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The effects of human-altered habitat on sloth activity

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Abstract

Deforestation and habitat degradation are an increasing threat to wildlife globally. The effects are particularly pronounced in regions where they are compounded by the expansion of human settlements and land-use changes. As behavioural adaptations are often the initial response of wildlife to environmental change, this study explores how human disturbance affects the activity of two sloth species, Choloepus hoffmanni and Bradypus variegatus. By comparing the activity of sloths living in secondary forest habitats and human-impacted forest habitats, the objective is to determine whether sloths exhibit adaptive behaviours in response to habitat degradation and human presence. Tri-axial accelerometer data loggers were fitted to sloths inhabiting secondary forest and human-impacted forest. With this tri-axial accelerometer data, three key locomotive behaviours in sloths – arboreal vertical and horizontal locomotion, and terrestrial locomotion – were identified and quantified. Linear mixed-effects (LME) model analyses of these activity budgets with respect to environmental factors (temperature, precipitation, windspeed) and habitat type indicated significant individual variation in behaviour, with the environmental factors exhibiting limited but notable effects. Individual variability may be explained by reproductive age, genetic differences and/or fine-scale microhabitat characteristics. Bradypus variegatus in human-impacted forest habitats displayed increased levels of nocturnal activity, suggesting a possible adaptive behavioural response to human presence. The response of sloths to human-impacted forest habitat is multifaceted, influenced by anthropogenic disturbance, environmental factors and individual needs, suggesting that activity patterns may be shaped through balancing external pressures and internal constraints. This study highlights the importance of individual variability in shaping sloth behaviour and underscores the need for more comprehensive studies including fine-scale habitat structure to inform conservation strategies.

Lay Abstract

Tropical rainforests globally are being cut down to make space for human activities, severely affecting the wildlife living within these regions. Sloths, known for their slow movements, are especially vulnerable as they live in the tree canopy and cannot move quickly to avoid danger or jump to cross gaps between trees. This study looks at how two species of sloth - Choloepus hoffmanni and Bradypus variegatus – adjust their behaviour when their habitats are disturbed by humans. This is done by comparing the activity of sloths living rainforest impacted by humans and sloths living in more optimal rainforest habitats which are protected from human activity. Sloths were fitted with data-logging devices which recorded their movement over time. Through the measurements recorded by these devices, it could be determined how long each sloth spent climbing up and down tree trunks, moving along branches, and crawling along the ground, and at what time of day they performed these behaviours. The results showed that sloths living in habitats were there was human activity may be more active at night, possibly to avoid humans. Sloth behaviour varied significantly between individuals, possibly due to small differences in their habitats, genetic or age differences. Factors like temperature, rainfall, and wind speed did have some effect, however these were minor in comparison to the differences between individuals. Understanding these differences in behaviour can help conservationists protect sloths and ensure their habitats are safe from being cut down to make space for human activities.
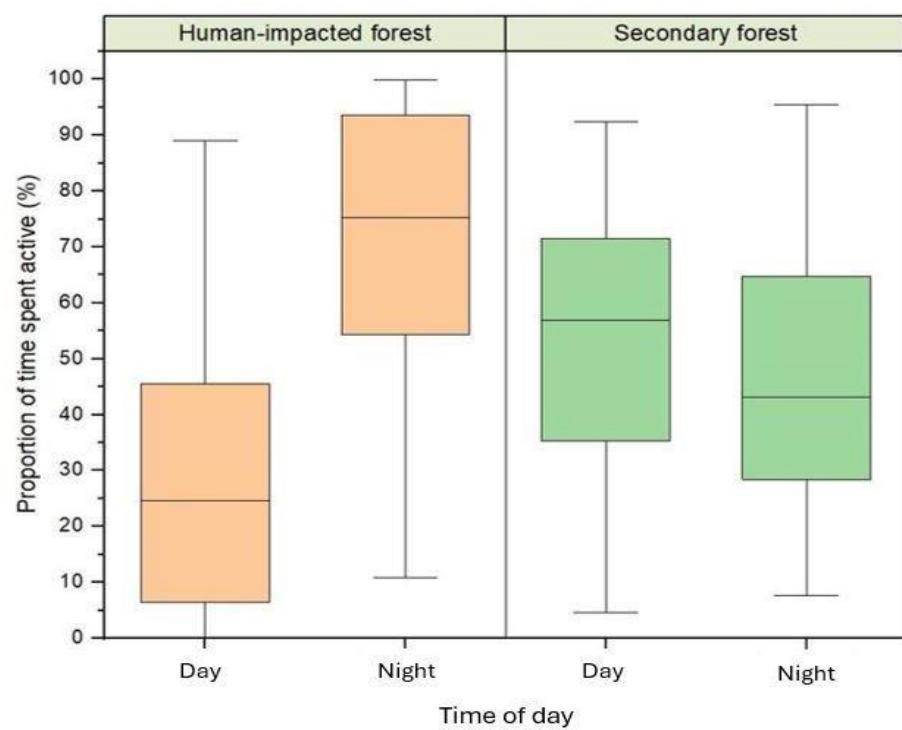
Figure: Proportions of the total time spent active in the day (diurnal) and night (nocturnal) in each habitat by three-toed sloths. Orange indicates human-impacted habitat, green indicates secondary forest habitat.

Declarations

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed

Amelia Symeou

Date 25/09/2024

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed

Amelia Symeou

Date 25/09/2024

I hereby give consent for my thesis, if accepted, to be available for electronic sharing

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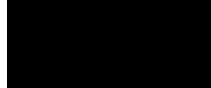
Amelia Symeou

Date 25/09/2024

The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

Signed

Amelia Symeou

Date 25/09/2024

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Abbreviations

N.B. all specialized terms and abbreviations are defined at first mention throughout

TNZ	Thermoneutral zone
IPCC	Intergovernmental Panel on Climate Change
FOA	Food and Agriculture organization of the United Nations
VHF	Very High Frequency
MINAE	Ministerio de Ambiente y Energía Ministry of Environment and Energy
SINAC	Sistema Nacional de Áreas de Conservación National System of Conservation Areas
ACLAC	Área de Conservación La Amistad Caribe La Amistad Caribe Area of Conservation
DD	Daily Diary Data Logger
Axy	TechnoSmart Axy 5S tri-axial accelerometers
VeDBA	Vectorial sum of dynamic body acceleration
LoCoD	Lowest Common Denominator Method
BEs	Behavioural Elements
Δ	Rate of change
LME	Linear mixed-effects
AIC	Akaike Information Criterion
SD	Standard deviation
SE	Standard error
HIH	Human-impacted habitat
R^2m	Marginal R^2
R^2c	Conditional R^2

The effects of human-altered habitat on sloth activity

Introduction

Deforestation and habitat degradation present an increasingly pervasive threat to wildlife globally (Hoang and Kanemoto 2021). The effects are especially pronounced in tropical rainforests, where these pressures are compounded by the expansion of human settlements and land-use changes (Hoang and Kanemoto 2021). To date, an estimated 50% of tropical rainforest has been deforested (Wright 2005), contributing to global biodiversity loss (Laurance 2007) and creating forest fragments among human settlements. With tropical forests acting as significant carbon sinks (IPCC 2023), there are global consequences associated with deforestation. However, the drivers of deforestation are directly related to the livelihoods of local families and the financial incentives of corporations (Pain et al. 2021), making deforestation an inevitability despite the environmental impact.

The diverse range of social factors contributing to the erosion of primary tropical rainforest have resulted in the growth of 'secondary' forest (Fig. 2) (Perz and Skole 2003). Secondary forest is regarded as immature forest, regenerated following significant disturbance of the original vegetation (Perz and Skole 2003). Although secondary forest ecosystems now account for approximately 70% of the earth's tropical forest (FOA 2010) and are an important stage in forest regeneration, they have lower levels of ecosystem functionality, diversity and structural complexity compared to mature forest (Perz and Skole 2003; FOA 2018).

Areas of forest with frequent and ongoing anthropogenic disturbance is termed 'human-

impacted' forest in this study, with the constant threat of deforestation (Fig. 2). These areas are characterised by extensive fragmentation, little canopy connectivity and the presence of roads, human settlements and domestic animals. This type of habitat lacks the structural complexity and biodiversity to maintain arboreal mammals, potentially increasing the incidence of terrestrial movement and exposure to threats such as human interference, domestic dog attacks, and vehicle collisions (Young et al. 2023).

Responses of tropical rainforest wildlife to deforestation include either relocating from disturbed areas (Sergio et al. 2018) or adapting to life in disturbed forests with a notable trend towards increased nocturnal activity as a possible adaptive strategy to avoid conflict with humans (Gaynor et al. 2018). Among mammals, sloths (genera: Bradypus and Choloepus), slow-moving Xenarthrans native to Neotropical rainforests in Central and South America, are predicted to be among the most affected. Due to the structural differences present in each habitat type, it is reasonable to hypothesise that sloths inhabiting the different habitat types will perform different levels of activity.

Bradypus variegatus and Choloepus hoffmanni, the focal species of this study, inhabit neotropical forest throughout central America at risk of anthropogenic change and are likely to be affected by these changes. Both sloth species have a low dispersal ability (Schloss et al. 2012) accompanied by exceptionally slow speeds, with a maximum of 0.05 – 0.15 m/s in trees (Young et al. 2023). This speed further decreases to 0.02 – 0.06 m/s when forced into terrestrial locomotion (Young et al. 2023). As a result, their movement away from forest disturbances is remarkably slow for a mammal, and when on the ground (such as when traversing between forest patches), sloths are highly vulnerable to human interference, attacks by dogs, and vehicle collisions (Young et al. 2023). While both species share most ecological and behavioral characteristics there are several key differences. C. hoffmanni is generally the larger of the two with a healthy adult weighing between 4 and 8 kg and exhibit

cathemeral activity patterns, while B. variegatus is generally smaller at 3 – 6 kg and are considered diurnal (Peery and Pauli 2014).

Deforestation is expected to affect the sloths that remain in disturbed areas, primarily due to their unusually slow rate of energy acquisition and metabolic rate (Nagy and Montgomery 1980). Sloths are suited to the highly biodiverse and structurally complex environment of primary rainforest, where they forage and digest their chosen food plants extremely slowly as part of their evolved strategy for critical energy conservation (Cliffe et al. 2015). Additionally, sloths rely on the structural complexity of primary rainforests to regulate their body temperature due to their poikilothermal nature, alternating between shaded areas and basking in sunlight (Cliffe et al. 2018). This behaviour allows them to adjust both body temperature and metabolic rate in response to environmental changes (Levesque et al. 2016; Cliffe et al. 2018). The ongoing deforestation of these natural habitats may restrict the sloth's ability to perform these critical behaviours.

The effect of deforestation on sloths' ability to perform thermoregulatory behaviours may be compounded by adverse weather conditions, such as low temperatures, increased precipitation and windspeed. Increased precipitation has been linked to decreased activity levels in sloths (Cliffe et al. 2018), while ambient temperatures below 22 °C severely reduce a sloths ability to maintain body temperature within their thermoneutral zone (TNZ) of 30.2 – 34.9 °C (McNab 1985; Gilmore et al. 2000). In both studies, environmental factors linked to reductions in body temperature and activity are linked to the reduced ability of microbes within the foregut to breakdown food, impacting their ability to acquire energy (King et al. 2011).

Given that human disturbance often alters the activity patterns of mammals (Gaynor et al. 2018), potential behavioural changes in sloths could hinder their ability to practice effective

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heterothermy, potentially increasing their energy costs while reducing the choice of food plants. In summary, while the full impact of reduced biodiversity and the loss of structural complexity in both secondary forests and human-impacted forest fragments on sloth ecology remains unknown, it is likely to be significant.

Studying wild sloth behaviour poses significant challenges due to their cryptic nature and highly specialized arboreal lifestyle—sloth behaviours are rarely observable, and their movements are minimal. However, accelerometers have been well-documented as effective tools for tracking an animal's activity (Wilson et al. 2008, Mortlock et al. 2024), eliminating the need for continuous human observation, which is particularly difficult in well-camouflaged, tree-dwelling animals such as sloths (Sunquist and Montgomery 1973).

This study therefore aims to investigate whether habitat degradation and the establishment of human settlements are affecting the activity levels of sloths living in these altered environments. Specifically, it will assess whether, during active periods, the proportion of time spent in key locomotive behaviours—horizontal, vertical, and terrestrial locomotion—differs significantly from that of sloths in more optimal, secondary forest habitats. Additionally, the study will examine whether B. variegatus sloths in human-impacted forest fragments are shifting their activity patterns toward increased nocturnal activity, potentially as a strategy to avoid human contact.

These findings will contribute to a deeper understanding of sloth behavioural ecology and inform conservation strategies which aim to mitigate the impact of habitat fragmentation on arboreal mammals with low-dispersal abilities.

Methods

Data collection

Study sites

Data were collected from two locations; one dominated by secondary forest and one with high rates of human-impact and habitat degradation (referred to as human-impacted forest) (Fig. 1, 2). Data collection was conducted in the privately owned secondary forest of the Sloth Sanctuary of Costa Rica (N 09°47'56.47" W 082°54'47.20") of approximately 95 hectares, between April 2014 and August 2015. Data from human-impacted rainforest fragments was collected between November 2020 and July 2023 from four different sites along the south Caribbean coast of Costa Rica: the Cocles Maritime Zone (N 09°39'22.3" W 082°44'30.1"), Playa Cocles (9°39'05.8"N 082°44'17.9"W), Chiquita (N 09°38'16.8" W 082°42'36.0"), and Playa Negra (N 09°39'25.2" W 082°46'12.0").
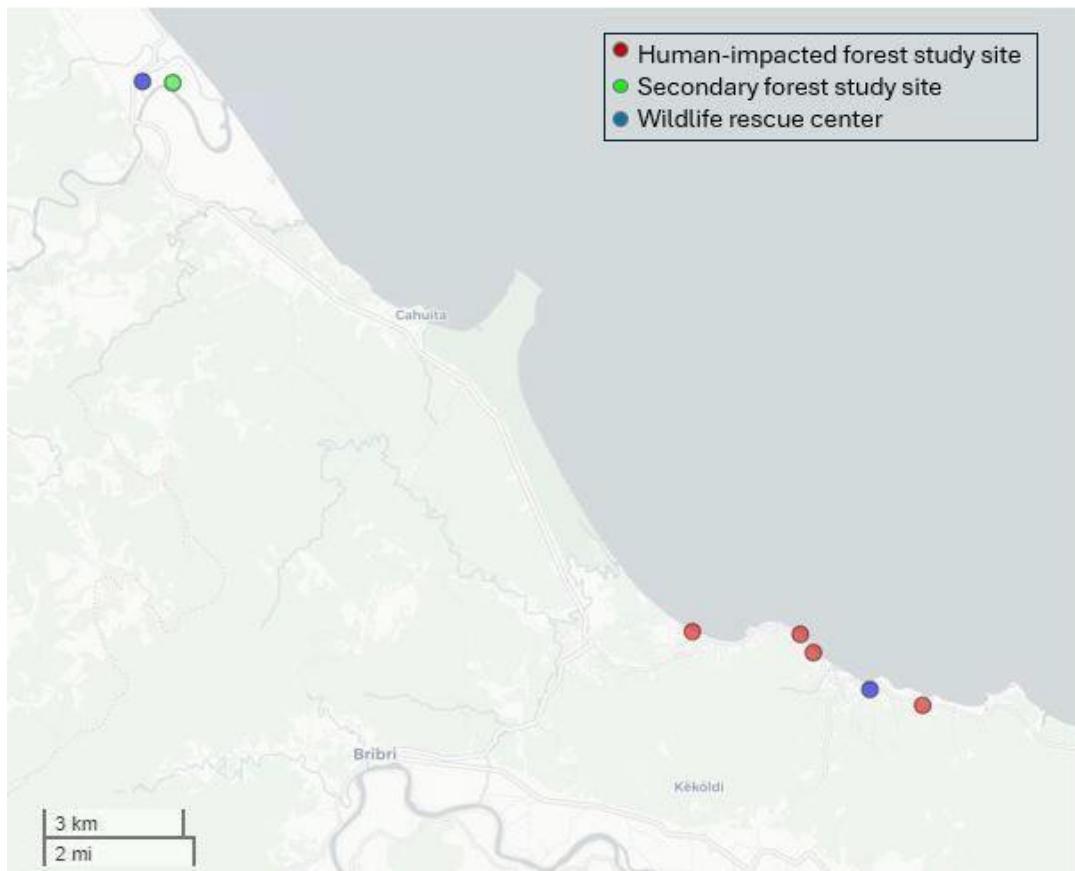
Figure 1. Map of the South Caribbean coast of Costa Rica marking the study sites and the two wildlife rescue centers. Human-impacted forest study sites are indicated in red, the secondary forest study site is indicated in green, and the rescue centers are indicated in blue.
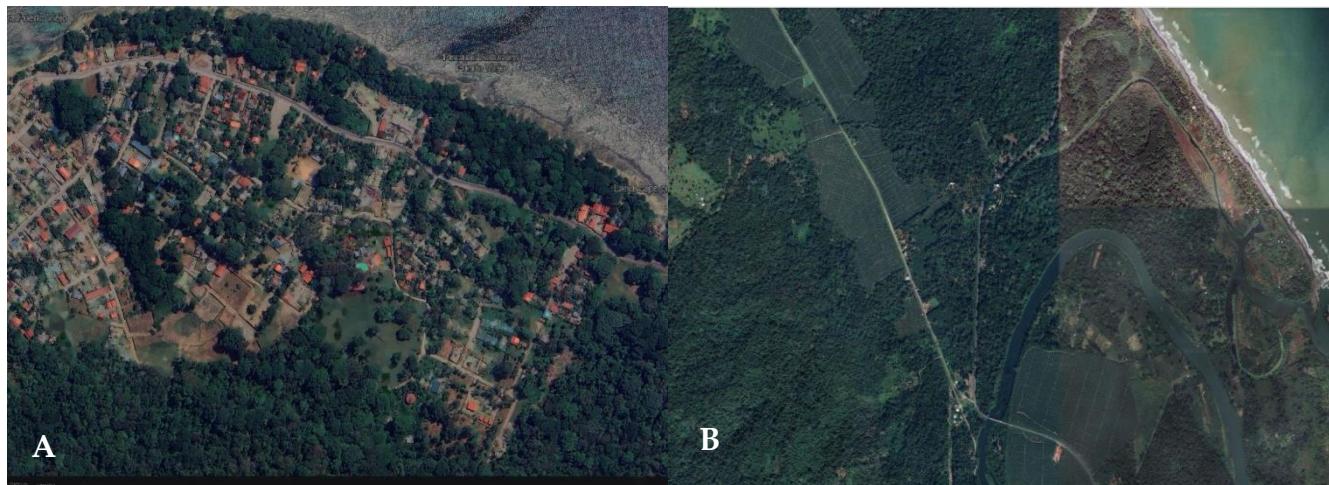
Figure 2. Aerial photographs of human-impacted habitat (A) and secondary forest habitat (B).

Weather data

Weather data were collected from Station ID MRLM (Visual Crossing Weather, https://www.visualcrossing.com/). Station ID MRLM is located at Limon International Airport (9°57'45.1"N 83°01'32.9"W). Mean daily temperature (°C), precipitation (mm), and wind speed (mph) for the recording period of each data logger was collected for statistical analysis against the key behaviours (Appendix A, Table 1, 2).

