from the first 5 h after releasing the sloths were discarded to eliminate the effects of handling on HR and T_{skin}. The trends in HR, T_{skin}, and T_a were compared individually, and the mean hourly HR for the day was calculated for each sample.

To analyse the relationship between Ta and Tskin, six models were established: (1) null linear model, (2) linear model, (3) null linear mixed-effects model, (4) linear mixed-effects model, (5) Gompertz least squares model, and (6) Gompertz mixed-effects model. These statistical analyses were conducted using R statistical software version 4.1.0 (R Core Team, 2021). Linear models were calculated with the ‘glm’ function in the ‘stats’ package, linear mixed-effects models were calculated with the ‘lmer’ function in the ‘lme4’ package (Bates et al., 2015), Gompertz least squares model was calculated with the ‘nls’ function in the ‘stats’ package, and Gompertz mixed-effects model was calculated with the ‘nlme’ function in the ‘nlme’ package (Pinheiro et al., 2021). T_{skin} was fitted as the response variable, T_a was fitted as an explanatory variable, and individual ID was fitted as a random factor. The Akaike information criterion (AIC; Akaike, 1974) values of each model was calculated, and the model with the smallest AIC values was selected as the best model.

To analyse the relationship between T_a and HR, four models were established: (1) null linear model, (2) linear model, (3) null linear mixed-effects model, and (4) linear mixed-effects model. Linear models were calculated with the ‘glm’ function in the ‘stats’ package, and linear mixed-effects models were calculated with the ‘lmer’ function in the ‘lme4’ package (Bates et al., 2015). HR was fitted as the response variable, T_a was fitted as an explanatory variable, and individual ID was fitted as a random factor. The pseudo-coefficients of determination for the linear mixed-effects models were calculated using the ‘MuMIn’ package (Bartoń, 2020). The AIC values of each model were calculated, and the model with the smallest AIC values was selected as the best model.

Previously obtained data on mammals (Noujaim et al., 2004) were collected to analyse the relationship between body mass and HR; the body mass and HR of sloths obtained in the present study were compared with that of other mammals as reported by Noujaim et al. (2004). The regression line on a double-logarithmic graph was calculated, and data for *B. tridactylus* and other mammals were compared.

3. Results

We collected 68 sets of T_{skin} and HR data samples from 27 individuals. Some loggers did not record the data owing to mechanical issues; therefore, the number of complete datasets was different for each analysis. The mean body mass of the *B. tridactylus* was 3.1 ± 1.2 kg (mean ± SD; range: 0.7–4.5 kg; $N = 26$).

3.1. Time series of HR, T_{skin}, and T_a

The HR of some individuals followed a rhythmic pattern (Fig. 2a); however, this periodicity was not apparent in other individuals (Fig. 2b). T_{skin} changed with T_a, and T_{skin} tended to be higher than T_a. However, when T_a was extremely high, T_{skin} was lower than T_a (Fig. 2b; 3 and 4 September). At times, T_{skin} rapidly increased without any apparent increase in HR or T_a (indicated by black arrows in Fig. 2). Sudden declines in T_a and T_{skin} (indicated by white arrows in Fig. 2) may have been the result of rainfall incidents.

3.2. Daily HR trends

In total, 49 sets of HR samples were collected from 34 individuals. No apparent circadian rhythm was observed in the HR trend, but the mean HR tended to be low around 0600 hours and high around 1900 hours (Fig. 3).

3.3. Relationship between T_a and T_{skin}

Within the six models established to analyse the relationship between T_a and T_{skin}, Gompertz mixed-effect model was selected as the best model (Table 1). The slope of the approximate curve relating T_a to T_{skin} was steep when T_a was low, but became more gradual as T_a increased [$Y = 37.680 \times \exp(-12.902 \times 0.848^X)$; Table 1, 2; Fig. 4]. The approximate curves for males [$Y = 37.986 \times \exp(-15.595 \times 0.844^X)$] and females [$Y = 37.822 \times \exp(-9.783 \times 0.858^X)$] were similar. In general, T_{skin} was higher than T_a, but T_{skin} tended to be lower than T_a when T_a exceeded 36 °C. Specifically, T_{skin} was higher than T_a in 99.2% of cases (184,478/186,005) but only in 26.8% of cases (193/720) when T_a exceeded 36 °C. The interquartile range of T_{skin} was 30.1–33.7 °C, and 90.5% (168,412/186,005) of the data points were within a range of 27.6–36.0 °C. In some cases, T_{skin} reached 45–60 °C even though the concurrent T_a was 26–34 °C.