Equipping the sloths

Sloths were selected opportunistically according to their ease of capture, with animals being captured when they were less than 4 m from the ground. Sloths included in the sample were weighed (E-PRANCE® Portable Hanging Scale (±0.01 g)) to ensure they fell within the expected healthy adult range for their respective species (Peery and Pauli 2014) and showed no outward symptoms of injury or disease.

Protocols for the capture, handling and instrumentation of both species followed Cliffe et al., 2023. In summary, B. variegatus were equipped with backpacks or collars without the use of

anaesthesia before being immediately returned to the tree they were found in. C. hoffmanni were anaesthetised during capture by a licensed veterinarian using 1 mg/kg of ketamine (Ketamina 50®, Holliday Scott) and 0.008 mg/kg of dexmedetomidine (Dexdomitor®, Zoetis) administered intramuscularly. If required, anaesthesia was reversed prior to release using 0.008 mg/kg of anti-sedante (atipamezol; Antisedan®, Zoetis) before individuals were returned to the tree where they were found. The capture, handling and instrumentation of sloths was approved by the Costa Rican government and its associated departments (MINAE, SINAC, ACLAC), permit numbers; R-033-2015, R-032-2020, R-025-2021, R-018-2023.

Individuals tagged prior to 2023 were equipped with Very High Frequency (VHF) radio transmitters and Daily Diary Data Loggers (DD) recording tri-axial acceleration (g) at 40 Hz, barometric pressure (mbar) at 2 Hz, tri-axial magnetometry (gauss) at 13 Hz, external temperature (°C), and relative humidity (%). These were held within non-lubricated condoms containing 0.5 g silica gel to protect the electronics from moisture damage and then placed in custom 3D-printed cases combined with VHF pip transmitter (TW3 10-28) and attached firmly on the upper back via an elastic harness that was adjusted according to the measurements of each individual (Fig. 3). The whole package weighed 90 g (Cliffe et al. 2023), which represented a maximum of 4.6% of the body mass of B. variegatus and 2.4% of the body mass of C. hoffmanni.

Individuals tagged in 2023 were equipped with a different tag type, here an accelerometer (TechnoSmart Axy 5S)recorded tri-axial acceleration (g) and barometric pressure (mbar) at 10 Hz. These accelerometers (hereafter referred to as Axy) were attached to VHF radio collars (SirTrack V6C 173C) parallel to the VHF emitter using duct tape (Fig. 3). Combined, the collar weighed 50 g, which represented a maximum of 2.6% of the body mass of B. variegatus and 1.4% of the body mass of C. hoffmanni.

Both accelerometers recorded the movements of the sloths in the three orthogonal axes. Sloths were equipped with a VHF radio transmitter (Biotrack PIP3 VHF tag) enabling tagged sloths to be relocated through telemetry.

Figure 3. Top left panel: 3D printed case measuring 4 cm x 5 cm 2cm with DD (A), battery (B) and VHF pip transmitter used in human-impacted forest (C). Top right panel: case and harness used in secondary forest (Cliffe et al. 2023). Bottom panel: Axy attached to VHF radio collar

Post-release monitoring and device recovery

All sloths were observed for a minimum of ten minutes immediately post-release. Observational notes recording key locomotive behaviours were logged during this time to aid in the initial stages of accelerometer analysis. Sloths were monitored and located using the VHF radio transmitters via a 4 MHz Sika receiver. Sloths in secondary forest were monitored daily (Cliffe et al. 2023) and sloths in human-impacted forest were monitored three times per week. Once a sloth was located the GPS location of the sloth was recorded, along with notes on the three locomotive behaviours sloths display – terrestrial locomotion, and arboreal horizontal and vertical locomotion (Young et al. 2023). Terrestrial locomotion describes crawling along the ground, where a sloth's abdomen is lifted, and their body weight is supported by the hindlimb plantar surfaces, either supporting their upper body through the forelimb palmar surface or the elongated radius and ulna (Mendel 1981; Mendel 1985). Arboreal horizontal locomotion describes suspensory quadrupedal locomotion occurring within the canopy (Fig. 4), while vertical locomotion describes traversing up or down the trunk of a tree in either an upright or inverted posture.

The DD backpacks had a battery life of approximately two weeks and the Axy collar battery life was approximately two months. Device retrieval was only attempted after these respective durations. The VHF battery life was approximately one year, allowing for location and retrieval of the devices after the accelerometer batteries had run out.

Three backpacks (SCH1, SCH2 and SCH3, Appendix A Table. 3) incorporated small links of water-soluble film (Aquatics ROMEO) to allow the DD to fall off in heavy rain (Cliffe et al 2023), eliminating the need for additional anaesthesia. This was not a viable option in rainforest environments, as the frequent rainfall might have resulted in the DD being released well before the accelerometer has ceased recording.

Data Analysis

Identifying key behaviours

Tagging data were visualised and processed using DDMT software (http://www.swansea.ac.uk/biosci/researchgroups/slam/slamsoftware/), which has been custom-developed by the Swansea Lab for Animal Movement for work with multi-dimensional, high-frequency tagging data. Behaviours were identified using (i) pressure data, as pressure changes over scales of seconds to minutes indicate changes in height above the ground, and hence periods when sloths were moving up or down, or (ii) acceleration data and their derivatives. Pressure data were smoothed over 7.5 s and rates of change in the smoothed pressure variable was calculated over a 12.5 s period.

Acceleration was recorded in three orthogonal axes: surge, heave, sway (Fig. 4). Acceleration data were smoothed over 2.5 s and the rates of change in each of the smoothed acceleration axes were calculated over a period of 12.5 s. The smoothing intervals were chosen to reduce irregularities in the data caused by noise and aid in behaviour identification by increasing the uniformity of predictable patterns in acceleration during the key behaviours. Previous studies have shown rates of change of acceleration to be more powerful than raw acceleration values in characterising the movements of slow-moving animals (Hopkins et al. 2021). The differential values also reduce any systematic differences in absolute values that may result from device placement, which in turn, should make algorithms perform better when applied across individuals (Shepard et al. 2008).
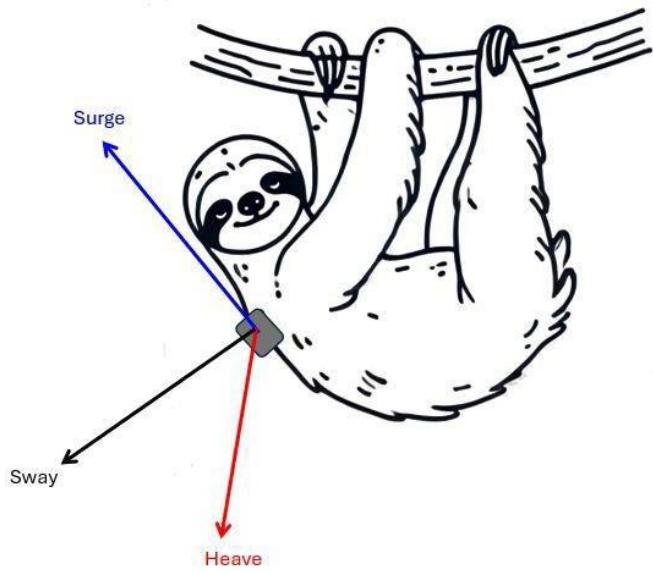
Figure. 4: Diagram showing how acceleration in the three orthogonal axes - Surge (x axis, blue), Sway (y axis, black), Heave (z axis, red) – relate to the sloth's orientation and movements. The grey rectangle represents the DD backpack.

The acceleration values in each channel change in relation to both the static and dynamic components. When stationary, the vectorial sum of the raw acceleration in the three axes is 1 g, which is acceleration due to gravity only, often referred to as the static component (Shepard et al. 2008). When the tag changes orientation (i.e. the animal moves), the static component measured in each axis changes, allowing body posture to be quantified (Shepard et al. 2010). The static component can be estimated within the data by smoothing the data in each channel over 2 seconds (Shepard et al., 2008). Dynamic body acceleration (DBA) is the component of the signal due to body motion. This can be estimated by subtracting the smoothed data from the raw data in each channel. Acceleration values in each axis change with movement, resulting in the vectorial sum (the total summation of the x, y and z axis values at a specified point) being higher or lower than 1 g depending on the direction and intensity of the movement (Wilson et al. 2020b). The vectorial sum of dynamic body acceleration (VeDBA) is the vectoral sum of the dynamic acceleration values from all three

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orthogonal axes (Fig. 4). VeDBA is often utilised as a proxy for energy expenditure as it is strongly correlated with oxygen consumption during activity across a range of species (Wilson et al. 2008; Gleiss et al. 2011; Wilson et al. 2018; Wilson et al. 2020a). VeDBA data was smoothed over 2 s and the rates of change in smoothed VeDBA variable was calculated over a 12.5 s period.

The key behaviours were initially identified within the data using observations from the individual with the most extensive period of ground-truthing: UCH3. Movements associated with each behaviour produced clear patterns in acceleration and pressure (i.e. surge, heave, sway, pressure, and VeDBA) (Fig. 5). Identifying the key behaviours in the data enables the durations of these behaviours to be exported from the DDMT software, allowing for the analysis of the activity budgets of sloths living in different habitat types.
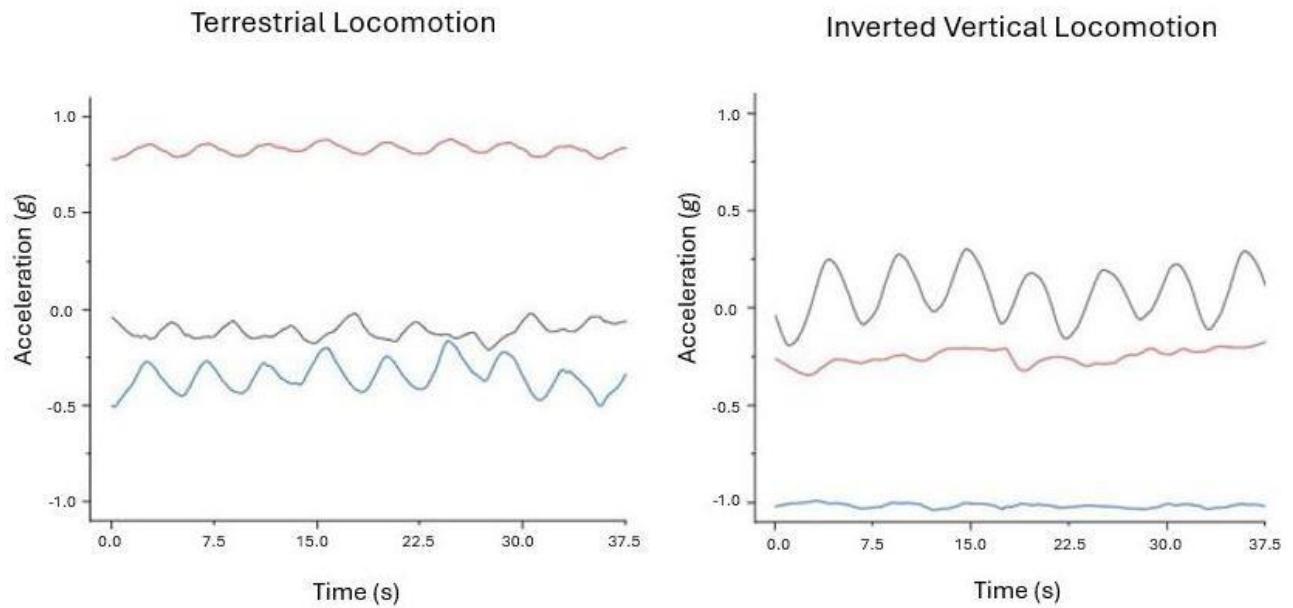
Figure. 4: Temporal patterns (37.5 s) in the three acceleration signals for two key behaviours,
(i)   terrestrial locomotion, (ii) inverted vertical arboreal locomotion. The surge signal is in blue, the sway signal is in black, and the surge signal is in red.

Algorithms to identify behaviour

The Lowest Common Denominator Method (LoCoD) described in Wilson et al. 2018 was employed to define the identifying features (Behavioural Elements) of each key behaviour. Behavioural Elements (BEs) of a behaviour are generally multiple and occur in a defined sequence over a specified time period. This study utilised the 'behaviour builder' function in DDMT to search for defined BEs in sequence. The behaviour builder is a Boolean conditional search function (Redcliffe and Holton 2022) which highlights places in the data where all conditions of the search are met (each of these sections are hereafter referred to as 'Marked Events').

The value and working of the method can be illustrated by describing its use to identify one behaviour – here vertical locomotion. Where organised wave patterns were visible in a specific smoothed acceleration trace over time (i.e. vertical locomotion, Fig. 5, 5), the rates of change values for the chosen acceleration variable were isolated at the peaks and troughs (BE1 and BE2). Since use of the rate of change data in search terms results in better performing algorithms than non-derivatives (which are particularly subject to variation in device positioning and calibration (Shepard et al. 2008)), the same search algorithm could be used across individuals (Table 1). The differential sway acceleration values were analysed using a histogram (Fig. 7) as the data follows a normal distribution, indicated by the bell-shaped curve. The histogram serves as a visual representation of the distribution, facilitating the identification of the most appropriate values for identifying the BEs within the data through a Boolean conditional search function.
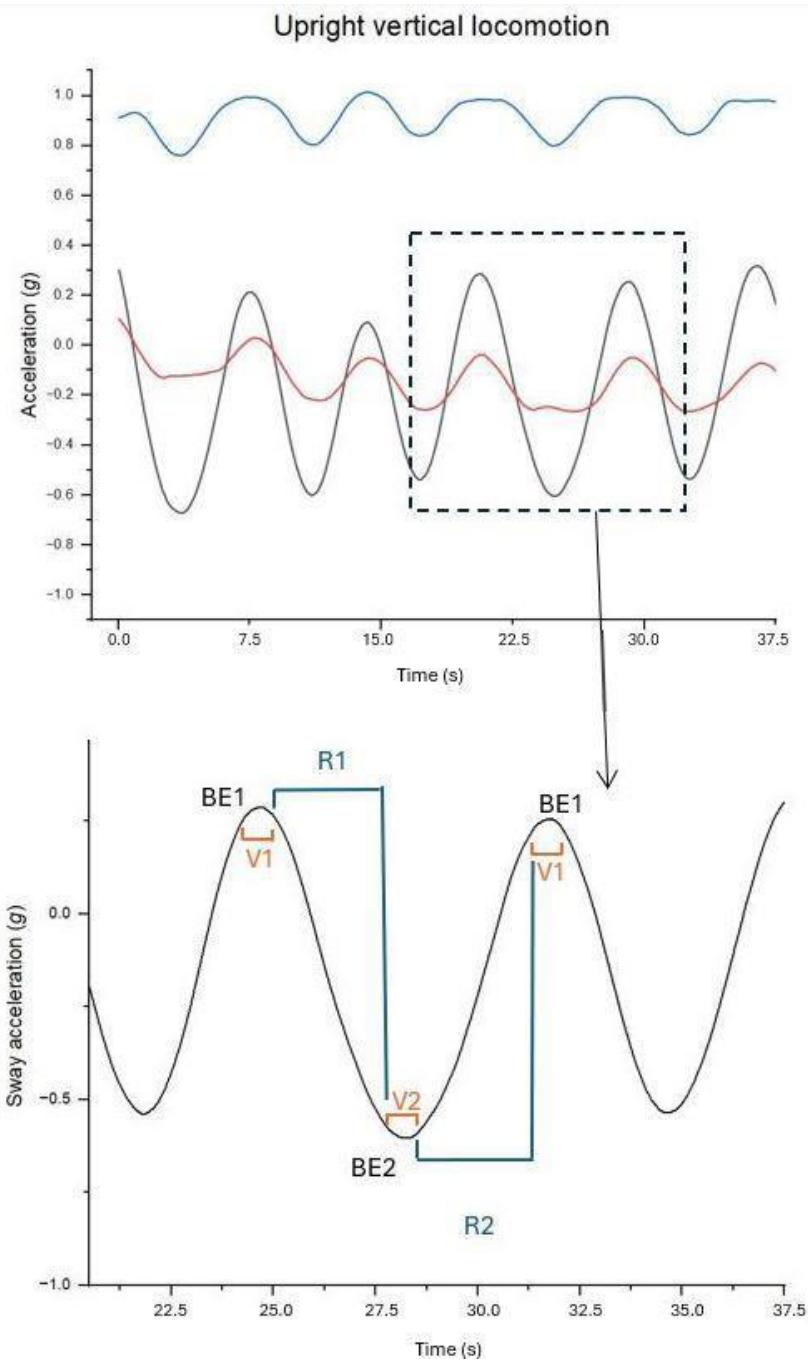
Figure. 6: Top panel: Acceleration signals for upright vertical locomotion (surge in blue, sway in black and heave signal in red). Bottom panel: 17.5 s of upright vertical locomotion in the sway acceleration channel (black line). The Lowest Common Denominator Method uses a search function through the data to identify features characteristic of certain behaviours. In

this case, there is an obvious characteristic signal in the sway axis and a particular range of values define the differential of the sway acceleration peak (see Fig. 7) for the first Behavioural Element (BE1). Specifically, once these differential values are approached by scanning the data through time, the peak is searched for within a defined period (V1).

Subsequently, the program skips another defined period (R1) before searching for the second BE (BE2). The sway acceleration trough is the key feature of BE2 (again defined via the differential of the smoothed sway acceleration), and once detected, is isolated specifically by minimum values within another defined period (V2). Following this, there is another period (R2) during which data are skipped before the program reverts to searching for BE1 again. When the conditions for vertical locomotion are met, the data is highlighted as a Marked Event, i.e. upright vertical locomotion is occurring.

Figure. 7: Histogram representing the distribution of the rate of change of the smoothed sway axis at BE1 within upright Vertical Locomotion. This shows that an appropriate value choice for the Boolean search function should lie between -0.5 and +0.5 g/s

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Where one axes exhibits a small range due to the orientation of the sloth during that locomotive behaviour (e.g. surge during terrestrial locomotion, Fig. 5), that is utilised as a part of the BE and makes the Boolean formula more specific to that that locomotive behaviour, reducing the incidence of false positives. Where a behaviour exhibits multiple consecutive (i.e. where the trace has periodicity with peaks and troughs) it is necessary to include time within the algorithm, introducing sub-conditions to each BE. An example is given in Fig. 6 where, for the behaviour to be recognised, the defined channel conditions need to be maintained over a specified time period. Once this has occurred, a further time period can be introduced, which is the range to next BE, which specifies a time to be skipped before searching for the next BE.

Inactivity

Inactivity, encompassing rest and sleep, was identified by very low axial differentials, indicating no or very little movement. Inactivity was visually identified within the tri-axial acceleration trace of dataset UCH3 and the smoothed VeDBA values were extracted. The smoothed VeDBA values were analysed through a histogram (cf. Fig. 7) to identify the most appropriate values for identifying inactivity within the data using a Boolean conditional search function (Table 1).

Marked Events with less than 1 s duration were removed to allow for brief pauses in activity. Marked events within 10 s of each other were merged to allow for minimal posture changes which occur during rest.

Activity

With inactivity accounted for in UCH3, the smoothed VeDBA values were extracted from the remaining data, i.e. activity. These values were analysed using a histogram (cf. Fig. 7) to identify the most appropriate values for identifying activity within the data using a Boolean

conditional search function (Table 1).

Marked Events with less than 1 second duration were removed to allow for noise and minimal posture changes which occur during inactivity. Marked events within 2 seconds of each other were merged to allow for brief pauses in activity.

Terrestrial locomotion

Terrestrial locomotion, or crawling, exhibits organised and predictable traces in all three acceleration axes (Fig. 5). The key identifying feature is a posture unique to ground locomotion, with heave maintaining a high value (mean = 0.79 g). The addition of a minimum smoothed VeDBA parameter (smoothed VeDBA > 0.03) eliminated this posture during rest (Table 1).

Marked Events of less than 1 s duration were removed to account this posture being sometimes briefly present during horizontal canopy locomotion. Marked Events within 5 s of each other were merged to account for pauses in movement along the ground.

Upright vertical locomotion

Vertical locomotion up or down the trunk exhibited an organised and predictable trace in the sway acceleration. The most frequent peak and trough values were used to differentiate BE1 and BE2 (Fig. 6), while the surge acceleration was relatively high and constant (mean = 0.92 g) relative to other locomotive postures. Ascent and descent were distinguished through the addition of a rate of change of pressure parameter, with a negative pressure differential indicating ascent and a positive pressure differential indicating descent (Table 1).

Marked events within 2.5s of each other were merged to account for pauses in movement.

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Inverted vertical descent

Descent can occur with the animal adopting an inverted posture, exhibiting a defined pattern in the sway axis. The most frequent peak and trough values in the sway were used to differentiate BE1 and BE2 (cf. Fig. 6), while surge was constant maintaining a low value (mean = -0.81 g) (Table 1).

Marked events within 2.5s of each other were merged to account for pauses in movement.

Table 1: Key behaviour, behavioural elements (BE) number, and the corresponding Boolean conditional search formula, where Δ denotes a rate of change for that variable.

Behaviour	BE	BE Formula
Activity	1	VeDBA $> 0.03\,g$
Inactivity	1	$-0.0007\,g\ <\ \Delta\,\text{surge}\ <\ 0.0007\,g$
		AND
		$-0.0007\,g\ <\ \Delta\,\text{heave}\ <\ 0.0007\,g$
		AND
		$-0.0007\,g\ <\ \Delta\,\text{sway}\ <\ 0.0007\,g$
Ground locomotion	1	Heave $>\ 0.8\,g$
		AND
		VeDBA $>\ 0.03\,g$
Upright vertical locomotion - Ascent	1	$\Delta\,\text{Sway}\ <\ -0.05\,g$
		AND
		$\Delta\,\text{Pressure}\ <\ -0.05\,g$
		AND

	2	Surge > 0.7 g Δ Sway > 0.07 g AND Δ Pressure < -0.05 g AND Surge > 0.7 g
Upright vertical locomotion – Descent	1	Δ Sway < -0.05 g AND Δ Pressure > 0.05 g AND Surge > 0.7 g
	2	Δ Sway > 0.07 g AND Δ Pressure > 0.05 AND Surge > 0.7 g
Inverted vertical locomotion - descent	1	Δ Sway < 0.15 g AND Δ Pressure > 0.05 g AND Surge < -0.6 g

2   Δ Sway > -0.21 g

AND

Δ Pressure > 0.05 g

AND

Surge < -0.6 g

Statistical analysis

The behavioural and environmental data was standardised prior to preforming any statistical tests to improve the interpretability of the coefficients and mitigate multicollinearity (Schielzeth 2010). The Tukey Interquartile Range method was used to identify outliers in the behavioural data, where data falling outside of the upper and lower bounds were eliminated from the statistical analysis (upper bound = 3rd quartile – (1.5 x interquartile range), lower bound = 1st quartile – (1.5 x interquartile range)).

An initial Welch's Two-Sample T-Test was conducted on the environmental data to determine if a significant difference was present between the temperature, precipitation levels, and windspeed during the two study periods.

The first objective was to explore whether habitat and environmental factors affected the length of time spent active. Time spent active and inactive was calculated per 24-hour period for each individual (Appendix A, Table 4, 5). A linear mixed-effects (LME) model was conducted using the 'lmer' from the "lme4" package in R. The LME was fitted using restricted maximum likelihood (REML) to investigate the relationship between time spent active and the following environmental predictors: habitat type, temperature, windspeed and precipitation. Interactions between habitat type and environmental factors were also

explored, AIC values were used to select the best fitting model, and hence the interactions that were included. With activity the inverse of inactivity the AIC values determined whether a model was run for activity or inactivity. The model included random intercepts for species and individual nested within species to account for species imbalance and repeated measures within the samples.

The second objective was to test whether environmental parameters predicted variation in time spent in the key behaviours: terrestrial, vertical and horizontal locomotion. Time spent in each behaviour was calculated per 24-hour period for each individual. This followed the same approach as that for activity, with a separate model being run for each of the key behaviours.

The final objective was to explore whether habitat and environmental factors affected the level of activity performed by B. variegatus in the diurnal and nocturnal diel phases. Time spent active in the nocturnal and diurnal diel phases was calculated for each individual (Appendix A, Table 9, 10). This followed the same approach as that for activity and the key locomotive behaviours, with a separate model being run for the diurnal and nocturnal diel phases. The diurnal and nocturnal diel phases were determined to occur between 05:30 - 18:00, and 18:00 – 05:30 respectively. The models included individual sloth as a random effect to account for repeated measures within the samples. C. hoffmanni was excluded from this analysis due to the species imbalance present in both samples and previous studies indicating a difference in circadian rhythm between the two species (Sunquist and Montgomery 1973).

The AIC values for each model and the possible fixed-effect interaction were compared to determine the most appropriate model selection, with lower AIC values indicating more appropriate and better fitting model selection (Table 3). The model assumptions were

evaluated using the 'performance' package in R, ensuring that the data linearity, collinearity and normality of residuals fit the LME model assumptions.

RESULTS

Device durations and recovery

Ten sloths were tagged in human impacted forest habitat: six B. variegatus of which three were male and three were female, and four C. hoffmanni of which two were male and two were female. Ten sloths were tagged in secondary forest habitat: seven B. variegatus of which six were male and one was female, and three C. hoffmanni, all of which were female (Appendix A Table. 3)

Backpack S13 of SCH1 (Table. 2) recorded for 100.6 hours, however 14.3 mm of rain was recorded on day 3 of deployment (Appendix A Table. 2), resulting in the ROMEO link dissolving and the DD backpack releasing after 48.8 hours of recording. This is the only C. hoffmanni data logger to reach the 48-hour threshold for analysis. SCH2 was fitted with a DD which recorded for 12 hours before releasing in 3.3 mm of rainfall. SCH3 was fitted with a DD twice, the first released after 6.8 hours of recording despite zero daily precipitation being recorded, and the second stopped recording after 29.5 hours. SCH2 and SCH3 were not included in this study.

Table. 2 Individual IDs, data logger type and recording durations (hr) of each data logger and individual sloths. Specific sloths are referred to within the text by their ID: S denotes secondary forest habitat, U denotes human-mediated forest habitat, BV denotes Bradypus variegatus and CH denotes Choloepus hoffmanni. DD denotes Daily Diary Data Loggers, AXY denotes Axy S5 accelerometers.

Individual ID	Sex	Data logger type	Recording duration (hrs)
UBV1	M	DD	57.6
UBV2	M	DD	95.2
UBV3	F	DD	209.7
UBV4	M	AXY	1200.0
UBV5	F	AXY	552.0
UBV6	F	AXY	504.0
UCH1	F	AXY	488.5
UCH2	M	DD	150.6
UCH3	M	DD	157.5
UCH4	F	AXY	467.0
SBV1	M		513.1
		DD	105.9
		DD	95.2
		DD	144.0
		DD	168.0
SBV2	M		345.1
		DD	187.4
		DD	157.7
SBV3	F		241.4
		DD	109.2
		DD	132.2
SBV4	M	DD	169.7

SBV5	M	DD	47.2
SBV6	M	DD	189.0
SBV7	M	DD	157.3
SCH1	F	DD	48.8

A total of 3882.1 hours of behavioural data was recorded from ten sloths inhabiting human-impacted forest, 3315.8 hours of this was categorised as either active or inactive. Sloths in human-impacted forest spent 60.1% of this time inactive at a daily mean of 9.3 hours per day (range 7.6 – 11.2 hours). A daily mean of 6.9 hours per day was spent active (range 5.9 - 8.8 hours per day) (Fig. 8, Appendix A Table. 4). Individuals varied in their mean total diurnal activity (range 8.1 – 56.1%) and exhibited a large level of intra-variation in their mean daily diurnal activity (Fig. 9, 10). The majority of active behaviour was spent moving within the canopy (defined as horizontal canopy movement, 94%), with a daily average of 6.5 hours.

On average 12.2 minutes per day were allocated to vertical locomotion, with ascent and descent accounting for 54% and 46% respectively (Appendix A, Table. 7). Terrestrial locomotion accounted for 0.04% of the total active behaviour (Table. 3).

A total of 1704.4 hours of behavioural data was recorded for eight sloths inhabiting secondary rainforest habitats. 1551.6 hours of this was categorised as either active or inactive. Sloths in secondary forest spent 66.5% of this time inactive at a daily mean of 7 hours per day (range 8.4 – 14.2 hours). A daily mean of 8.6 hours per day was spent active (range 5.5 - 8.8 hours) (Fig. 8, Appendix A Table. 4). Individuals varied in their mean diurnal activity (range 23.6 – 77.4%) and also exhibited variation within the individual daily diurnal activity (Fig. 9, 9). The majority of active behaviour was spent performing horizontal canopy movement (94%), with a daily average of 6.6 hours. On average 28.8 minutes per day were allocated to vertical locomotion (Table. 3), with ascent and descent accounting for 61.3% and

38.7% respectively (Appendix A, Table. 7, 8). Terrestrial locomotion accounted for 0.2% of the total active behaviour. (Table. 3)
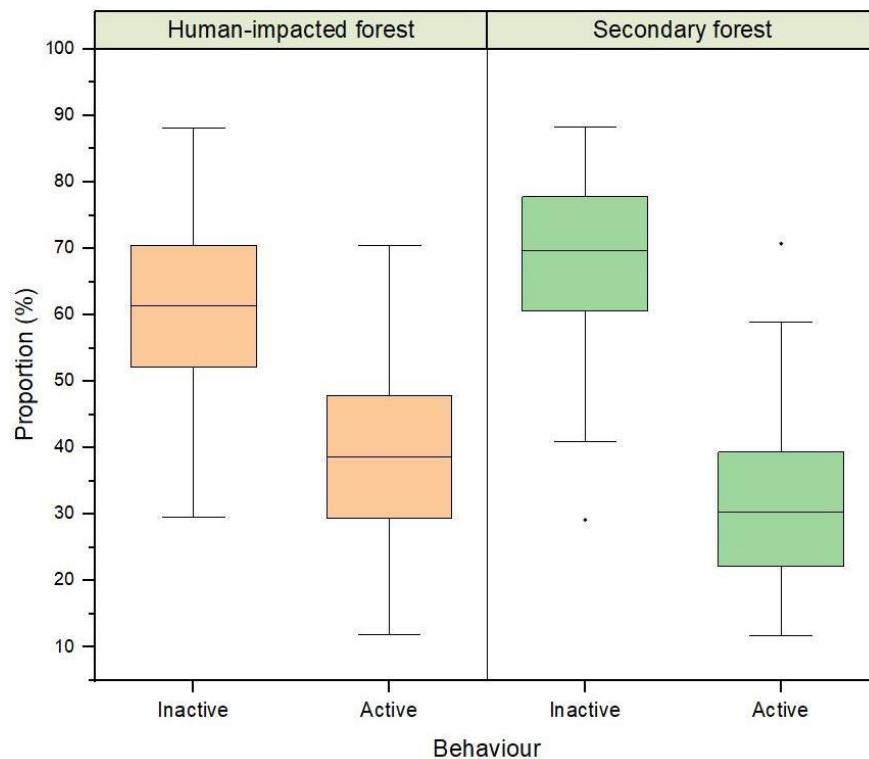
Figure. 8: Proportions of total time spent Inactive and Active in human-impacted forest habitat and secondary forest habitat (n = 18). Orange indicates human-impacted habitat, green indicates secondary forest habitat. ▪ = outlier
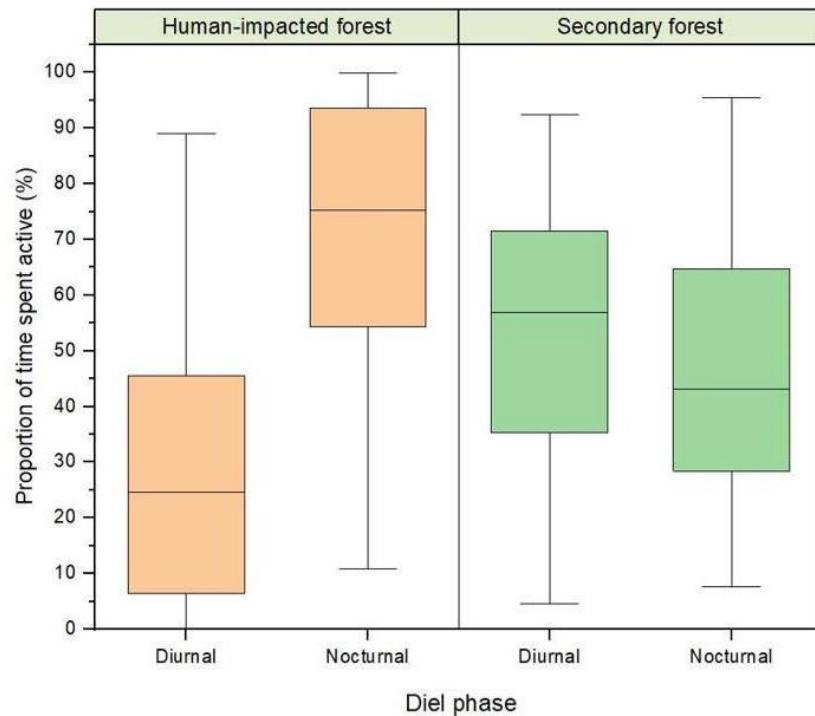
Figure. 9: Proportions of Bradypus variegatus total time spent active in the diurnal and nocturnal diel phases in each habitat. Orange indicates human-impacted habitat, green indicates secondary forest habitat.
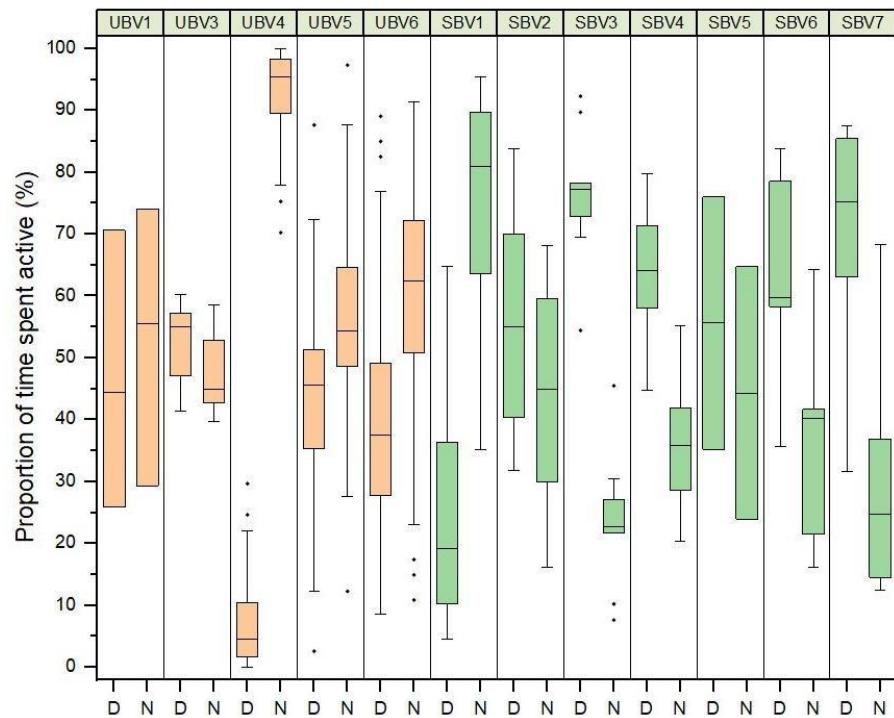
Figure. 10: Proportions of Bradypus variegatus total time spent active in the diurnal and nocturnal diel phases for each individual (n = 12). Orange indicates human-impacted habitat, green indicates secondary forest habitat. D = diurnal, N = nocturnal, ▪ = outlier

Table. 3 Individual ID, data logger ID, the daily mean (hrs), total recorded (hrs) and total proportion (%) of Active behaviour spent performing the key locomotive behaviours (ground locomotion, horizontal locomotion, vertical locomotion) for each individual (n = 18) and data logger (n = 23)

Individual	Data Logger	Terrestrial			Horizontal			Vertical		
		Daily mean (hrs)	Total (hrs)	% of active total	Daily mean (hrs)	Total (hrs)	% of active total	Daily mean (hrs)	Total (hrs)	% of active total
SBV1		0.0	0.0	0.0	6.1	134.5	93.0	0.5	10.0	7.0
	s1	0.0	0.0	0.0	5.4	26.8	97.0	0.2	0.8	3.0
	s2	0.0	0.0	0.0	5.9	23.8	93.4	0.4	1.7	6.6
	s3	0.0	0.0	0.0	6.4	38.5	89.9	0.7	4.3	10.1
	s4	0.0	0.0	0.0	6.5	45.3	93.4	0.5	3.2	6.6
SBV2		0.0	0.0	0.0	5.8	86.7	94.9	0.3	4.7	5.1
	s5	0.0	0.0	0.0	5.8	46.3	93.9	0.4	3.0	6.1
	s6	0.0	0.0	0.0	5.8	40.5	96.0	0.2	1.7	4.0
SBV3		0.0	0.0	0.0	7.1	78.6	97.1	0.2	2.3	2.9
	s7	0.0	0.0	0.0	6.7	33.6	96.1	0.3	1.3	3.9

	s8	0.0	0.0	0.0	7.5	45.1	97.9	0.2	1.0	2.1
SBV4	s9	0.01	0.1	0.1	6.2	49.8	96.8	0.2	1.6	3.1
SBV5	s10	0.2	0.3	1.9	7.8	15.7	89.1	0.8	1.6	3.3
SBV6	s11	0.0	0.0	0.0	7.1	64.1	95.7	0.2	2.9	4.3
SBV7	s12	0.0	0.0	0.0	7.0	49.1	95.6	0.2	2.3	4.4
SCH1	s13	0.2	0.4	2.5	7.6	15.2	88.2	0.4	1.6	9.4
UBV3	u3	0.0	0.0	0.0	5.9	53.3	94.1	0.2	3.3	5.9
UBV4	u4	0.0	0.0	0.0	7.5	374.5	90.8	0.4	37.9	9.2
UBV5	u5	0.0	0.0	0.0	6.7	161.8	95.2	0.2	8.2	4.8
UBV6	u6	0.003	0.1	0.02	8.4	176.6	96.0	0.2	7.4	4.0
UCH1	u7	0.0	0.0	0.0	5.8	121.9	97.1	0.1	3.6	2.9
UCH2	u8	0.0	0.0	0.0	6.4	44.8	93.9	0.2	2.9	6.1
UCH3	u9	0.04	0.3	0.2	7.1	49.4	95.0	0.2	2.3	4.5

UCH4	u10	0.0	0.0	0.0	6.3	126.6	94.0	0.2	8.0	6.0

Environmental factors

The results of the two-sample t-test indicates a significant difference in temperature between human-impacted forest study period (mean = 26.5 °C, SD = 1.14) and secondary forest study period (mean = 26.1 °C, SD = 1.06); t(157.91) = -2.85, p = 0.0049). No significant difference in precipitation was identified between the human-impacted forest study period (mean = 7.2 mm, SD = 13.89) and the secondary forest study period (mean = 14.1 mm, SD = 33.96); t(87.94) = 1.57, p = 0.1204). Wind speed was not found to be significantly different between human-impacted forest study period (mean = 16.9 mm, SD = 4.2) and secondary forest study period (mean = 17.7 mm, SD = 6.28); t(108.44) = 1.15, p = 0.2514). (Appendix A Table. 1, 2)

Statistical analysis of key locomotive behaviours

Model selection

AIC values were used to select the best fitting model; no interaction between habitat type and environmental variables was the most appropriate model for inactivity, terrestrial and horizontal locomotion, while the model including an interaction between habitat type and precipitation was the most appropriate for modelling vertical locomotion (Table. 4).