3.4. Relationship between T_a and HR

Within the four models established to analyse the relationship between T_a and HR, a linear mixed-effect model was selected as the best model (Table 3). There was a gradual positive correlation between T_a and HR, but the relationship was unclear, and the pseudo-coefficient of determination was small ($Y = 0.383X + 60.282$, pseudo-$R^2 = 0.004$; Table 4, Fig. 5).

3.5. Relationship between HR and body mass

Noujaim et al. (2004) indicated a clear double-logarithmic relationship between body mass and HR in mammals ($Y = 919.48X^{-0.203}$; Fig. 6). The mean body mass and mean HR of sloths were 3.1 ± 1.1 kg (mean ± SD; range: 0.9–4.5 kg) and 70.0 ± 6.6 bpm (mean ± SD; range: 58.3–83.3 bpm), respectively. Thus, their HR was 38.4% (30.6–45.8%) of the expected value calculated based on their body mass (Fig. 6).

4. Discussion

The results showed that the T_{skin} of *Bradypus tridactylus* changed with T_a; however, T_{skin} tended to be higher than T_a (Fig. 2). Similar trends have been reported in two other sloth species, *B. variegatus* and *Choloepus hoffmanni* (Pauli et al., 2016). The increase in T_{skin} did not coincide with an increase in HR in this study (Fig. 2); therefore, it is unlikely that *B. tridactylus* increased their T_{skin} by heat production. Instead, they presumably preferred to inhabit warm microhabitats and bask in the sun, as the rapid increase in T_{skin} during daytime (Fig. 2) and the instances of extremely high T_{skin} that greatly exceeded T_a (Fig. 4) suggest sunbathing behaviour. Basking behaviour (extending the forearms and hindlegs and turning the ventral surface toward the sun; see Urbani and Bosque, 2007) was often observed during the daytime, further suggesting that sloths sunbathe to increase T_{skin}. Here, the temperature loggers measuring T_{skin} were located on the ventral surface of the neck where *B. tridactylus* faces the sun during sunbathing. Consequently, direct sunlight increased T_{skin} and the logger, and the loggers occasionally recorded extremely high temperatures up to 59.4 °C (Fig. 4). Increases of T_{skin} by sunbathing may contribute to increase the core body temperature (Geiser and Drury, 2003), which should enhance the fermentation in their forestomach (Urbani and Bosque, 2007). In addition to sunbathing, sloths may move between sunny and shaded areas as their body temperature changes (Montgomery and Sunquist, 1978). These results indicate that sloths are able to manage their body temperature within a narrow range without utilising their energy stores.

Pauli et al. (2016) showed that the range of T_{skin} was 30.7–34.8 °C in *B. variegatus*. This range is much narrower than our findings (22.8–59.4 °C). These differences might be caused by species or environmental differences, however, we believe they are more likely owing to the differences in research methods. First, Pauli et al. (2016) attached temperature loggers to the dorsum of each individual. Since *B. variegatus* individuals face the ventral surface toward the sun during sunbathing (Urbani and Bosque, 2007), as in *B. tridactylus*, temperature loggers attached on the dorsum are not exposed to solar radiation during sunbathing and thus less likely to record high temperature. Second, Pauli et al. (2016) investigated the T_{skin} of six individuals at 1 h intervals for five days (≤720 data points) while we recorded T_{skin} at 5 min intervals for 14 days and obtained 186,005 data points from 19 individuals. Therefore, it would be less likely for Pauli et al. (2016) to record the momentary high T_{skin}. Presumably, sloths change their posture if their T_{skin} reaches high enough during sunbathing; therefore, extremely high T_{skin} are less likely to be recorded at 1 h intervals.