Table. 4 Potential LME models and fixed effect interactions, AIC values used in model selection for the key behaviours. * Indicates the chosen fixed effect interaction

Model interaction	Inactivity*	Terrestrial	Horizontal	Vertical	Diurnal	Nocturnal

Habitat*precipitation	644.569	632.641	670.983	638.083*	419.175	350.413
Habitat*temperature	645.188	630.940	670.791	644.749	419.175	350.695
Habitat*windspeed	646.143	633.117	671.155	645.616	417.639	349.676
Habitat*precipitation & Habitat*temperature	649.089	NA	674.549	NA	423.632	354.003
Null interaction	644.570*	629.137*	668.872*	641.310	415.843*	346.938*

Model results

In the LME model predicting levels of inactivity, the analysis indicates that both temperature (β = 0.269, SE = 0.083, t(220) = 3.24, p = 0.0014) and precipitation (β = 0.0916, SE = 0.055, t(220) = 1.66, p = 0.049) have significant positive effects on inactivity. The LME indicates that a 1.1 °C increase in temperature was associated with a 17.8 minute increase in inactive behaviour, and a 22.1 mm increase in precipitation was associated with a 6.0 minute increase in inactive behaviour (Table. 6). The fixed effects accounted for 5.9% of the variance (R^2m = 0.059), while 52.2% of the variance is accounted for by the random effects (R^2c = 0.522) (Table. 6).

The model analysis indicates that the interaction between habitat type and precipitation had a significant effect on vertical locomotion (β = 0.359, SE = 0.13, t(220) = 2.76, p = 0.0063), suggesting a 22.1 mm increase in precipitation was associated with an overall 14.9 minute increase in vertical locomotion in human-impacted forest habitats. This significance is supported in the analysis of ascent (β = 0.337, SE = 0.133, t(220) = 2.53, p = 0.012) and descent (β = 0.336, SE = 0.13, t(220) = 2.58, p = 0.0106). Individually, habitat type (β = -0.012, SE = 0.243, t(15) = –0.05, p = 0.9615) and precipitation (β = -0.064, SE = 0.063, t(220) = –1.01, p = 0.313) do not have a significant effect on vertical locomotion (Table. 5). The fixed effects

account for 4.3% of the variance (R2m = 0.0434), while 20.3% of the variance is accounted for by the random effects (R2c = 0.246) (Table. 6).

The analyses do not suggest that terrestrial or horizontal locomotion is affected by habitat type, precipitation, temperature, or windspeed (p < 0.05) (Table. 5). The model analysis for terrestrial locomotion indicates that habitat type and environmental factors account for 11.8% of the variance (R2m = 0.118), while 73.8% of the variance is accounted for by the random effects (R2c = 0.8564) (Table. 6).

Table. 5: Value (β), standard error (SE), degrees of freedom, t-value, and p-values of fixed effects of key behaviour LME models: inactivity, activity, terrestrial locomotion, horizontal locomotion, vertical locomotion, vertical ascent and vertical descent. HIH = Human-impacted habitat, * = interaction

	Value (β)	SE	Degrees of freedom	t-value	p-value
Inactivity					
Temperature	0.2692	0.0831	220	3.2386	0.0014
Windspeed	-0.0673	0.0539	220	-1.2503	0.2125
HIH	-0.0261	0.3984	15	-0.0654	0.9487
Precipitation	0.0916	0.0551	220	1.6625	0.0493
Terrestrial locomotion					
Temperature	-0.112	0.0801	220	-1.3983	0.1634
Windspeed	-0.0123	0.0502	220	-0.2447	0.8069
HIH	-1.3846	0.7284	15	-1.9008	0.0767
Precipitation	-0.0158	0.0514	220	-0.3080	0.7584

Horizontal

locomotion

Temperature	0.0532	0.0846	220		0.6287	0.5302
Windspeed	0.0851	0.0582	220		1.4606	0.1455
HIH	0.1765	0.2747	15		0.6428	0.5301
Precipitation	0.0196	0.0595	220		0.3289	0.7423

Vertical

locomotion

Temperature	0.1160	0.0796	220		1.4563	0.1467
Windspeed	0.0713	0.0546	220		1.3051	0.1932
HIH	-0.0119	0.2430	15		-0.0491	0.9615
Precipitation	-0.0636	0.0629	220		-1.0112	0.3130
HIH * precipitation	0.3592	0.1301	220		2.7609	0.0063

Table. 6: LME models of the key behaviours, marginal R2 (variance explained by the fixed effects), conditional R2 (variance explained by the fixed and random effects), and variance explained by the random effects as a percentage (individual nested within species)

LME Model	R^2m	R^2c	Variance explained by random effects (%)
Inactivity	0.0592	0.5220	46.3
Terrestrial locomotion	0.1181	0.8564	73.8

Horizontal locomotion	0.0167	0.2528	24.0
Vertical locomotion	0.0434	0.2465	23.6

Statistical analysis of *Bradypus variegatus* diurnal and nocturnal behaviour

Model selection

AIC values were used to select the best fitting model; no interaction between habitat type and environmental variables was the most appropriate model for diurnal and nocturnal activity in *B. variegatius* (Table. 4).

Model results

The model analysis indicated that windspeed (β = 0.231, SE = 0.059, t(150) = 3.91, p = 0.0001) had a significantly positive effect on diurnal activity, suggesting that a 4.4 mph increase in windspeed was associated with an overall 1.02 hour increase in the diurnal activity of B. variegatus (Table. 7). The fixed effects account for 6.9% of the variance ($R2m$ = 0.069), while 43.8% of the variance is accounted for by the random effects ($R2c$ = 0.507) (Table. 8).

The model analysis indicated that temperature (β = 0.154, SE = 0.073, t(150) = 2.12, p = 0.0355) had a significantly positive effect on nocturnal activity, suggesting that a 1.2 C increase in temperature was associated with an overall 10.2 minute increase in nocturnal activity of B. variegatus. Habitat type also showed a significantly positive effect on nocturnal activity, suggesting that inhabiting human-impacted forest can be associated with a 39 minute increase in the nocturnal activity of B. variegatus (Table. 7). The fixed effects account for

21.5% of the variance (R2m = 0.215), while 31.5% of the variance is accounted for by the random effects (R2c = 0.53) (Table. 8).

Table. 7 Value (β), standard error (SE), degrees of freedom, t-value, and p-values of fixed effects of diel phase LME models (diurnal and nocturnal)

	Value (β)	Standard error	Degrees of freedom	t-value	p-value
Diurnal activity					
Temperature	-0.01444	0.090067	150	-0.16032	0.8728
Windspeed	0.230652	0.05892	150	3.914705	0.0001
Precipitation	-0.0433	0.060162	150	-0.71967	0.4728
HIH	-0.24799	0.381693	15	-0.6497	0.5257
Nocturnal activity					
Temperature	0.15393	0.072537	150	2.12203	0.0355
Windspeed	0.061673	0.048165	150	1.280449	0.2024
Precipitation	0.032778	0.049075	150	0.667907	0.5052
HIH	0.648859	0.277627	15	2.337165	0.0337

Table. 8: LME models of B. variegatus activity during the diurnal and nocturnal diel phases, marginal R2 (variance explained by the fixed effects), conditional R2 (variance explained by the fixed and random effects), and variance explained by the random effects as a percentage (individual sloth)

LME Model	R^2m	R^2c	Variance explained by random effects (%)
Diurnal activity	0.0692	0.5072	43.8
Nocturnal activity	0.215456	0.530077	31.5

Discussion

The majority of published research on the activity of sloths has been conducted on captive individuals (e.g. Cliffe et al. 2018; Young et al. 2023) due to the difficult nature of observing these animals in the wild. This is the first study to compare the activity budgets of free-living sloths living in two distinct habitat types and is the first to use tri-axial accelerometers to analyse the activity of sloths living among anthropogenic stressors. As part of this, it is also the first to specify the acceleration parameters that define key locomotive behaviours. The analysis of acceleration in the three orthogonal axes to determine posture played a crucial role in identifying the key behaviours in this study. In particular, posture allowed for a clear distinction between terrestrial and vertical locomotion when utilised alongside VeDBA.

Individual variation

The variation in behaviour and activity was much more linked to the identity of the individual sloth than it was to environmental factors. Significant individual variation in

activity and rest has been exhibited in other species (e.g. Mortlock et al. 2024). The large variation in behaviour across individuals may be due to reproductive age, genetic differences or fine-scale microhabitat characteristics. It is difficult to tease these apart as drivers of behaviour, however. For example, there are difficulties in aging wild sloths, although studies on captive sloths estimate that sexual maturity occurs at 2-3 years (Lara-Ruiz and Chiarello 2005) and there are regionally variable and distinct mating seasons (Garcés-Restrepo et al. 2017) which presumable affects activity. Generally, males have larger home ranges than females, with male home ranges encompassing the home range of multiple females (Pauli et al. 2012) which presumable increases their activity too. However, mate selection is determined by female sloths, and during oestrus female sloths are considered to be potentially more active as they shift their home ranges to access different males (Garcés-Restrepo et al. 2017).

The significant influence of individuality on sloth behaviour in this study may be due to the translocation of sloths from other regions, with distinct regional behavioural features. While to the knowledge of the researchers no sloth included in the study was specifically translocated, the human-impacted forest study sites were within 1.6 and 5.4 km of a wildlife rescue center, while the secondary forest study site was within 300 m of a sloth-specific rescue center (Fig. 1), both of which receive sloths from other regions of the country. A recent study on genetic divergence of C. hoffmanni throughout Costa Rica has identified distinct genetic differences between C. hoffmanni populations in different regions (Cliffe et al. 2020). As a consequence of the lack of suitable habitats in the sloth's original location or lack of support, funding and education, the sloths admitted into the rescue centres may not be released back to their original regions. While no study on the genetic divergence of B. variegatus in Costa Rica has been conducted, the species shares the same low dispersal ability as C. hoffmanni. Sloths originating from different regions translocated to the study sites that differ in their responses to environmental conditions may therefore contribute to

the observed variation of individuals and genetic differences may amplify these behavioural responses to their environment.

Differences in fine-scale forest structural complexity within the microhabitat of individual sloths may also have contributed to the high individual variability. For instance, fine-scale forest structural complexity, encompassing variation in floristic composition, tree height, trunk diameter, canopy cover, epiphyte presence, tree to tree connectivity, and tree density can all have substantive impacts on habitat selection and use in Bradypus (Vaughan et al. 2007; Falconi et al. 2015; Neam and Lacher 2018). As highly specialised locomotors (specifically, obligatory quadrupedal suspensory locomotors) the daily activity of sloths involves both vertical and horizontal movement to avoid interspecific aggression, while continuous canopy connectivity aids access to resources (Cassano et al. 2011). In particular, high tree density has been indicated as a significant predictor of sloth presence as it is linked to increased connectivity (Falconi et al. 2015). Anthropogenic disturbances reduce the structural complexity of tropical forests and have a significant negative impact on tree density (Hansen et al. 2020), with the impact of deforestation being particularly severe when combined with the establishment of human settlements and land use changes (Hoang and Kanemoto 2021).

The low frequency of terrestrial locomotion observed in this study aligns with the highly specialised arboreal nature of sloths. Terrestrial locomotion is both energetically costly and encounters high risks of mortality from predators, including domestic dogs (Young et al. 2023). However terrestrial locomotion was unexpectedly identified in three individuals inhabiting secondary forest (SBV4, SBV5, SCH1) (Table. 2), despite the seemingly well-connected forest canopy. This highlights the need for data on fine-scale forest structure data collection, it is possible there were gaps in connectivity that elicited the need for terrestrial locomotion, but fine-scale forest structural composition data is required to confirm this.

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It is known that even well-developed secondary forest is not as structurally complex as primary forest (Perz and Skole 2003), so micro-fragmentation may be present. At device retrieval there was no visually identifiable injury or disease for the individuals that engaged in terrestrial movement (Appendix A, Table 3). Within human-impacted forest habitats, terrestrial locomotion was identified in two individuals (UCH3, UBV6); one month after device retrieval for this study individual UCH3 was admitted to the local wildlife rescue centre having suffered aggression from multiple domestic dogs during terrestrial locomotion and later died from associated secondary infections. These findings underscore the risks associated with terrestrial locomotion and the importance of forest connectivity in minimising mortality risks.

Environmental factors

Although environmental factors (habitat type, precipitation, temperature and windspeed) explained little of the variance in sloth activity and behaviour, there were significant effects nonetheless. Precipitation was the most important predictor of activity, with reduced activity as precipitation increased. Prolonged exposure to precipitation can cause a sloth's body temperature to fall below its optimal 30.2 – 34.9 °C TNZ (Giné et al. 2015; Cliffe et al. 2018) due to evaporate cooling (Voigt et al. 2011). This may affect activity per se, as is the case in reptiles (Huey 1988) but is also more likely to affect the physiology of digestion. As foregut fermenters, the microbes present in a sloth's foregut function best within the sloth's TNZ (King et al. 2011). Following Q10 theory, a concept used to describe how an organisms physiological processes are influenced by external environmental conditions (Hochachka and Somero 2002), a reduction in body temperature below the TNZ can reduce the ability of microbes to break down leaves and effectively metabolise plant matter to derive energy (Foley et al. 1995; King et al. 2011). This effectively reduces the rate at which animals acquire energy. Laboratory studies have established that mammals experiencing large fluctuations

in body temperature are vulnerable to reduced gut fermentation efficiency when experiencing low body temperature (Yahav and Buffenstein 1991), potentially explaining the reduced activity of sloths during heightened precipitation. This may also be linked to the increased vertical locomotion in human-impacted forest. Specifically, the lower structural complexity present in human-impacted forest habitats may result in sloths being more exposed to adverse weather conditions. I speculate that the associated increased vertical locomotive behaviour is part of a shelter-seeking strategy as a part of adaptive thermoregulatory behaviour.

Activity also decreased with temperature, which aligns with previous research suggesting that sloths reduce their metabolic rate with temperature (Cliffe et al. 2018). Aligning with Q10 theory, as endothermic heterotherms this is almost certainly linked to their inability to maintain body temperature within their TNZ at low ambient temperatures (Cliffe et al. 2018). The optimal ambient temperature for sloths is suggested to be between 26 – 30 °C, which corresponds to the average daily rainforest temperatures (Cliffe et al. 2015; Giné et al. 2015). This is also the temperature range at which sloths living in well-connected forest habitats are most active (Chiarello 1998; Cliffe et al. 2015; Giné et al. 2015). Temperatures below 22 °C reportedly curtail activity severely (McNab 1985; Gilmore et al. 2000). Notably, the lowest temperature recorded in this study was 23.7 °C. The limited global distribution of sloths (Voss et al. 2009) places them in environments where, currently, temperatures rarely deviate from their optimal range. The findings here therefore align with previous research suggesting that sloths reduce activity when environmental conditions are unfavourable to avoid the high energetic costs associated with thermoregulation (Gilmore et al. 2000; Cliffe et al. 2015; Giné et al. 2015).

The temperatures recorded during the 2020 – 2023 study period were significantly higher than the temperatures recorded during the 2014 – 2015 study period. Elevated energy

demands due to significantly increasing ambient temperatures are likely to influence activity budgets and movement patterns. In human-impacted forest where resources are limited, and canopy connectivity and fine-scale structural complexity are reduced, higher temperatures as a result of climate change are likely to only exacerbate sloths' energetic constraints.

Behavioural adaptations

Nocturnal activity and vertical locomotion in sloths appear to be influenced by a combination of environmental factors, anthropogenic disturbances, and individual variability. Globally, wildlife has shown increased nocturnality, possibly as an adaptive strategy to avoid conflicts with humans and domesticated animals (Gaynor et al. 2018). The results of this study support this, showing that B. variegatus in human-disturbed forest habitats are more likely to be active during the nocturnal period (Fig. 9). Additionally, the study indicates that temperature and windspeed play a role in determining the time of day sloths are most active, with animals being generally more active during the day at higher windspeeds and more active at night at higher temperatures (Table. 6). It is unclear what advantages there are to the diel shifts in these behaviours. The observed variation among individuals (Fig. 10) suggests that the shift to nocturnal activity may be a complex adaptation, driven by a mix of anthropogenic disturbances, environmental conditions, and individual needs. This implies that sloth activity patterns are shaped by the need to balance external pressures with internal constraints.

Behavioural adaptations are often the initial response of wildlife to environmental change (Sergio et al. 2018). With deforestation and habitat degradation posing a growing and widespread threat to wildlife worldwide (Hoang and Kanemoto 2021), understanding how habitat change may affect the behaviour of sloths is vital. Both sloth species are considered of special conservation concern in Costa Rica (Vaughan et al. 2007), with sloths being the

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most frequently admitted animals admitted to rescue centers on the South Caribbean coast of Costa Rica, accounting for a quarter of all animals (JRC, 2023).

Despite the insights gained from this study, there are several limitations in the study design. The imbalance of individuals per species restricted interspecies comparison within the statistical models. While recent findings suggest that both species have similar levels of activity (Cliffe et al. 2023) this imbalance may limit the broader application of these findings across both species. The gender imbalance present in the secondary forest sample population restricted the analysis of gender within the statistical models and potential differences in activity between the genders resulting in the males searching for receptive females was not able to be explored. Additionally, the current inability to accurately age sloth's limits analysis of reproductive age on activity. These limitations alongside the lack of fine-scale forest structure data within the microhabitats of each sloth reduced the ability of this study to fully investigate how environmental factors and habitat type influence sloth behaviour. Addressing these limitations in future research would provide a more comprehensive understanding of the factors affecting sloth behaviour across habitats with different levels of anthropogenic disturbance.