The trend of T_{skin} clearly followed that of T_a; however, the HR trends were relatively unclear, and no apparent sleeping periods were indicated by solid blocks of low HR (Fig. 2). Rapid increases in HR for short periods may indicate locomotion; however, such trends occurred infrequently and were observed irrespective of time (Fig. 2). Although the mean HR tended to be lower at around 0600 hours and higher at around 1900 hours, the overall trend was unclear (Fig. 3); therefore, we could not conclude whether this species is diurnal, nocturnal, or crepuscular. In our 24 h observations at 10 min intervals on *B. tridactylus*, three out of eight individuals showed both diurnal and nocturnal activities (moving or feeding) (Leandro Vieira Vidal, Daisuke Muramatsu, Tsuneaki Yabe, and Marcelo Gordo, unpublished data). These activity patterns may reflect their 'cathemeral' habits [i.e. polyphasic activity patterns that are roughly evenly distributed throughout the 24 h cycle (Curtis and Rasmussen, 2006; Tattersall, 2006)]; however, further investigations are necessary to prove whether they are indeed cathemeral. *Bradypus variegatus* also shows diurnal and nocturnal activities (Castro-Sa et al., 2021), with an observed reduction in activity at approximately 0600 hours (Sunquist and Montgomery, 1973). These results contrast with those observed in the two-toed sloth *C. hoffmanni*, which is nocturnal (Gilmore et al., 2001; Montgomery and Sunquist, 1978; Sunquist and Montgomery, 1973).

T_a and HR show a weak positive correlation (Fig. 5), which is commonly observed in ectotherms (Bartholomew and Tucker, 1964; Hiebert and Noveral, 2007) but rarely seen in mammals. However, the relationship between T_a and HR was unclear, and the pseudo-coefficient of determination was low (pseudo-$R^2 = 0.004$). Moreover, the AIC value was only slightly smaller than that of the null linear mixed-effects model (Table 3). Therefore, we could not conclude that a positive relationship between T_a and HR was characteristic of this species. Considering that no apparent increase in HR was observed at high or low T_a (Fig. 5), *B. tridactylus* did not seem to suffer from temperature stress within the observed T_a range (21.5–42.9 °C).

The HR of sloths under laboratory conditions has been reported in other studies. The HRs of *B. tridactylus* under minimally restrained and unrestrained conditions are 83.6 and 78.1 bpm (body mass: 2.3–4.7kg, $N = 13$), respectively (Duarte et al., 1982). The HRs of free-ranging and habitually positioned *B. variegatus* are 73.0 ± 6.5 bpm [24 h mean ± SE, body mass: 4.4 ± 0.2 kg, $N = 6$ (Duarte et al., 2003)] and 81.0 ± 4.4 bpm [mean ± SE, body mass: 3.9 ± 0.1 kg, $N = 17$ (Silva et al., 2005)], respectively. These previously reported values of the HRs of individual sloths were higher than those found in this study under wild conditions (70.0 ± 1.5 bpm; range: 58.3–83.3); however, these results are not directly comparable because our data included active, resting, and sleeping HRs, whereas those of previous studies did not. The 1-h mean HR of each sample sometimes decreased below 50 bpm (Fig. 3), possibly indicating sleeping HR, which may have caused the low mean HR observed under wild conditions. It is also possible that the HR under laboratory conditions was higher than that under natural conditions owing to the effects of handling and/or artificial circumstances. Even under the same T_a conditions, animals in laboratory conditions without access to radiation heat (including sunbathing) may require higher amounts of energy to increase body temperature (Geiser and Drury, 2003).

The low metabolic rate of sloths has been reported in several studies (Gilmore et al., 2001; McNab, 1978; Pauli et al., 2014, 2016; Vendl et al., 2016). As HR is closely correlated with metabolic rate regarding oxygen consumption (Bartholomew and Tucker, 1964; Currie et al., 2014; Green, 2011; Tattersall et al., 2016), the low HR of *B. tridactylus* observed in this study may reflect its low metabolic rate. The HR of *B. tridactylus* is much lower than that of other mammals; that is, it is approximately one-third of the expected value calculated based on their body mass (Fig. 6). This may be due to passive thermoregulation, as endothermy is energetically expensive (Geiser, 2004; Nagy, 2005; Pauli et al., 2016).

5. Conclusions

Although the T_{skin} of *B. tridactylus* changed with T_a, over 90% of T_{skin} remained within a temperature range of 27.6–36.0 °C while the T_a ranged between 21.5–42.9 °C. Additionally, T_{skin} was higher than T_a in 99.2% of cases. These traits may contribute to successful fermentation, which aids in the bacterial breakdown of structural carbohydrates and the detoxification of secondary compounds in the leaf-heavy diet of sloths. Moreover, the increase in T_{skin} did not correspond with an increase in HR, suggesting that *B. tridactylus* does not rely on thermogenesis to increase T_{skin}. Instead, they may passively increase T_{skin} by selecting warmer microhabitats and sunbathing. Therefore, *B. tridactylus* can maintain a high T_{skin} without expending their own energy. Consequently, their energy expenditure is lower than that of other mammals, as shown by their low HRs.

Data availability

The data and R code used in the present study are available at https://doi.org/10.17632/jy3ghfm37h.3.

Compliance with ethical standards

Marking and capturing sloths were authorised by the Biodiversity Authorization and Information System (SISBIO-60116-1) and the Ethics Committee of the Federal University of Amazonas (006/2018-CEUA/UFAM).

Author contributions

Daisuke Muramatsu: Conceptualization, Investigation, Methodology, Formal analysis, Visualization, Writing - Original Draft, Writing - Review and Editing. **Leandro Vieira Vidal:** Investigation, Methodology. **Edson Rodrigues Costa:** Investigation. **Ken Yoda:** Writing - Review and Editing. **Tsuneaki Yabe:** Supervision, Project administration. **Marcelo Gordo**: Supervision, Project administration, Writing - Review and Editing.

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Declaration of competing interest

The authors declare that they have no conflicts of interest.

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Table 1: Comparison of six models established to analyse the relationship between ambient temperature (T_a) and body surface temperature (T_{skin}). Models were sorted by the Akaike information criterion (AIC) values ranked in increasing order. X and Y in the estimated models indicate T_a and T_{skin}, respectively.

AIC	Model description	Estimated model
701474.6	Gompertz mixed-effects model	$Y = 37.680 \times \exp(-12.902 \times 0.848X)$
718161.4	Linear mixed-effects model	$Y = 0.715X + 12.712$
728692.3	Gompertz least squares model	$Y = 38.152 \times \exp(-8.474 \times 0.864X)$
739534.0	Linear model	$Y = 0.693X + 13.289$
876898.8	Null linear mixed-effects model	$Y = 32.102$
888371.0	Null linear model	$Y = 31.956$

Table 2: Maximum-likelihood estimates and their standard errors (SEs) for the best model calculated using nonlinear mixed-effects models explaining the relationship between ambient temperature (T_a) and body surface temperature (T_{skin}). The variance and residual variance estimated for random effect were 3.046 and 2.541, respectively.

Model term	Estimate	SE
Asym	37.680	0.039
b2	12.902	0.516
b3	0.848	0.001

Table 3: Comparison of four models established to analyse the relationship between ambient temperature (T_a) and heart rate (HR). Models were sorted by the Akaike information criterion (AIC) values ranked in increasing order. X and Y in the estimated models indicate T_a and HR, respectively.

AIC	Model description	Estimated model
462992.5	Linear mixed-effects model	$Y = 0.383X + 60.282$
463247.3	Null linear mixed-effects model	$Y = 70.545$
470868.7	Linear model	$Y = 0.238X + 62.701$
470964.4	Null linear model	$Y = 69.091$

Table. 4: Maximum-likelihood estimates and their standard errors (SEs) for the best model calculated using linear mixed-effects models explaining the relationship between ambient temperature (T_a) and heart rate (HR). The variance and residual variance estimated for random effect were 46.88 and 226.71, respectively.

Model term	Estimate	SE
Intercept	60.282	1.662
T_a	0.383	0.024

Fig. 1: Attached devices. Heart rate and temperature loggers were attached to the collar with heat-shrink tubes (a), and a very-high-frequency (VHF) transmitter and global positioning system (GPS) logger were attached to the harness (b).

Fig. 2: Example time series of heart rate, body surface temperature, and ambient temperature of one male (a) and one female (b). Black arrows indicate the breaks in the relationship between ambient and body surface temperatures. White arrows indicate concurrent decreases in ambient and body surface temperatures.