Conclusion

This study provides valuable insights into the importance of accounting for individual variability in shaping sloth behaviour, with a notable proportion of variance in key behaviours and diel phase activity explained by individual differences. Genetic differences and microhabitat complexities likely contribute to this variability, emphasising the need for future studies to investigate these influences further.

While some environmental conditions affected sloth activity, particularly in relation to thermoregulation, the overall impact of these variables seemed limited in this study.

Nonetheless, the significant increase in temperature recorded between the two study periods coupled with the detected decrease in activity with increasing temperature highlights the vulnerability of sloths to climate change as higher temperatures are likely to become more frequent as climate change continues. Shifts in nocturnal behaviour in human-impacted habitats, likely driven by anthropogenic stressors, highlight a multifaceted adaptation to external and internal constraints. The infrequent but risky terrestrial locomotion unexpectedly observed in both habitat types underscores the importance of fine-scale habitat structure in understanding the drivers of sloth behaviour.

Despite its contributions, this study acknowledges several limitations. Addressing these gaps in future research will greatly aid our understanding of how sloths navigate climate change, habitat disturbance and anthropogenic stressors, contributing to more effective conservation strategies.

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Appendix A

Table. 1 Individual ID, data logger ID, mean temperature (°C), precipitation (mm) and windspeed (mph) of each individual and data logger recording period (Visual Crossing Weather, https://www.visualcrossing.com/)

Individual		Temperature (°C)	Precipitation (mm)	Windspeed (mph)
UBV1	u1	26.4	23.4	16.7
UBV2	u2	27.4	7.0	18.5
UBV3	u3	27.6	1.5	15.9
UBV4	u4	27.7	9.6	18.2
UBV5	u5	25.9	10.2	16.0
UBV6	u6	25.8	8.7	15.8
UCH1	u7	25.7	3.1	16.3
UCH2	u8	25.9	3.6	16.7
UCH3	u9	25.9	3.6	16.7
UCH4	u10	25.7	3.3	16.4
SBV1		26.1	27.1	17.7
	s1	26.1	60.1	18.2
	s2	25.6	14.2	21.3
	s3	26.2	24.8	17.2
	s4	26.4	13.0	15.6
SBV2		27.1	5.6	15.4
	s5	27.7	3.7	16.2
	s6	26.5	7.7	14.6
SBV3		24.9	9.6	19.2
	s7	24.6	2.3	18.9
	s8	25.2	15.7	19.6
SBV4	s9	24.7	18.2	21.1
SBV5	s10	26.4	11.5	17.3
SBV6	s11	26.4	3.1	19.8
SBV7	s12	26.7	9.8	14.3

Data logger	Recording day #	Temperature (°C)	Precipitation (mm)	Windspeed (mph)
SCH1 s13		25.6	10.7	15.9

Table. 2 Data logger ID, data logger recording day number, mean daily temperature (°C), precipitation and windspeed (Visual Crossing Weather, https://www.visualcrossing.com/)

Data logger	Recording day #	Temperature (°C)	Precipitation (mm)	Windspeed (mph)
S5	1	27	0.1	16.6
	2	26.5	4.1	14.8
	3	27.9	0.1	14.8
	4	28.4	1.5	13
	5	28.7	8.2	18.4
	6	28.4	0.5	16.6
	7	27.8	2	20.5
	8	27.1	13.2	14.8
S6	2	27	8	15.1
	3	25.9	7	11.2
	4	26.4	0.1	20.5
	5	26.3	7.1	13
	6	27.4	6.6	16.6
	7	25.5	14.3	14.8
	8	26.7	10.7	10.8
S1	1	25.3	15	22.3
	2	25.8	283	25.9
	3	26.1	0.1	14.8
	4	26.6	1.9	13
	5	26.6	0.4	14.8
S2	2	26.2	1.2	11.2
	3	26.3	15.4	25.9
	4	24.7	25.1	27.7
	5	25.3	15	20.5
S3	2	26.1	11	22.3
	3	26	62.4	15.8
	4	25.5	45	14.8
	5	26.1	4	16.6
	6	26.7	0.1	20.5
	7	26.6	26	13

s4	2	27.1	17	16.6
	3	27.1	4.7	15.5
	4	25.7	36	14.4
	5	26.5	7	14.8
	6	25.7	12.3	14
	7	26.3	2	18.4
	8	26.6	11.7	15.5
S9	1	24.7	0.5	53.6
	2	25	0.3	16.6
	3	25.4	13.4	22.3
	4	25.2	49	20.5
	5	24.6	1.6	14.8
	6	24.7	56.4	13
	7	23.7	23.4	16.6
	8	24	1	11.2
S7	2	24.4	8.4	19.6
	3	24.5	0	19.8
	4	24.5	1	14.2
	5	25	0	14.8
	6	24.8	2	25.9
S8	2	25.3	0.1	16.6
	3	23.7	38	15.5
	4	25.4	0.2	22.3
	5	24.2	46.9	29.5
	6	26.6	8.8	24.1
	7	25.8	0	9.4
S11	1	26.9	0	20.5
	2	27	1	11.2
	3	25.6	12.3	27.7
	4	26	1	31.7
	5	25.8	9.4	16.6
	6	26.4	0.3	18.4
	7	26.7	0.3	20.5
	8	26.8	0.3	16.6
	9	26.4	3	14.8
S10	2	25.9	10	13
	3	26.9	13	21.6
S13	2	25.3	7	13.3
	3	25.9	14.3	18.4
S12	2	26.5	17	14.8
	3	26.3	3	11.2
	4	26.4	11.3	13

	5	26.9	14	16.6
	6	27.6	9.1	14.8
	7	27.3	1.7	14.8
	8	26.2	12.3	14.8
U2	1	28	0	16.6
	2	28	3.5	18.4
	3	27.4	0.6	16.6
	4	27.3	18.8	22.3
	5	26.5	12	18.4
U1	2	27.6	7.2	18.4
	3	26	20	20.5
	4	25.7	43	11.2
U8	1	26.2	0.1	16.6
	2	25.9	1.3	9.4
	3	26.4	0.4	13
	4	25.6	0.1	13
	5	26	0.8	25.9
	6	26	0.4	16.6
	7	24.9	22	22.3
U4	2	29	4.2	16.6
	3	28	1.4	30.6
	4	28.2	0.4	13.6
	5	28.7	1	12.9
	6	28.7	2	14.8
	7	29	0.6	14.1
	8	28.3	0.6	14.8
	9	28.7	0.4	18.4
	10	29	3	14.1
	11	28.1	1	16
	12	28.1	1.7	16.9
	13	26.5	14.6	16
	14	27.4	19.1	28.8
	15	25.8	35	29.5
	16	28.1	4.9	18.4
	17	27.6	4.8	14.4
	18	28.5	6.9	13
	19	28.3	4	15.9
	20	27.4	0.7	27.7
	21	26.7	14	21.5
	22	27.4	0.1	24.1
	23	28	0.1	16.6

24	27.6	4.3	20.2
25	27.6	0.5	15.3
26	27.5	0.5	13.4
27	28.4	1	15.4
28	27.9	3.6	14
29	27	9	25.9
30	28.1	2	25.9
31	26.6	3	14.4
32	27.7	2.7	14.8
33	27.7	2	11.8
34	28.3	1.2	17.3
35	27.1	0.5	16.6
36	28.2	5.9	29.5
37	28.2	4.5	16.6
38	26.8	7	16.6
39	27.2	11.9	19
40	27.6	0.4	20.9
41	27	77.1	14.7
42	26.2	10	28.2
43	27.7	1.2	22.3
44	25.9	28.2	20.9
45	26.3	17.9	20.5
46	26.1	87.3	18
47	27.6	2.6	16.5
48	27.6	27.4	12.5
49	28.3	5.6	11.2
50	28.3	3.4	14.8
51	28	41	12.2
U6	2	25.2	14	13.7
	3	26.2	1.5	15.3
	4	26.2	3.5	14.8
	5	26	0.6	18.4
	6	26.2	2.1	22.3
	7	26.5	10	18.5
	8	25.9	28	14.8
	9	25.5	3.1	14.8
	10	24.3	6	19.1
	11	24.7	0.3	11.5
	12	24.8	3	13
	13	26.3	7.8	19
	14	25.6	37	16.6

	15	26.5	8	14.8
	16	25.2	12	12.3
	17	24.9	0.1	22.6
	18	26.2	1.3	11.2
	19	26.1	37	16.6
	20	26.3	3.3	11.9
	21	26.4	0.8	15.6
	22	26.6	3	16
U10	1	24.9	2	14.1
	2	25.2	3	18.9
	3	25.9	0.3	15.4
	4	25.8	4	20.6
	5	25.1	1	20.5
	6	26.4	3.1	16.6
	7	24.5	24	13
	8	24.6	11	12.6
	9	24.7	3.8	23
	10	25.6	3	9.4
	11	25.5	1.5	21.1
	12	25.5	1	13.6
	13	25.5	1.2	13
	14	25.6	0.8	13
	15	26.3	1.6	17.3
	16	26	1.2	16.5
	17	26.6	0.3	18.6
	18	26.7	2.1	16.6
	19	26.4	0.6	15.9
	20	26.6	0.3	18.4
U9	1	26.2	0.1	16.6
	2	25.9	1.3	9.4
	3	26.4	0.4	13
	4	25.6	0.1	13
	5	26	0.8	25.9
	6	26	0.4	16.6
	7	24.9	22	22.3
U5	2	25.2	14	13.7
	4	26.2	3.5	14.8
	5	26	0.6	18.4
	6	26.2	2.1	22.3
	7	26.5	10	18.5
	8	25.9	28	14.8

	9	25.5	3.1	14.8
	10	24.3	6	19.1
	11	24.7	0.3	11.5
	12	24.8	3	13
	13	26.3	7.8	19
	14	25.6	37	16.6
	15	26.5	8	14.8
	16	25.2	12	12.3
	17	24.9	0.1	22.6
	18	26.2	1.3	11.2
	19	26.1	37	16.6
	20	26.3	3.3	11.9
	21	26.4	0.8	15.6
	22	26.6	3	16
	23	26.7	3	18.4
	24	26.4	51	16.6
	25	26.9	0.4	14.8
U7	1	24.9	2	14.1
	2	25.2	3	18.9
	3	25.9	0.3	15.4
	4	25.8	4	20.6
	5	25.1	1	20.5
	6	26.4	3.1	16.6
	7	24.5	24	13
	8	24.6	11	12.6
	9	24.7	3.8	23
	10	25.6	3	9.4
	11	25.5	1.5	21.1
	12	25.5	1	13.6
	13	25.5	1.2	13
	14	25.6	0.8	13
	15	26.3	1.6	17.3
	16	26	1.2	16.5
	17	26.6	0.3	18.6
	18	26.7	2.1	16.6
	19	26.4	0.6	15.9
	20	26.6	0.3	18.4
	21	26.7	0.1	14.8
U3	2	27.6	0.9	13.5
	3	27.8	4	13.6
	4	27.6	0.7	14.8

5	27.4	0.2	14.7
6	28	0.2	16.6
7	27.9	1.5	18.4
8	27.5	5	18.4
9	26.8	1	18.2
10	27.5	0.1	14.8

Table. 3 Habitat type (sample), study site, individual sloth IDs, species, sex, and weights (kg) of each sloth fitted with data logging equipment (n = 20). Specific sloths are referred to within the text by their ID: S denotes secondary forest habitat, U denotes human-mediated forest habitat, BV denotes Bradypus variegatus and CH denotes Choloepus hoffmanni. *UCH1 + offspring, approximately 1kg

Sample	Site	Individual ID	Species	Sex	Weight (kg)	Date
Secondary Forest	Sloth Sanctuary Forest	SBV1	*Bradypus variegatus*	M	2.2	20/02/2015
					2.5	04/03/2015
					3.2	09/07/2015
					3.2	25/07/2015
		SBV2	*Bradypus variegatus*	M	4.8	24/04/2024
					4.7	07/08/2015
		SBV3	*Bradypus variegatus*	F	3.8	20/11/2014
					4.0	11/02/2015
					3.9	17/02/2015
					3.9	09/05/2015
					4.0	18/05/2015
					3.9	06/06/2015
		SBV4	*Bradypus variegatus*	M	5.0	08/09/2014

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						5.0	26/07/2015
						5.0	03/08/2015
		SBV5	*Bradypus variegatus*	M	3.45		04/08/2015
		SBV6	*Bradypus variegatus*	M	4.3		27/03/2015
		SBV7	*Bradypus variegatus*	M	3.9		15/04/2015
		SCH1	*Choloepus hoffmanni*	F	6.9		10/03/2015
		SCH2	*Choloepus hoffmanni*	F	7.3		10/03/2015
		SCH3	*Choloepus hoffmanni*	F	8.2		26/07/2015
						8.25	03/08/2015
Human Impacted Forest	Chiquita	UBV1	*Bradypus variegatus*	M	4.85		20/04/2021
	Chiquita	UBV2	*Bradypus variegatus*	M	2.31		18/01/2021
	Playa Negra	UBV3	*Bradypus variegatus*	F	2.28		02/09/2022
					2.6		19/09/2022
					3.6		28/05/2023
	Cocles Maritime Zone	UBV4	*Bradypus variegatus*	M	1.96		03/06/2023
					2.94		26/02/2024
	Cocles Maritime Zone	UBV5	*Bradypus variegatus*	F	3.61		22/03/2023
					4.52		06/09/2023
					4.57		29/04/2024
	Cocles Maritime Zone	UBV6	*Bradypus variegatus*	F	3.82		22/03/2023
	Playa Negra	UCH1	*Choloepus hoffmanni*	F	13.7 *		05/09/2022
					9.25		27/02/2023
					9.83		26/04/2023

					10.03	23/06/2023
Playa Cocles	UCH2	*Choloepus hoffmanni*	M		3.7	22/01/2021
Playa Cocles	UCH3	*Choloepus hoffmanni*	M		5.7	22/01/2021
Playa Negra	UCH4	*Choloepus hoffmanni*	F		4.15	01/08/2022
					4.3	15/09/2022
					6	27/02/2023
					6.2	25/04/2023

Table. 4 Individual ID, data logger ID, total recorded data categorised into Active and Inactive behaviour, the daily mean (hrs), total recorded (hrs) and total proportion (%) of Active and Inactive behaviour for each individual (n = 18) and data logger (n = 23)

Individual	Data Logger	Categorised (hrs)	Inactive Daily mean (hrs)	Total (hrs)	%	Active Daily mean (hrs)	Total (hrs)	%
SBV1		369.4	10.0	220.6	59.7	6.6	144.6	39.1
	s1	82.2	10.9	54.5	66.3	5.5	27.7	33.7
	s2	75.3	12.5	49.8	66.2	6.4	25.5	33.8
	s3	101.7	9.1	54.6	53.7	7.1	42.9	42.1
	s4	110.2	8.8	61.7	56.0	6.9	48.5	44.0
SBV2		315.6	11.7	224.2	71.0	6.1	91.4	29.0
	s5	162.7	14.2	113.4	69.7	6.2	49.3	30.3
	s6	153.0	9.3	110.8	104.2	6.0	42.2	39.6
SBV3		177.8	8.8	96.8	54.5	7.3	81.0	45.5
	s7	81.5	9.3	46.6	57.2	7.0	34.9	42.8
	s8	96.2	8.4	50.2	52.2	7.7	46.0	47.8
SBV4	s9	158.4	13.4	106.9	67.5	6.4	51.5	32.5
SBV5	s10	36.4	9.4	18.8	51.7	8.8	17.6	48.3
SBV6	s11	160.9	10.4	93.9	58.4	7.4	67.0	41.6
SBV7	s12	123.4	10.3	72.0	58.3	7.3	51.4	41.7
SCH1	s13	39.8	11.3	22.5	56.6	8.6	17.3	43.4
UBV1	u1	40.4	7.6	22.8	56.5	5.9	17.6	43.5

UBV2	u2	73.7	8.6	43.1	58.5	6.1	30.6	41.5
UBV3	u3	157.3	11.2	100.6	64.0	6.3	56.6	36.0
UBV4	u4	862.8	9.0	450.4	52.2	8.2	412.4	47.8
UBV5	u5	374.5	8.5	204.5	54.6	7.1	169.9	45.4
UBV6	u6	381.8	9.4	197.7	51.8	8.8	184.0	48.2
UCH1	u7	322.1	9.4	196.6	61.0	6.0	125.5	39.0
UCH2	u8	115.8	9.7	68.1	58.8	6.8	47.7	41.2
UCH3	u9	124.0	10.3	72.0	58.1	7.4	52.0	41.9
UCH4	u10	312.1	8.9	177.5	56.9	6.7	134.6	43.1

Table. 5 Individual ID, data logger ID, data logger recording day number, corresponding date, daily time (hours) and proportion of categorised time spent active and inactive

Individual	Data logger	Recording day	Date	Active		Inactive	
				%	(hrs)	%	(hrs)
SBV1	s1	1	20/02/2015	36.1	3.4	63.9	6.0
		2	21/02/2015	32.8	5.9	67.2	12.1
		3	22/02/2015	35.0	7.5	65.0	14.0
		4	23/02/2015	35.4	6.2	64.6	11.4
		5	24/02/2015	29.6	4.6	70.4	11.0
	s2	2	05/03/2015	34.3	6.6	65.7	12.7
		3	06/03/2015	24.2	4.9	75.8	15.4
		4	07/03/2015	34.1	6.1	65.9	11.9
		5	08/03/2015	44.2	7.8	55.8	9.8
	s3	2	10/07/2015	51.1	9.2	48.9	8.8
		3	11/07/2015	30.1	4.9	69.9	11.3
		4	12/07/2015	44.2	6.2	55.8	7.9
		5	13/07/2015	41.4	7.0	58.6	9.9
		6	14/07/2015	48.7	8.1	51.3	8.5
		7	15/07/2015	47.8	7.5	52.2	8.2
	s4	2	26/07/2015	32.4	5.3	67.6	11.1
		3	27/07/2015	48.5	9.0	51.5	9.6
		4	28/07/2015	35.3	5.6	64.7	10.3
		5	29/07/2015	49.3	7.9	50.7	8.1
		6	30/07/2015	51.3	7.6	48.7	7.2