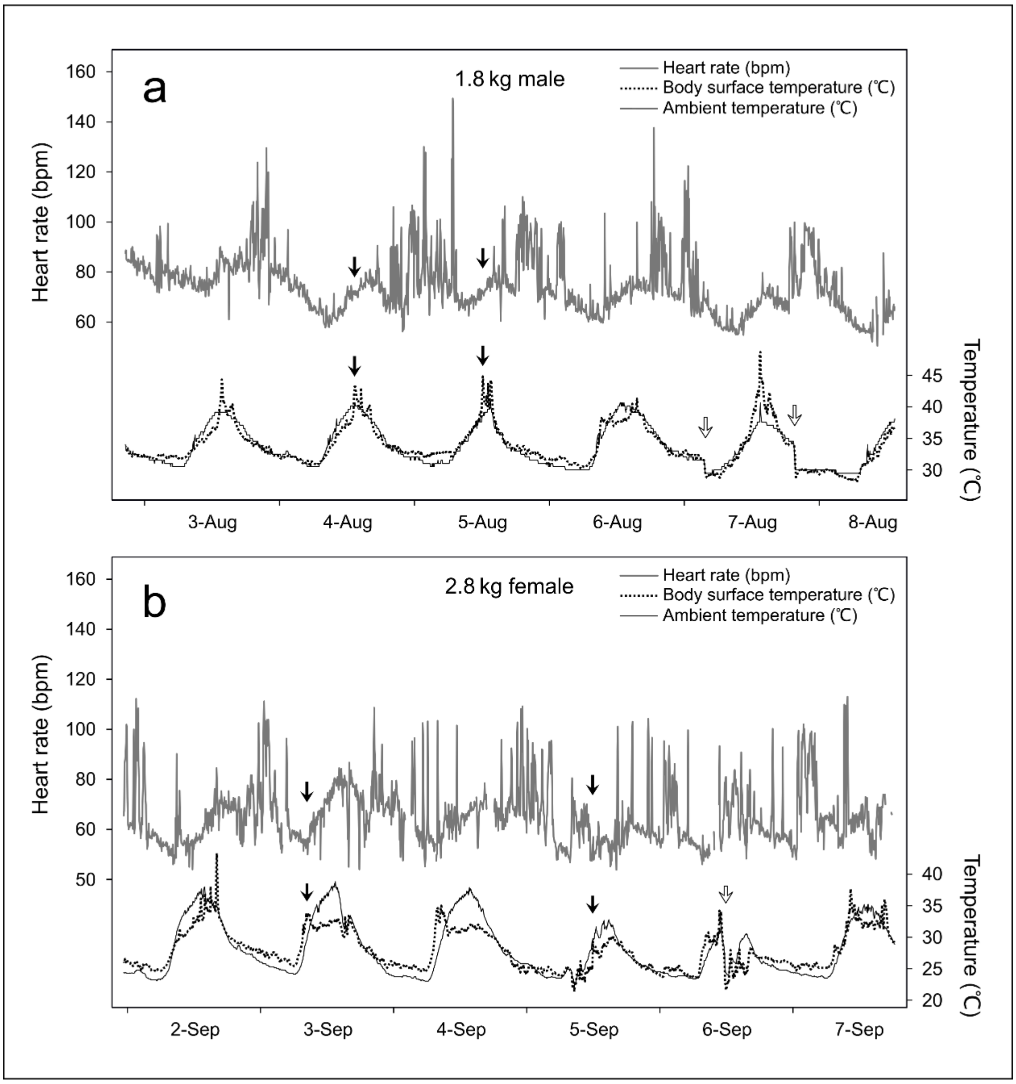

Fig. 3: Daily heart rate trend. Thin grey lines indicate the mean heart rate of each sample throughout the day. The thick black line indicates the mean heart rate of all samples, and the shaded area indicates 95% confidence interval.

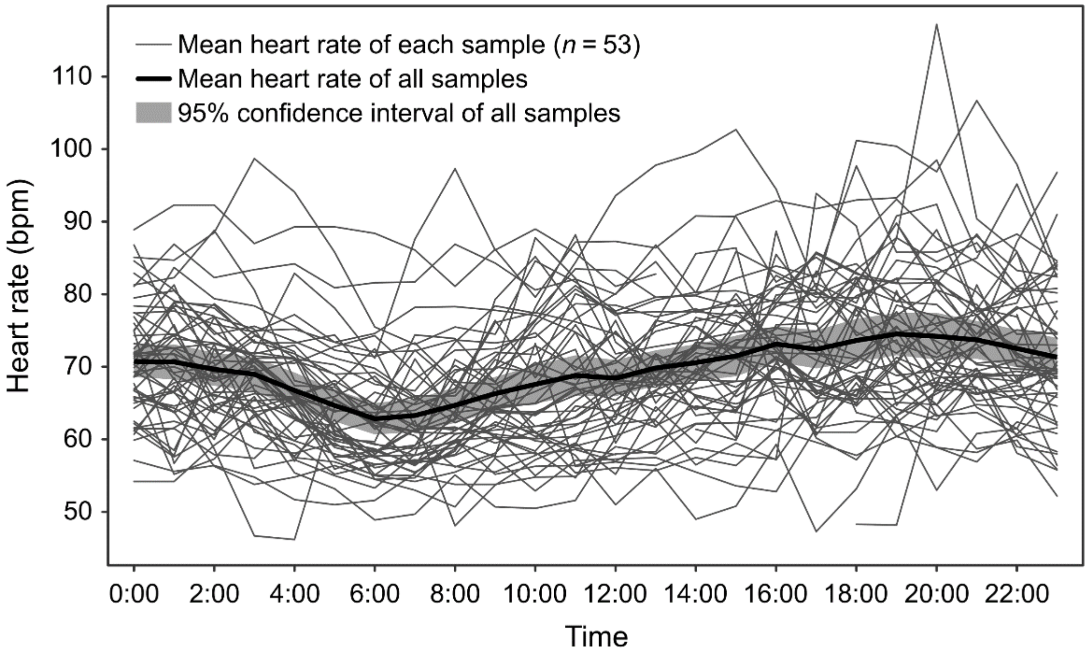

Fig. 4: Relationship between ambient and body surface temperatures. Each data point is plotted in a transparent colour; darker areas represent high density of points. The dashed grey line indicates equality between ambient and body surface temperatures; therefore, points above the line indicate that the body surface temperature is higher than the ambient temperature. The curved grey line indicates the approximate Gompertz curve calculated using the nonlinear mixed-effects model.