		7	31/07/2015	52.9	8.1	47.1	7.2
		8	01/08/2015	38.0	5.0	62.0	8.2
SBV2	s5	1	24/04/2014	23.5	3.5	76.5	11.3
		2	25/04/2014	32.2	6.9	67.8	14.5
		3	26/04/2014	31.4	7.0	68.6	15.3
		4	27/04/2014	36.1	8.2	63.9	14.5
		5	28/04/2014	22.7	4.7	77.3	15.9
		6	29/04/2014	34.2	6.3	65.8	12.1
		7	30/04/2014	35.0	7.8	65.0	14.4
		8	01/05/2014	24.6	5.0	75.4	15.4
	s6	2	09/08/2015	43.3	6.6	56.7	8.7
		3	10/08/2015	43.2	7.4	56.8	9.7
		4	11/08/2015	39.0	6.5	61.0	10.1
		5	12/08/2015	41.2	5.5	58.8	7.9
		6	13/08/2015	42.3	6.6	57.7	9.0
		7	14/08/2015	33.3	5.3	66.7	10.6
		8	15/08/2015	31.6	4.3	68.4	9.2
SBV3	s7	2	21/11/2014	35.1	6.8	64.9	12.6
		3	22/11/2014	35.9	5.9	64.1	10.6
		4	23/11/2014	55.1	8.1	44.9	6.6
		5	24/11/2014	42.2	7.9	57.8	10.9
		6	25/11/2014	51.0	6.1	49.0	5.9
	s8	2	12/02/2015	57.4	8.6	42.6	6.4
		3	13/02/2015	51.0	7.4	49.0	7.1
		4	14/02/2015	47.8	8.7	52.2	9.5
		5	15/02/2015	37.8	7.3	62.2	12.0
		6	16/02/2015	43.9	7.3	56.1	9.3
		7	17/02/2015	53.6	6.8	46.4	5.9
SBV4	s9	1	08/09/2014	45.1	7.0	54.9	8.5
		2	09/09/2014	29.1	6.5	70.9	15.7
		3	10/09/2014	32.0	7.0	68.0	14.8
		4	11/09/2014	35.2	7.5	64.8	13.7
		5	12/09/2014	39.5	7.7	60.5	11.8
		6	13/09/2014	28.4	5.6	71.6	14.0
		7	14/09/2014	17.8	3.7	82.2	17.1
		8	15/09/2014	37.0	6.7	63.0	11.3
SBV5	s10	2	06/08/2015	50.4	8.1	49.6	8.0
		3	07/08/2015	46.7	9.5	53.3	10.8
SBV6	s11	1	27/03/2015	46.6	8.2	53.4	9.4
		2	28/03/2015	32.5	6.8	67.5	14.0
		3	29/03/2015	46.9	9.5	53.1	10.8

		4	30/03/2015	54.0	9.6	46.0	8.2
		5	31/03/2015	51.7	10.2	48.3	9.5
		6	01/04/2015	38.1	7.5	61.9	12.1
		7	02/04/2015	37.0	7.5	63.0	12.8
		8	03/04/2015	32.0	5.2	68.0	11.1
		9	04/04/2015	29.5	2.5	70.5	6.0
SBV7	s12	2	16/04/2015	45.7	8.3	54.3	9.8
		3	17/04/2015	46.8	8.9	53.2	10.1
		4	18/04/2015	42.9	7.6	57.1	10.1
		5	19/04/2015	38.3	6.6	61.7	10.7
		6	20/04/2015	38.1	7.4	61.9	12.1
		7	21/04/2015	47.6	10.5	52.4	11.6
		8	22/04/2015	21.4	2.1	78.6	7.6
SCH1	s13	2	11/03/2015	47.6	11.1	52.4	12.2
		3	12/03/2015	37.4	6.2	62.6	10.3
UBV1	u1	2	20/04/2021	28.7	5.1	71.3	12.8
		3	21/04/2021	55.7	9.5	44.3	7.5
		4	22/04/2021	53.8	2.9	46.2	2.5
UBV2	u2	1	19/05/2021	41.6	4.1	58.4	5.7
		2	20/05/2021	41.2	6.5	58.8	9.2
		3	21/05/2021	37.4	7.2	62.6	12.0
		4	22/05/2021	37.7	6.8	62.3	11.3
		5	23/05/2021	55.5	6.0	44.5	4.8
UBV3	u3	2	20/09/2022	41.5	7.4	58.5	10.4
		3	21/09/2022	30.9	5.5	69.1	12.2
		4	22/09/2022	50.8	6.7	49.2	6.5
		5	23/09/2022	39.0	7.8	61.0	12.2
		6	24/09/2022	29.4	5.7	70.6	13.7
		7	25/09/2022	39.9	6.3	60.1	9.4
		8	26/09/2022	35.6	7.2	64.4	13.1
		9	27/09/2022	41.0	7.6	59.0	11.0
		10	28/09/2022	17.0	2.5	83.0	12.2
UBV4	u4	2	04/06/23	51.4	8.8	48.6	8.4
		3	05/06/23	56.5	8.6	43.5	6.6
		4	06/06/23	50.4	8.0	49.6	7.9
		5	07/06/23	59.6	10.2	40.4	6.9
		6	08/06/23	45.7	7.9	54.3	9.4
		7	09/06/23	43.2	7.5	56.8	9.9
		8	10/06/23	38.9	6.3	61.1	9.9
		9	11/06/23	35.1	6.3	64.9	11.6
		10	12/06/23	48.2	6.7	51.8	7.2

11	13/06/23	45.6	8.4	54.4	10.0
12	14/06/23	40.0	7.3	60.0	10.9
13	15/06/23	40.7	7.7	59.3	11.2
14	16/06/23	41.2	7.0	58.8	9.9
15	17/06/23	44.8	6.6	55.2	8.1
16	18/06/23	55.0	8.3	45.0	6.8
17	19/06/23	57.5	9.8	42.5	7.3
18	20/06/23	51.7	9.6	48.3	9.0
19	21/06/23	51.9	8.5	48.1	7.9
20	22/06/23	59.4	9.7	40.6	6.6
21	23/06/23	55.4	7.0	44.6	5.6
22	24/06/23	53.0	9.5	47.0	8.4
23	25/06/23	62.2	9.0	37.8	5.4
24	26/06/23	54.0	9.0	46.0	7.7
25	27/06/23	52.2	9.6	47.8	8.8
26	28/06/23	49.4	10.0	50.6	10.2
27	29/06/23	40.7	7.6	59.3	11.1
28	30/06/23	43.9	9.2	56.1	11.8
29	01/07/23	36.7	5.9	63.3	10.2
30	02/07/23	33.8	5.8	66.2	11.3
31	03/07/23	39.0	5.8	61.0	9.2
32	04/07/23	41.3	7.3	58.7	10.3
33	05/07/23	39.5	8.1	60.5	12.4
34	06/07/23	40.9	7.3	59.1	10.6
35	07/07/23	38.8	6.9	61.2	10.9
36	08/07/23	49.6	7.1	50.4	7.2
37	09/07/23	38.1	6.3	61.9	10.2
38	10/07/23	42.0	5.1	58.0	7.0
39	11/07/23	48.1	9.5	51.9	10.3
40	12/07/23	57.4	9.9	42.6	7.3
41	13/07/23	47.5	9.0	52.5	10.0
42	14/07/23	51.5	9.6	48.5	9.0
43	15/07/23	55.5	10.4	44.5	8.4
44	16/07/23	44.1	7.9	55.9	9.9
45	17/07/23	54.6	8.7	45.4	7.3
46	18/07/23	52.2	9.6	47.8	8.8
47	19/07/23	47.7	9.1	52.3	10.0
48	20/07/23	49.3	10.5	50.7	10.8
49	21/07/23	54.5	10.8	45.5	9.0
50	22/07/23	58.2	9.1	41.8	6.5
51	23/07/23	48.1	8.5	51.9	9.1

UBV5	u5	2	23/03/23	49.7	8.7	50.3	8.8
		3	24/03/23	55.4	11.0	44.6	8.9
		4	25/03/23	64.3	9.4	35.7	5.2
		5	26/03/23	55.1	7.8	44.9	6.3
		6	27/03/23	46.8	7.9	53.2	8.9
		7	28/03/23	38.3	4.5	61.7	7.2
		8	29/03/23	34.0	5.1	66.0	9.8
		9	30/03/23	48.5	4.9	51.5	5.2
		10	31/03/23	42.8	4.7	57.2	6.2
		11	01/04/23	27.2	3.6	72.8	9.6
		12	02/04/23	38.2	5.0	61.8	8.0
		13	03/04/23	23.6	3.3	76.4	10.7
		14	04/04/23	33.6	4.3	66.4	8.4
		15	05/04/23	32.2	5.2	67.8	10.9
		16	06/04/23	31.6	4.7	68.4	10.3
		17	07/04/23	59.0	8.7	41.0	6.1
		18	08/04/23	48.8	8.1	51.2	8.5
		19	09/04/23	56.0	10.2	44.0	8.1
		20	10/04/23	43.5	7.9	56.5	10.3
		21	11/04/23	50.5	9.2	49.5	9.1
		22	12/04/23	50.2	9.4	49.8	9.3
		23	13/04/23	53.9	8.5	46.1	7.3
		24	14/04/23	45.3	9.0	54.7	10.9
		25	15/04/23	45.9	8.9	54.1	10.5
UBV6	u6	2	23/03/2023	48.3	8.8	51.7	9.5
		3	24/03/2023	41.6	8.4	58.4	11.8
		4	25/03/2023	42.3	9.1	57.7	12.4
		5	26/03/2023	45.2	8.3	54.8	10.1
		6	27/03/2023	45.2	8.9	54.8	10.8
		7	28/03/2023	46.5	7.2	53.5	8.3
		8	29/03/2023	57.4	10.5	42.6	7.8
		9	30/03/2023	51.7	9.8	48.3	9.2
		10	31/03/2023	44.5	8.6	55.5	10.7
		11	01/04/2023	50.9	9.3	49.1	9.0
		12	02/04/2023	50.2	9.3	49.8	9.3
		13	03/04/2023	55.8	8.8	44.2	7.0
		14	04/04/2023	50.1	9.4	49.9	9.3
		15	05/04/2023	47.1	8.1	52.9	9.1
		16	06/04/2023	50.7	9.1	49.3	8.8
		17	07/04/2023	50.3	9.0	49.7	8.9
		18	08/04/2023	46.9	8.8	53.1	9.9

		19	09/04/2023	50.6	8.4	49.4	8.2
		20	10/04/2023	42.9	8.0	57.1	10.6
		21	11/04/2023	51.1	10.3	48.9	9.9
		22	12/04/2023	44.9	5.8	55.1	7.1
UCH1	u7	1	27/02/23	46.4	5.4	53.6	6.3
		2	28/02/23	47.0	7.7	53.0	8.7
		3	01/03/23	31.7	4.6	68.3	9.9
		4	02/03/23	34.1	5.1	65.9	9.8
		5	03/03/23	28.8	4.3	71.2	10.7
		6	04/03/23	31.3	4.5	68.7	9.9
		7	05/03/23	32.0	4.5	68.0	9.7
		8	06/03/23	34.9	5.1	65.1	9.4
		9	07/03/23	42.2	5.3	57.8	7.3
		10	08/03/23	29.2	4.1	70.8	9.9
		11	09/03/23	38.6	4.5	61.4	7.2
		12	10/03/23	19.2	2.5	80.8	10.5
		13	11/03/23	45.3	7.7	54.7	9.3
		14	12/03/23	51.6	8.9	48.4	8.3
		15	13/03/23	43.5	8.2	56.5	10.7
		16	14/03/23	45.5	7.5	54.5	8.9
		17	15/03/23	41.9	6.2	58.1	8.5
		18	16/03/23	44.3	8.3	55.7	10.4
		19	17/03/23	39.1	7.6	60.9	11.8
		20	18/03/23	43.8	7.9	56.2	10.2
		21	19/03/23	38.1	5.6	61.9	9.1
UCH2	u8	1	22/01/2021	32.6	4.0	67.4	8.3
		2	23/01/2021	38.9	7.3	61.1	11.5
		3	24/01/2021	45.5	7.5	54.5	9.0
		4	25/01/2021	40.9	7.0	59.1	10.1
		5	26/01/2021	38.3	6.7	61.7	10.8
		6	27/01/2021	41.8	6.3	58.2	8.7
		7	28/01/2021	47.9	8.9	52.1	9.7
UCH3	u9	1	23/01/2021	40.1	4.9	59.9	7.4
		2	24/01/2021	51.3	8.8	48.7	8.4
		3	25/01/2021	36.1	7.6	63.9	13.5
		4	26/01/2021	37.7	6.2	62.3	10.2
		5	27/01/2021	51.5	9.1	48.5	8.6
		6	28/01/2021	34.0	6.8	66.0	13.3
		7	29/01/2021	44.1	8.5	55.9	10.7
UCH4	u10	1	27/02/2023	63.5	8.3	36.5	4.8
		2	28/02/2023	46.4	8.5	53.6	9.8

3	01/03/2023	45.5	6.5	54.5	7.8
4	02/03/2023	45.1	8.7	54.9	10.6
5	03/03/2023	62.5	8.8	37.5	5.3
6	04/03/2023	42.4	9.2	57.6	12.5
7	05/03/2023	53.5	8.3	46.5	7.2
8	06/03/2023	55.9	6.6	44.1	5.2
9	07/03/2023	53.8	6.4	46.2	5.5
10	08/03/2023	30.2	4.8	69.8	11.0
11	09/03/2023	36.1	5.6	63.9	10.0
12	10/03/2023	41.6	6.2	58.4	8.6
13	11/03/2023	30.6	6.1	69.4	13.8
14	12/03/2023	34.1	6.2	65.9	12.0
15	13/03/2023	56.1	6.6	43.9	5.2
16	14/03/2023	28.7	3.8	71.3	9.4
17	15/03/2023	29.2	4.2	70.8	10.2
18	16/03/2023	47.8	6.1	52.2	6.7
19	17/03/2023	38.2	6.3	61.8	10.2
20	18/03/2023	38.5	7.3	61.5	11.7

Table. 6 Individual ID (n = 18), data logger ID (n = 23), data logger recording day number, breakdown of daily activity into horizontal, terrestrial and vertical locomotion by time (hours) and proportion.

Individual	Data logger	Recording day	Date	Horizontal %	(hr)	Terrestrial %	(hr)	Vertical %	(hr)
SBV1	s1	1	20/02/15	94.1	3.2	0.0	0.00	5.9	0.2
		2	21/02/15	97.4	5.7	0.0	0.00	2.6	0.2
		3	22/02/15	98.5	7.4	0.0	0.00	1.5	0.1
		4	23/02/15	97.4	6.1	0.0	0.00	2.6	0.2
		5	24/02/15	95.4	4.4	0.0	0.00	4.6	0.2
	s2	2	05/03/15	93.5	6.2	0.0	0.00	6.5	0.4
		3	06/03/15	95.8	4.7	0.0	0.00	4.2	0.2
		4	07/03/15	88.3	5.4	0.0	0.00	11.7	0.7
		5	08/03/15	95.8	7.4	0.0	0.00	4.2	0.3
	s3	2	10/07/15	85.4	7.8	0.0	0.00	14.6	1.3
		3	11/07/15	93.0	4.5	0.0	0.00	7.0	0.3

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		4	12/07/15	88.6	5.5	0.0	0.00	11.4	0.7
		5	13/07/15	90.0	6.3	0.0	0.00	10.0	0.7
		6	14/07/15	91.6	7.4	0.0	0.00	8.4	0.7
		7	15/07/15	92.8	7.0	0.0	0.00	7.2	0.5
	s4	2	26/07/15	95.4	5.1	0.0	0.00	4.6	0.2
		3	27/07/15	95.5	8.6	0.0	0.00	4.5	0.4
		4	28/07/15	90.4	5.1	0.0	0.00	9.6	0.5
		5	29/07/15	91.2	7.2	0.0	0.00	8.8	0.7
		6	30/07/15	95.3	7.2	0.0	0.00	4.7	0.4
		7	31/07/15	92.9	7.5	0.0	0.00	7.1	0.6
		8	01/08/15	92.1	4.6	0.0	0.00	7.9	0.4
SBV2	s5	1	24/04/14	89.6	3.1	0.0	0.00	10.4	0.4
		2	25/04/14	96.9	6.7	0.0	0.00	3.1	0.2
		3	26/04/14	95.0	6.7	0.0	0.00	5.0	0.3
		4	27/04/14	96.1	7.9	0.0	0.00	3.9	0.3
		5	28/04/14	89.9	4.2	0.0	0.00	10.1	0.5
		6	29/04/14	94.6	5.9	0.0	0.00	5.4	0.3
		7	30/04/14	91.6	7.1	0.0	0.00	8.4	0.7
		8	01/05/14	94.3	4.7	0.0	0.00	5.7	0.3
	s6	2	09/08/15	90.4	6.0	0.0	0.00	9.6	0.6
		3	10/08/15	98.6	7.3	0.0	0.00	1.4	0.1
		4	11/08/15	99.6	6.4	0.0	0.00	0.4	0.0
		5	12/08/15	98.5	5.5	0.0	0.00	1.5	0.1
		6	13/08/15	88.7	5.8	0.0	0.00	11.3	0.7
		7	14/08/15	98.7	5.2	0.0	0.00	1.3	0.1
		8	15/08/15	99.0	4.2	0.0	0.00	1.0	0.0
SBV3	s7	2	21/11/14	99.4	6.8	0.0	0.00	0.6	0.0
		3	22/11/14	92.6	5.5	0.0	0.00	7.4	0.4
		4	23/11/14	93.4	7.6	0.0	0.00	6.6	0.5
		5	24/11/14	96.1	7.6	0.0	0.00	3.9	0.3
		6	25/11/14	99.7	6.1	0.0	0.00	0.3	0.0
	s8	2	12/02/15	98.4	8.5	0.0	0.00	1.6	0.1
		3	13/02/15	97.2	7.2	0.0	0.00	2.8	0.2
		4	14/02/15	97.7	8.5	0.0	0.00	2.3	0.2
		5	15/02/15	98.7	7.2	0.0	0.00	1.3	0.1
		6	16/02/15	97.2	7.1	0.0	0.00	2.8	0.2
		7	17/02/15	98.2	6.7	0.0	0.00	1.8	0.1
SBV4	s9	1	08/09/14	94.8	6.6	1.8	0.05	4.4	0.3

		2	09/09/14	99.1	6.4	0.0	0.00	0.9	0.1
		3	10/09/14	97.7	6.8	0.0	0.00	2.3	0.2
		4	11/09/14	95.6	7.1	0.0	0.00	4.4	0.3
		5	12/09/14	95.4	7.4	0.0	0.00	4.6	0.4
		6	13/09/14	94.6	5.3	0.0	0.00	5.4	0.3
		7	14/09/14	97.7	3.6	0.0	0.00	2.3	0.1
		8	15/09/14	100.0	6.7	0.0	0.00	0.0	0.0
SBV5	s10	2	06/08/15	85.2	6.9	4.1	0.30	11.1	0.9
		3	07/08/15	92.5	8.7	0.6	0.04	7.1	0.7
SBV6	s11	1	27/03/15	97.1	8.0	0.0	0.00	2.9	0.2
		2	28/03/15	98.4	6.6	0.0	0.00	1.6	0.1
		3	29/03/15	90.9	8.7	0.0	0.00	9.1	0.9
		4	30/03/15	92.9	8.9	0.0	0.00	7.1	0.7
		5	31/03/15	95.8	9.8	0.0	0.00	4.2	0.4
		6	01/04/15	98.5	7.3	0.0	0.00	1.5	0.1
		7	02/04/15	97.0	7.3	0.0	0.00	3.0	0.2
		8	03/04/15	96.0	5.0	0.0	0.00	4.0	0.2
		9	04/04/15	99.4	2.5	0.0	0.00	0.6	0.0
SBV7	s12	2	16/04/15	98.0	8.1	0.0	0.00	2.0	0.2
		3	17/04/15	98.6	8.8	0.0	0.00	1.4	0.1
		4	18/04/15	96.3	7.3	0.0	0.00	3.7	0.3
		5	19/04/15	97.5	6.5	0.0	0.00	2.5	0.2
		6	20/04/15	95.1	7.1	0.0	0.00	4.9	0.4
		7	21/04/15	91.7	9.7	0.0	0.00	8.3	0.9
		8	22/04/15	85.8	1.8	0.0	0.00	14.2	0.3
SCH1	s13	2	11/03/15	84.6	9.4	4.4	0.42	11.6	1.3
		3	12/03/15	94.6	5.9	0.0	0.00	5.4	0.3
UBV1	u1	2	20/04/21	99.5	5.1	0.0	0.00	0.5	0.0
		3	21/04/21	90.9	8.6	0.0	0.00	9.1	0.9
		4	22/04/21	80.2	2.4	0.0	0.00	19.8	0.6
UBV2	u2	1	19/05/21	94.0	3.8	0.0	0.00	6.0	0.2
		2	20/05/21	91.6	5.9	0.0	0.00	8.4	0.5
		3	21/05/21	94.6	6.8	0.0	0.00	5.4	0.4
		4	22/05/21	89.4	6.1	0.0	0.00	10.6	0.7
		5	23/05/21	95.9	5.8	0.0	0.00	4.1	0.2
UBV3	u3	2	20/09/22	93.2	6.8	0.0	0.00	6.8	0.5
		3	21/09/22	96.0	5.2	0.0	0.00	4.0	0.2
		4	22/09/22	94.0	6.3	0.0	0.00	6.0	0.4
		5	23/09/22	93.5	7.3	0.0	0.00	6.5	0.5
		6	24/09/22	92.2	5.3	0.0	0.00	7.8	0.4
		7	25/09/22	93.8	5.9	0.0	0.00	6.2	0.4

8	26/09/22	95.5	6.9	0.0	0.00	4.5	0.3
9	27/09/22	96.0	7.3	0.0	0.00	4.0	0.3
10	28/09/22	90.6	2.3	0.0	0.00	9.4	0.2
2	04/06/23	92.2	8.2	0.0	0.00	7.8	0.7
3	05/06/23	90.6	7.8	0.0	0.00	9.4	0.8
4	06/06/23	95.0	7.6	0.0	0.00	5.0	0.4
5	07/06/23	95.0	9.7	0.0	0.00	5.0	0.5
6	08/06/23	91.1	7.2	0.0	0.00	8.9	0.7
7	09/06/23	89.9	6.8	0.0	0.00	10.1	0.8
8	10/06/23	87.2	5.5	0.0	0.00	12.8	0.8
9	11/06/23	89.0	5.6	0.0	0.00	11.0	0.7
10	12/06/23	87.6	5.8	0.0	0.00	12.4	0.8
11	13/06/23	90.2	7.6	0.0	0.00	9.8	0.8
12	14/06/23	84.8	6.2	0.0	0.00	15.2	1.1
13	15/06/23	84.2	6.5	0.0	0.00	15.8	1.2
14	16/06/23	86.7	6.0	0.0	0.00	13.3	0.9
15	17/06/23	90.7	6.0	0.0	0.00	9.3	0.6
16	18/06/23	82.3	6.8	0.0	0.00	17.7	1.5
17	19/06/23	91.8	9.0	0.0	0.00	8.2	0.8
18	20/06/23	95.5	9.2	0.0	0.00	4.5	0.4
19	21/06/23	97.3	8.3	0.0	0.00	2.7	0.2
20	22/06/23	85.7	8.3	0.0	0.00	14.3	1.4
21	23/06/23	89.1	6.2	0.0	0.00	10.9	0.8
22	24/06/23	89.2	8.5	0.0	0.00	10.8	1.0
23	25/06/23	90.9	8.1	0.0	0.00	9.1	0.8
24	26/06/23	91.5	8.2	0.0	0.00	8.5	0.8
25	27/06/23	80.5	7.8	0.0	0.00	19.5	1.9
26	28/06/23	95.1	9.5	0.0	0.00	4.9	0.5
27	29/06/23	97.8	7.4	0.0	0.00	2.2	0.2
28	30/06/23	86.6	8.0	0.0	0.00	13.4	1.2
29	01/07/23	87.5	5.2	0.0	0.00	12.5	0.7
30	02/07/23	95.7	5.5	0.0	0.00	4.3	0.3
31	03/07/23	94.7	5.5	0.0	0.00	5.3	0.3
32	04/07/23	85.9	6.3	0.0	0.00	14.1	1.0
33	05/07/23	93.1	7.5	0.0	0.00	6.9	0.6
34	06/07/23	92.4	6.8	0.0	0.00	7.6	0.6
35	07/07/23	90.8	6.3	0.0	0.00	9.2	0.6
36	08/07/23	91.5	6.5	0.0	0.00	8.5	0.6
37	09/07/23	91.9	5.8	0.0	0.00	8.1	0.5
38	10/07/23	88.2	4.5	0.0	0.00	11.8	0.6
39	11/07/23	92.6	8.8	0.0	0.00	7.4	0.7

UBV4   u4

	40	12/07/23	96.1	9.5	0.0	0.00	3.9	0.4
	41	13/07/23	93.3	8.4	0.0	0.00	6.7	0.6
	42	14/07/23	91.8	8.8	0.0	0.00	8.2	0.8
	43	15/07/23	95.4	10.0	0.0	0.00	4.6	0.5
	44	16/07/23	90.5	7.1	0.0	0.00	9.5	0.7
	45	17/07/23	90.7	7.9	0.0	0.00	9.3	0.8
	46	18/07/23	87.6	8.4	0.0	0.00	12.4	1.2
	47	19/07/23	91.8	8.4	0.0	0.00	8.2	0.8
	48	20/07/23	94.0	9.9	0.0	0.00	6.0	0.6
	49	21/07/23	90.0	9.8	0.0	0.00	10.0	1.1
	50	22/07/23	90.7	8.2	0.0	0.00	9.3	0.8
	51	23/07/23	91.3	7.7	0.0	0.00	8.7	0.7
UBV5 u5	2	23/03/23	99.2	8.7	0.0	0.00	0.8	0.1
	3	24/03/23	93.0	10.2	0.0	0.00	7.0	0.8
	4	25/03/23	96.2	9.1	0.0	0.00	3.8	0.4
	5	26/03/23	99.0	7.7	0.0	0.00	1.0	0.1
	6	27/03/23	98.1	7.7	0.0	0.00	1.9	0.1
	7	28/03/23	90.4	4.1	0.0	0.00	9.6	0.4
	8	29/03/23	97.4	4.9	0.0	0.00	2.6	0.1
	9	30/03/23	99.4	4.8	0.0	0.00	0.6	0.0
	10	31/03/23	96.8	4.5	0.0	0.00	3.2	0.2
	11	01/04/23	97.1	3.5	0.0	0.00	2.9	0.1
	12	02/04/23	97.5	4.9	0.0	0.00	2.5	0.1
	13	03/04/23	93.5	3.1	0.0	0.00	6.5	0.2
	14	04/04/23	79.1	3.4	0.0	0.00	20.9	0.9
	15	05/04/23	95.7	4.9	0.0	0.00	4.3	0.2
	16	06/04/23	95.3	4.5	0.0	0.00	4.7	0.2
	17	07/04/23	98.9	8.6	0.0	0.00	1.1	0.1
	18	08/04/23	95.1	7.7	0.0	0.00	4.9	0.4
	19	09/04/23	94.6	9.7	0.0	0.00	5.4	0.6
	20	10/04/23	97.6	7.8	0.0	0.00	2.4	0.2
	21	11/04/23	95.5	8.8	0.0	0.00	4.5	0.4
	22	12/04/23	93.7	8.8	0.0	0.00	6.3	0.6
	23	13/04/23	86.9	7.4	0.0	0.00	13.1	1.1
	24	14/04/23	92.2	8.3	0.0	0.00	7.8	0.7
	25	15/04/23	98.0	8.7	0.0	0.00	2.0	0.2
UBV6 u6	2	23/03/23	99.6	8.8	0.0	0.00	0.4	0.0
	3	24/03/23	100.0	8.4	0.0	0.00	0.0	0.0
	4	25/03/23	100.0	9.1	0.0	0.00	0.0	0.0
	5	26/03/23	98.7	8.2	0.0	0.00	1.3	0.1
	6	27/03/23	98.4	8.8	0.0	0.00	1.6	0.1

		7	28/03/23	99.2	7.1	0.0	0.00	0.8	0.1
		8	29/03/23	97.8	10.3	0.0	0.00	2.2	0.2
		9	30/03/23	86.2	8.5	0.0	0.00	13.8	1.4
		10	31/03/23	93.5	8.0	0.0	0.00	6.5	0.6
		11	01/04/23	96.3	9.0	0.0	0.00	3.7	0.3
		12	02/04/23	96.2	9.0	0.0	0.00	3.8	0.4
		13	03/04/23	93.3	8.3	0.0	0.00	6.7	0.6
		14	04/04/23	90.4	8.5	0.0	0.00	9.6	0.9
		15	05/04/23	97.3	7.9	0.0	0.00	2.7	0.2
		16	06/04/23	98.4	8.9	0.0	0.00	1.6	0.1
		17	07/04/23	96.0	8.7	1.0	0.04	3.6	0.3
		18	08/04/23	96.4	8.4	0.0	0.00	3.6	0.3
		19	09/04/23	96.9	8.2	0.6	0.03	2.7	0.2
		20	10/04/23	95.5	7.6	0.0	0.00	4.5	0.4
		21	11/04/23	96.7	10.0	0.0	0.00	3.3	0.3
		22	12/04/23	86.9	5.0	0.0	0.00	13.1	0.8
UCH1	u7	1	27/02/23	99.8	5.4	0.0	0.00	0.2	0.0
		2	28/02/23	97.7	7.6	0.0	0.00	2.3	0.2
		3	01/03/23	96.2	4.4	0.0	0.00	3.8	0.2
		4	02/03/23	95.9	4.9	0.9	0.05	3.2	0.2
		5	03/03/23	97.3	4.2	0.0	0.00	2.7	0.1
		6	04/03/23	96.8	4.4	0.0	0.00	3.2	0.1
		7	05/03/23	96.3	4.4	0.0	0.00	3.7	0.2
		8	06/03/23	93.4	4.7	0.0	0.00	6.6	0.3
		9	07/03/23	93.6	5.0	0.0	0.00	6.4	0.3
		10	08/03/23	90.9	3.7	0.0	0.00	9.1	0.4
		11	09/03/23	96.4	4.3	0.0	0.00	3.6	0.2
		12	10/03/23	94.6	2.4	0.0	0.00	5.4	0.1
		13	11/03/23	99.0	7.6	0.0	0.00	1.0	0.1
		14	12/03/23	99.2	8.8	0.0	0.00	0.8	0.1
		15	13/03/23	97.7	8.1	0.0	0.00	2.3	0.2
		16	14/03/23	96.3	7.2	0.0	0.00	3.7	0.3
		17	15/03/23	98.6	6.1	0.0	0.00	1.4	0.1
		18	16/03/23	98.5	8.2	0.0	0.00	1.5	0.1
		19	17/03/23	97.8	7.4	0.0	0.00	2.2	0.2
		20	18/03/23	98.0	7.8	0.0	0.00	2.0	0.2
		21	19/03/23	97.7	5.5	0.0	0.00	2.3	0.1
UCH2	u8	1	22/01/21	99.2	4.0	0.0	0.00	0.8	0.0
		2	23/01/21	96.0	7.0	0.0	0.00	4.0	0.3
		3	24/01/21	95.6	7.2	0.0	0.00	4.4	0.3
		4	25/01/21	93.8	6.6	0.0	0.00	6.2	0.4

		5	26/01/21	95.7	6.4	0.0	0.00	4.3	0.3
		6	27/01/21	97.6	6.1	0.0	0.00	2.4	0.2
		7	28/01/21	84.7	7.5	0.0	0.00	15.3	1.4
UCH3	u9	1	23/01/21	88.4	4.4	0.4	0.02	11.3	0.6
		2	24/01/21	86.5	7.6	0.4	0.12	12.1	1.1
		3	25/01/21	99.3	7.6	0.0	0.00	0.7	0.1
		4	26/01/21	99.3	6.2	0.0	0.00	0.7	0.0
		5	27/01/21	99.7	9.1	0.0	0.00	0.3	0.0
		6	28/01/21	98.2	6.7	0.0	0.00	1.8	0.1
		7	29/01/21	92.8	7.8	3.2	0.13	5.6	0.5
UCH4	u10	1	27/02/23	97.9	8.1	0.0	0.00	2.1	0.2
		2	28/02/23	99.9	8.5	0.0	0.00	0.1	0.0
		3	01/03/23	87.5	5.7	0.0	0.00	12.5	0.8
		4	02/03/23	98.8	8.6	0.0	0.00	1.2	0.1
		5	03/03/23	98.2	8.6	0.0	0.00	1.8	0.2
		6	04/03/23	96.3	8.9	0.0	0.00	3.7	0.3
		7	05/03/23	95.4	7.9	0.0	0.00	4.6	0.4
		8	06/03/23	91.1	6.0	0.0	0.00	8.9	0.6
		9	07/03/23	91.0	5.8	0.0	0.00	9.0	0.6
		10	08/03/23	94.8	4.5	0.0	0.00	5.2	0.2
		11	09/03/23	88.1	5.0	0.0	0.00	11.9	0.7
		12	10/03/23	96.5	6.0	0.0	0.00	3.5	0.2
		13	11/03/23	85.9	5.2	0.0	0.00	14.1	0.9
		14	12/03/23	94.2	5.8	0.0	0.00	5.8	0.4
		15	13/03/23	95.7	6.3	0.0	0.00	4.3	0.3
		16	14/03/23	87.5	3.3	0.0	0.00	12.5	0.5
		17	15/03/23	91.9	3.9	0.0	0.00	8.1	0.3
		18	16/03/23	92.5	5.7	0.0	0.00	7.5	0.5
		19	17/03/23	92.5	5.9	0.0	0.00	7.5	0.5
		20	18/03/23	93.3	6.8	0.0	0.00	6.7	0.5

Table. 7 Individual ID, data logger ID, the daily mean (hrs), total recorded (hrs) and total proportion (%) of vertical locomotion spent ascending and descending for each individual (n = 18) and data logger (n = 23)

| Individual | Data Logger | Vertical ascent | | | Vertical descent | | |
		Daily mean (hrs)	Total (hrs)	% of vertical total	Daily mean (hrs)	Total (hrs)	% of vertical total
SBV1		0.3	6.1	60.4	0.2	4.0	39.6
	s1	0.1	0.4	53.2	0.1	0.4	46.8
	s2	0.2	0.7	42.3	0.2	1.0	57.7
	s3	0.5	2.8	65.4	0.2	1.5	34.6
	s4	0.3	2.1	65.1	0.2	1.1	34.9
SBV2		0.2	3.4	71.5	0.1	1.3	28.5
	s5	0.3	2.3	78.5	0.1	0.6	21.5
	s6	0.1	1.0	59.4	0.1	0.7	40.6
SBV3		0.1	0.8	32.8	0.1	1.6	67.2
	s7	0.1	0.3	20.7	0.2	1.1	79.3
	s8	0.1	0.5	49.6	0.1	0.5	50.4
SBV4	s9	0.1	1.0	63.5	0.1	0.6	36.5
SBV5	s10	0.5	1.1	66.7	0.3	0.5	33.3
SBV6	s11	0.2	1.7	59.2	0.1	1.2	40.8
SBV7	s12	0.2	1.4	63.5	0.1	0.8	36.5
SCH1	s13	0.6	1.1	12.2	0.2	0.5	29.3
UBV1	u1	0.2	0.7	50.2	0.2	0.7	49.8
UBV2	u2	0.2	1.1	52.4	0.2	1.0	47.6
UBV3	u3	0.2	1.9	56.1	0.2	1.5	43.9
UBV4	u4	0.4	20.4	54.0	0.3	17.4	46.0
UBV5	u5	0.2	4.9	59.5	0.1	3.3	40.5
UBV6	u6	0.2	4.3	58.9	0.1	3.0	41.1
UCH1	u7	0.1	2.1	57.4	0.1	1.5	42.6
UCH2	u8	0.1	0.6	22.3	0.3	2.3	77.7
UCH3	u9	0.1	1.0	41.6	0.2	1.4	58.4
UCH4	u10	0.2	4.6	57.5	0.2	3.4	42.5

Table. 8 Individual ID (n = 18), data logger ID (n = 23), data logger recording day number, breakdown of daily vertical locomotion into ascent and descent by time (hours) spent and proportion.