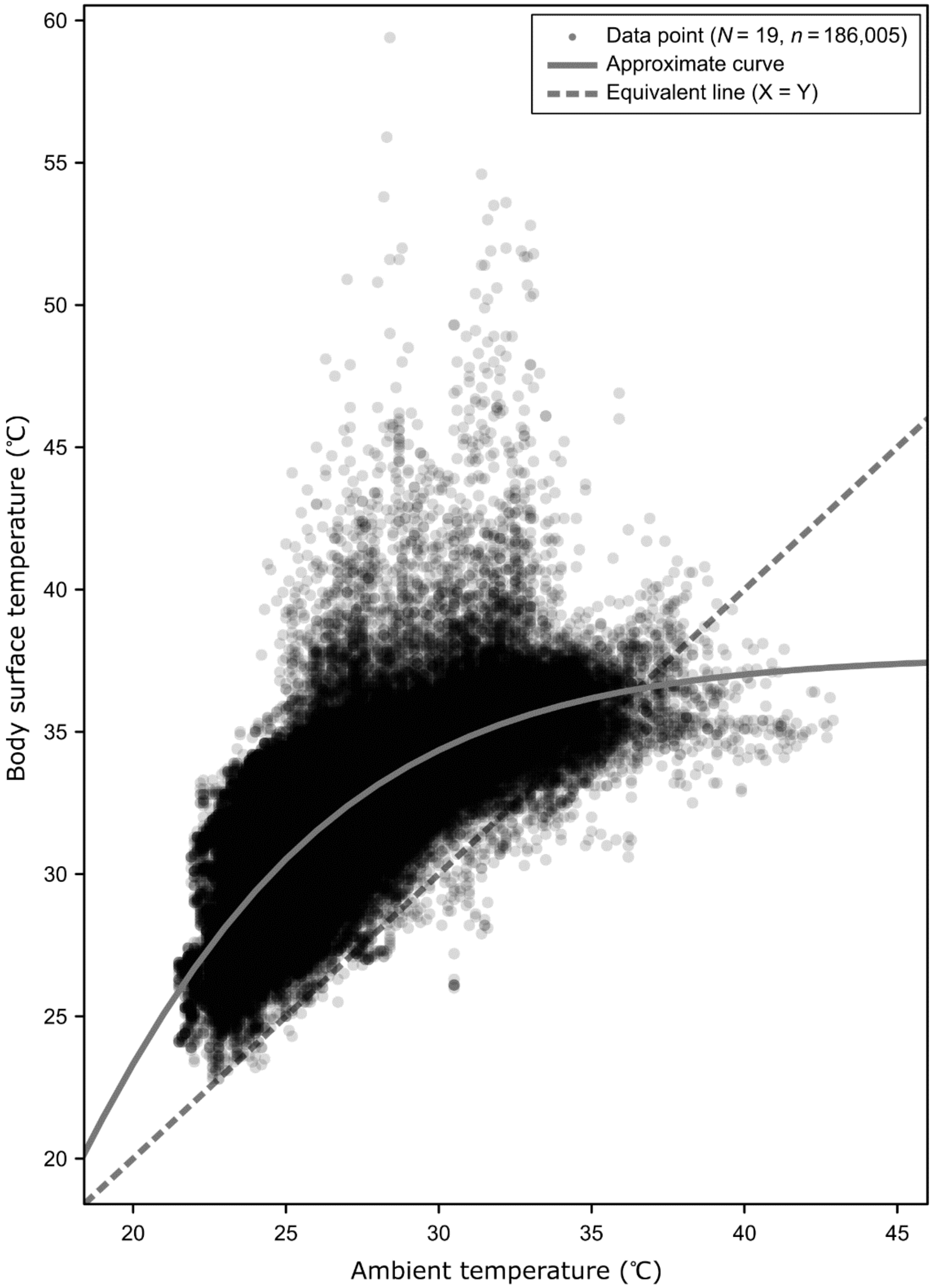

Fig. 5: Relationship between ambient temperature and heart rate. Each data point is plotted in a transparent colour; darker areas represent higher density of points. The grey line indicates the regression line calculated by the linear mixed-effects model.

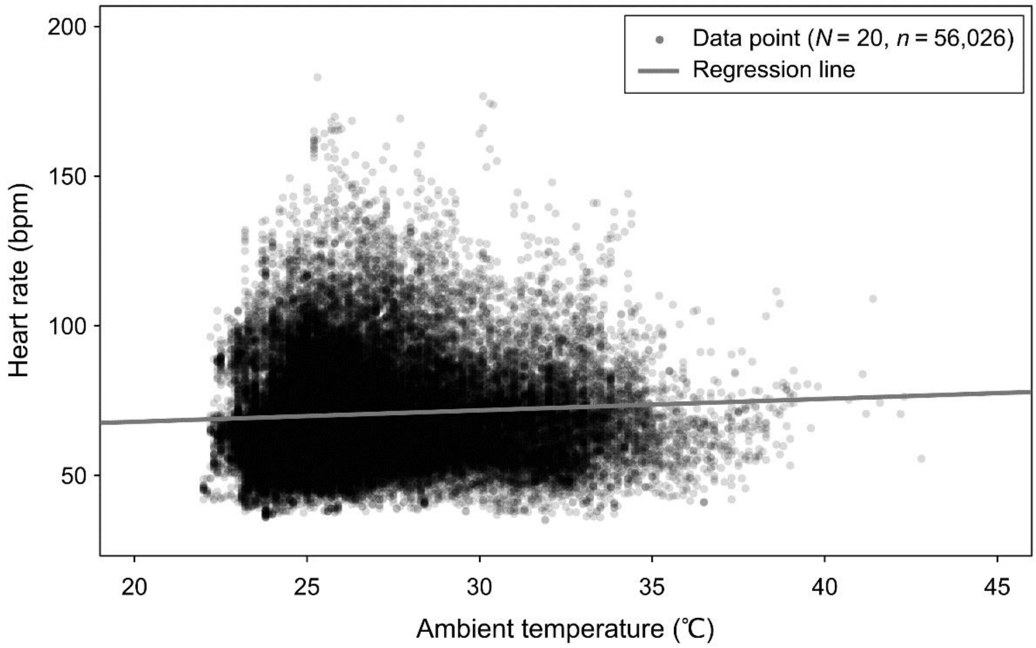

Fig. 6: Relationship between body mass and heart rate in mammals. Filled grey circles indicate the data of three-toed sloths from Duarte et al. (2003), Silva et al. (2005), and present study. Open diamonds and the regression line were drawn based on Noujaim et al. (2004), except for an apparent mistake (chimpanzee heart rate: 15 ± 20 bpm).