Individual	Dataset	Recording day	Date	Vertical ascent		Vertical descent	
				%	(hr)	%	(hr)
SBV1	s1	1	20/02/15	74.1	0.15	25.9	0.05
		2	21/02/15	49.8	0.08	50.2	0.08
		3	22/02/15	42.7	0.05	57.3	0.06
		4	23/02/15	50.7	0.08	49.3	0.08
		5	24/02/15	43.3	0.09	56.7	0.12
	s2	2	05/03/15	29.5	0.13	70.5	0.30
		3	06/03/15	18.0	0.04	82.0	0.17
		4	07/03/15	52.4	0.38	47.6	0.34
		5	08/03/15	52.7	0.17	47.3	0.15
	s3	2	10/07/15	58.5	0.79	41.5	0.56
		3	11/07/15	79.9	0.27	20.1	0.07
		4	12/07/15	66.1	0.47	33.9	0.24
		5	13/07/15	63.5	0.44	36.5	0.25
		6	14/07/15	68.6	0.46	31.4	0.21
		7	15/07/15	71.0	0.39	29.0	0.16
	s4	2	26/07/15	86.1	0.21	13.9	0.03
		3	27/07/15	47.9	0.19	52.1	0.21
		4	28/07/15	85.2	0.46	14.8	0.08
		5	29/07/15	50.2	0.35	49.8	0.34
		6	30/07/15	75.1	0.27	24.9	0.09
		7	31/07/15	47.0	0.27	53.0	0.30
		8	01/08/15	85.2	0.34	14.8	0.06
SBV2	s5	1	24/04/14	88.9	0.32	11.1	0.04
		2	25/04/14	68.5	0.15	31.5	0.07
		3	26/04/14	85.7	0.30	14.3	0.05
		4	27/04/14	74.6	0.24	25.4	0.08
		5	28/04/14	68.1	0.32	31.9	0.15
		6	29/04/14	94.6	0.32	5.4	0.02
		7	30/04/14	77.9	0.51	22.1	0.14
		8	01/05/14	67.6	0.19	32.4	0.09

		2	09/08/15	62.0	0.40	38.0	0.24
	s6						
		3	10/08/15	58.7	0.06	41.3	0.04
		4	11/08/15	79.4	0.02	20.6	0.01
		5	12/08/15	21.1	0.02	78.9	0.06
		6	13/08/15	60.0	0.45	40.0	0.30
		7	14/08/15	55.8	0.04	44.2	0.03
		8	15/08/15	77.9	0.03	22.1	0.01
SBV3	s7	2	21/11/14	0.0	0.00	100.0	0.04
		3	22/11/14	34.1	0.15	65.9	0.29
		4	23/11/14	15.0	0.08	85.0	0.45
		5	24/11/14	12.8	0.04	87.2	0.27
		6	25/11/14	47.0	0.01	53.0	0.01
	s8	2	12/02/15	65.7	0.09	34.3	0.05
		3	13/02/15	55.0	0.11	45.0	0.09
		4	14/02/15	39.1	0.08	60.9	0.12
		5	15/02/15	52.5	0.05	47.5	0.05
		6	16/02/15	58.4	0.12	41.6	0.09
		7	17/02/15	23.6	0.03	76.4	0.10
SBV4	s9	1	08/09/14	78.9	0.24	21.1	0.07
		2	09/09/14	71.8	0.04	28.2	0.02
		3	10/09/14	80.0	0.13	20.0	0.03
		4	11/09/14	61.1	0.20	38.9	0.13
		5	12/09/14	58.3	0.21	41.7	0.15
		6	13/09/14	52.6	0.16	47.4	0.14
		7	14/09/14	40.8	0.04	59.2	0.05
		8	15/09/14	0.0	0.00	0.0	0.00
SBV5	s10	2	06/08/15	64.6	0.58	35.4	0.32
		3	07/08/15	69.6	0.47	30.4	0.21
SBV6	s11	1	27/03/15	89.3	0.21	10.7	0.03
		2	28/03/15	68.1	0.08	31.9	0.04
		3	29/03/15	58.5	0.50	41.5	0.36
		4	30/03/15	56.0	0.38	44.0	0.30
		5	31/03/15	66.7	0.29	33.3	0.14
		6	01/04/15	43.7	0.05	56.3	0.06
		7	02/04/15	40.4	0.09	59.6	0.14
		8	03/04/15	47.6	0.10	52.4	0.11
		9	04/04/15	40.2	0.01	59.8	0.01
SBV7	s12	2	16/04/15	63.9	0.11	36.1	0.06
		3	17/04/15	50.7	0.06	49.3	0.06
		4	18/04/15	62.3	0.17	37.7	0.11
		5	19/04/15	62.2	0.10	37.8	0.06

		6	20/04/15	65.2	0.24	34.8	0.13
		7	21/04/15	58.3	0.51	41.7	0.37
		8	22/04/15	83.6	0.25	16.4	0.05
SCH1	s13	2	11/03/15	70.6	0.91	29.4	0.38
		3	12/03/15	71.0	0.24	29.0	0.10
UBV1	u1	2	20/04/21	55.9	0.01	44.1	0.01
		3	21/04/21	48.2	0.42	51.8	0.45
		4	22/04/21	52.9	0.31	47.1	0.28
UBV2	u2	1	19/05/21	91.2	0.22	8.8	0.02
		2	20/05/21	54.6	0.30	45.4	0.25
		3	21/05/21	41.3	0.16	58.7	0.23
		4	22/05/21	60.1	0.44	39.9	0.29
		5	23/05/21	4.6	0.01	95.4	0.24
UBV3	u3	2	20/09/22	67.5	0.34	32.5	0.16
		3	21/09/22	57.7	0.12	42.3	0.09
		4	22/09/22	67.7	0.27	32.3	0.13
		5	23/09/22	48.0	0.24	52.0	0.26
		6	24/09/22	50.1	0.22	49.9	0.22
		7	25/09/22	73.0	0.29	27.0	0.11
		8	26/09/22	25.9	0.08	74.1	0.24
		9	27/09/22	46.8	0.14	53.2	0.16
		10	28/09/22	65.7	0.16	34.3	0.08
UBV4	u4	2	04/06/23	58.6	0.40	41.4	0.29
		3	05/06/23	60.7	0.49	39.3	0.32
		4	06/06/23	63.7	0.25	36.3	0.14
		5	07/06/23	53.9	0.28	46.1	0.24
		6	08/06/23	53.7	0.38	46.3	0.32
		7	09/06/23	53.5	0.41	46.5	0.35
		8	10/06/23	67.1	0.54	32.9	0.26
		9	11/06/23	31.9	0.22	68.1	0.47
		10	12/06/23	62.1	0.51	37.9	0.31
		11	13/06/23	52.6	0.43	47.4	0.39
		12	14/06/23	43.7	0.49	56.3	0.63
		13	15/06/23	53.6	0.65	46.4	0.56
		14	16/06/23	47.5	0.44	52.5	0.49
		15	17/06/23	67.6	0.41	32.4	0.20
		16	18/06/23	49.4	0.72	50.6	0.74
		17	19/06/23	51.4	0.41	48.6	0.39
		18	20/06/23	54.7	0.24	45.3	0.20
		19	21/06/23	41.8	0.09	58.2	0.13
		20	22/06/23	66.2	0.91	33.8	0.47

21	23/06/23	39.1	0.30	60.9	0.46
22	24/06/23	59.7	0.61	40.3	0.41
23	25/06/23	55.1	0.45	44.9	0.37
24	26/06/23	54.6	0.42	45.4	0.35
25	27/06/23	49.1	0.92	50.9	0.95
26	28/06/23	43.9	0.21	56.1	0.27
27	29/06/23	39.4	0.07	60.6	0.10
28	30/06/23	56.8	0.70	43.2	0.53
29	01/07/23	63.8	0.47	36.2	0.27
30	02/07/23	24.2	0.06	75.8	0.19
31	03/07/23	59.1	0.18	40.9	0.13
32	04/07/23	65.5	0.67	34.5	0.35
33	05/07/23	54.2	0.30	45.8	0.26
34	06/07/23	50.8	0.29	49.2	0.28
35	07/07/23	58.3	0.37	41.7	0.27
36	08/07/23	50.3	0.30	49.7	0.30
37	09/07/23	68.0	0.35	32.0	0.16
38	10/07/23	51.8	0.31	48.2	0.29
39	11/07/23	71.9	0.51	28.1	0.20
40	12/07/23	40.2	0.16	59.8	0.23
41	13/07/23	53.2	0.32	46.8	0.28
42	14/07/23	47.3	0.37	52.7	0.42
43	15/07/23	40.7	0.19	59.3	0.28
44	16/07/23	58.7	0.44	41.3	0.31
45	17/07/23	56.0	0.45	44.0	0.36
46	18/07/23	50.6	0.60	49.4	0.59
47	19/07/23	46.4	0.35	53.6	0.40
48	20/07/23	74.3	0.47	25.7	0.16
49	21/07/23	52.5	0.57	47.5	0.51
50	22/07/23	45.4	0.39	54.6	0.46
51	23/07/23	47.9	0.35	52.1	0.38
UBV5 u5	2	23/03/23	50.9	0.04	49.1	0.03
	3	24/03/23	49.8	0.38	50.2	0.39
	4	25/03/23	67.0	0.24	33.0	0.12
	5	26/03/23	73.8	0.06	26.2	0.02
	6	27/03/23	57.2	0.09	42.8	0.06
	7	28/03/23	68.6	0.29	31.4	0.13
	8	29/03/23	31.1	0.04	68.9	0.09
	9	30/03/23	29.8	0.01	70.2	0.02
	10	31/03/23	88.6	0.13	11.4	0.02
	11	01/04/23	79.4	0.08	20.6	0.02

		12	02/04/23	37.6	0.05	62.4	0.08
		13	03/04/23	74.8	0.16	25.2	0.05
		14	04/04/23	57.3	0.51	42.7	0.38
		15	05/04/23	46.6	0.10	53.4	0.12
		16	06/04/23	87.7	0.19	12.3	0.03
		17	07/04/23	65.9	0.06	34.1	0.03
		18	08/04/23	57.6	0.23	42.4	0.17
		19	09/04/23	60.3	0.33	39.7	0.22
		20	10/04/23	30.3	0.06	69.7	0.13
		21	11/04/23	70.8	0.29	29.2	0.12
		22	12/04/23	60.2	0.36	39.8	0.24
		23	13/04/23	57.5	0.64	42.5	0.48
		24	14/04/23	58.2	0.41	41.8	0.30
		25	15/04/23	59.1	0.10	40.9	0.07
UBV6	u6	2	23/03/23	100.0	0.04	0.0	0.00
		3	24/03/23	0.0	0.00	0.0	0.00
		4	25/03/23	0.0	0.00	0.0	0.00
		5	26/03/23	84.1	0.09	15.9	0.02
		6	27/03/23	57.0	0.08	43.0	0.06
		7	28/03/23	67.3	0.04	32.7	0.02
		8	29/03/23	59.9	0.14	40.1	0.09
		9	30/03/23	60.0	0.81	40.0	0.54
		10	31/03/23	59.8	0.34	40.2	0.23
		11	01/04/23	57.2	0.20	42.8	0.15
		12	02/04/23	61.4	0.22	38.6	0.14
		13	03/04/23	47.9	0.29	52.1	0.31
		14	04/04/23	52.4	0.47	47.6	0.43
		15	05/04/23	62.3	0.13	37.7	0.08
		16	06/04/23	50.9	0.07	49.1	0.07
		17	07/04/23	57.7	0.19	42.3	0.14
		18	08/04/23	56.3	0.18	43.7	0.14
		19	09/04/23	57.3	0.13	42.7	0.10
		20	10/04/23	59.7	0.21	40.3	0.14
		21	11/04/23	60.8	0.21	39.2	0.13
		22	12/04/23	66.9	0.51	33.1	0.25
UCH1	u7	1	27/02/23	100.0	0.01	0.0	0.00
		2	28/02/23	100.0	0.18	0.0	0.00
		3	01/03/23	44.0	0.08	56.0	0.10
		4	02/03/23	87.0	0.14	13.0	0.02
		5	03/03/23	42.8	0.05	57.2	0.07
		6	04/03/23	85.5	0.12	14.5	0.02

		7	05/03/23	55.0	0.09	45.0	0.08
		8	06/03/23	71.6	0.24	28.4	0.10
		9	07/03/23	34.6	0.12	65.4	0.22
		10	08/03/23	49.7	0.18	50.3	0.19
		11	09/03/23	44.6	0.07	55.4	0.09
		12	10/03/23	64.5	0.09	35.5	0.05
		13	11/03/23	27.7	0.02	72.3	0.05
		14	12/03/23	62.9	0.05	37.1	0.03
		15	13/03/23	47.1	0.09	52.9	0.10
		16	14/03/23	48.7	0.14	51.3	0.14
		17	15/03/23	52.6	0.05	47.4	0.04
		18	16/03/23	59.9	0.08	40.1	0.05
		19	17/03/23	59.8	0.10	40.2	0.07
		20	18/03/23	60.8	0.10	39.2	0.06
		21	19/03/23	58.4	0.08	41.6	0.05
UCH2	u8	1	22/01/21	0.0	0.00	100.0	0.03
		2	23/01/21	45.6	0.13	54.4	0.16
		3	24/01/21	29.9	0.10	70.1	0.23
		4	25/01/21	32.2	0.14	67.8	0.30
		5	26/01/21	30.6	0.09	69.4	0.20
		6	27/01/21	48.3	0.07	51.7	0.08
		7	28/01/21	8.1	0.11	91.9	1.25
UCH3	u9	1	23/01/21	45.6	0.25	54.4	0.30
		2	24/01/21	40.2	0.43	59.8	0.64
		3	25/01/21	5.4	0.00	94.6	0.05
		4	26/01/21	20.2	0.01	79.8	0.03
		5	27/01/21	9.8	0.00	90.2	0.03
		6	28/01/21	34.4	0.04	65.6	0.08
		7	29/01/21	49.8	0.24	50.2	0.24
UCH4	u10	1	27/02/23	93.4	0.16	6.6	0.01
		2	28/02/23	100.0	0.01	0.0	0.00
		3	01/03/23	15.5	0.13	84.5	0.69
		4	02/03/23	88.9	0.09	11.1	0.01
		5	03/03/23	85.9	0.14	14.1	0.02
		6	04/03/23	70.0	0.24	30.0	0.10
		7	05/03/23	79.2	0.30	20.8	0.08
		8	06/03/23	48.0	0.28	52.0	0.30
		9	07/03/23	66.4	0.38	33.6	0.19
		10	08/03/23	58.7	0.15	41.3	0.10
		11	09/03/23	70.0	0.47	30.0	0.20
		12	10/03/23	73.7	0.16	26.3	0.06

13	11/03/23	46.3	0.40	53.7	0.46
14	12/03/23	65.4	0.24	34.6	0.13
15	13/03/23	59.7	0.17	40.3	0.11
16	14/03/23	65.4	0.31	34.6	0.16
17	15/03/23	53.3	0.18	46.7	0.16
18	16/03/23	48.2	0.22	51.8	0.24
19	17/03/23	67.8	0.32	32.2	0.15
20	18/03/23	54.7	0.27	45.3	0.22

Table. 9 Individual ID (n = 12), data logger ID (n = 17), the total proportion of time spent active in the diurnal and nocturnal diel phases

Individual	Data logger	Day %	Night %
UBV1	u1	43.4	56.6
UBV3	u3	52.8	47.2
UBV4	u4	8.1	91.9
UBV5	u5	45.1	54.9
UBV6	u6	41.3	58.7
SBV1		23.6	76.4
	s1	21.5	78.5
	s2	23.0	77.0
	s3	34.2	65.8
	s4	15.7	84.3
SBV2		55.1	44.9
	s5	61.5	38.5
	s6	48.7	51.3
SBV3		77.4	22.6
	s7	80.4	19.6
	s8	74.3	25.7
SBV4	s9	63.8	36.2
SBV5	s10	55.0	45.0
SBV6	s11	67.1	32.9
SBV7	s12	68.7	31.3

Table. 10 Individual ID (n = 12), data logger ID (n = 17), data logger recording day number, daily proportion of time spent active in the diurnal and nocturnal diel phases

Individual	Data logger	Recording day #	Day %	Night %
UBV1	U1	1	70.7	29.3
		2	25.9	74.1
		3	44.5	55.5
UBV3	U3	2	48.7	51.3
		3	41.4	58.6
		4	54.7	45.3
		5	55.5	44.5
		6	56.4	43.6
		7	58.3	41.7
		8	45.7	54.3
		9	60.3	39.7
UBV4	U4	2	8.1	91.9
		3	14.9	85.1
		4	9.8	90.2
		5	5.7	94.3
		6	4.3	95.7
		7	2.2	97.8
		8	6.5	93.5
		9	10.1	89.9
		10	4.7	95.3
		11	1.4	98.6
		12	8.7	91.3
		13	10.5	89.5
		14	22.0	78.0
		15	20.7	79.3
		16	15.2	84.8
		17	1.8	98.2
		18	4.1	95.9
		19	4.5	95.5
		20	14.5	85.5
		21	3.7	96.3
		22	29.7	70.3
		23	13.0	87.0

	24	0.6	99.4
	25	8.7	91.3
	26	0.1	99.9
	27	2.8	97.2
	28	3.5	96.5
	29	8.3	91.7
	30	15.2	84.8
	31	2.1	97.9
	32	18.3	81.7
	33	0.2	99.8
	34	0.5	99.5
	35	0.3	99.7
	36	8.2	91.8
	37	1.3	98.7
	38	0.4	99.6
	39	0.9	99.1
	40	9.1	90.9
	41	24.7	75.3
	42	14.7	85.3
	43	7.1	92.9
	44	0.6	99.4
	45	11.3	88.7
	46	2.5	97.5
	47	0.8	99.2
	48	0.6	99.4
	49	3.8	96.2
	50	2.6	97.4
	51	4.3	95.7
UBV5 U5	2	42.6	57.4
	3	45.6	54.4
	4	87.7	12.3
	5	53.8	46.2
	6	30.3	69.7
	7	49.1	50.9
	8	47.4	52.6
	9	51.8	48.2
	10	49.0	51.0
	11	50.9	49.1
	12	39.3	60.7
	13	58.1	41.9
	14	12.3	87.7
	15	21.1	78.9

		16	2.7	97.3
		17	41.6	58.4
		18	48.3	51.7
		19	58.1	41.9
		20	45.6	54.4
		21	32.1	67.9
		22	43.6	56.4
		23	72.4	27.6
		24	29.1	70.9
		25	38.6	61.4
UBV6	U6	1	25.5	74.5
		2	8.7	91.3
		3	40.2	59.8
		4	36.2	63.8
		5	37.1	62.9
		6	19.8	80.2
		7	89.1	10.9
		2	39.6	60.4
		3	30.0	70.0
		4	15.2	84.8
		5	25.4	74.6
		6	48.6	51.4
		7	31.7	68.3
		8	30.8	69.2
		9	76.9	23.1
		10	56.2	43.8
		11	55.8	44.2
		12	85.0	15.0
		13	36.2	63.8
		14	82.6	17.4
		15	42.1	57.9
		16	32.7	67.3
		17	39.6	60.4
		18	22.1	77.9
		19	37.9	62.1
		20	9.0	91.0
		21	39.2	60.8
		22	49.9	50.1
SBV1	s1	2	27.5	72.5
		3	10.2	89.8
		4	9.9	90.1

		5	35.5	64.5
SBV1	s2	2	20.9	79.1
		3	13.2	86.8
		4	19.1	80.9
		5	39.3	60.7
SBV1	s3	2	32.2	67.8
		3	56.8	43.2
		4	36.4	63.6
		5	7.0	93.0
		6	64.8	35.2
		7	12.7	87.3
SBV1	s4	2	10.4	89.6
		3	6.5	93.5
		4	4.6	95.4
		5	9.6	90.4
		6	49.5	50.5
		7	12.7	87.3
		8	53.1	46.9
SBV2	s5	1	77.6	22.4
		2	54.3	45.7
		3	71.6	28.4
		4	63.1	36.9
		5	40.4	59.6
		6	55.9	44.1
		7	70.0	30.0
		8	66.3	33.7
SBV2	s6	2	83.8	16.2
		3	39.5	60.5
		4	39.6	60.4
		5	31.8	68.2
		6	46.5	53.5
		7	49.1	50.9
SBV3	s7	2	77.3	22.7
		3	75.7	24.3
		4	89.7	10.3
		5	78.1	21.9
SBV3	s8	2	69.6	30.4
		3	72.8	27.2
		4	92.3	7.7
		5	54.5	45.5
		6	78.2	21.8

SBV4	s9	2	63.3	36.7
		3	79.7	20.3
		4	58.0	42.0
		5	71.3	28.7
		6	44.9	55.1
		7	64.9	35.1
SBV5	s10	2	35.3	64.7
		3	76.0	24.0
SBV6	s11	2	35.7	64.3
		3	83.8	16.2
		4	78.5	21.5
		5	59.1	40.9
		6	59.8	40.2
		7	58.3	41.7
		8	60.2	39.8
SBV7	s12	2	84.7	15.3
		3	85.5	14.5
		4	31.7	68.3
		5	87.4	12.6
		6	63.1	36.9
		7	65.9	34.1

Appendix B

I.   Statement of expenditure

Student name: Amelia Symeou
Student number: ███████

Category	Item	Description	Cost
Travel	Train	London to Swansea	£120
Accommodation	Flat	Short term rental in Swansea	£800 p/month

I hereby certify that the above information is true and correct to the best of my knowledge.

████████████████████
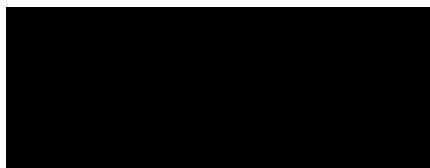
Amelia Symeou

II.   Research ethics approval

An investigation into how human disturbance affects the activity budgets of Choloepus hoffmanni and Bradypus variegatus: a comparison study **10948**

Project Tree

- An investigation into how human disturbance affects the activity budgets of Choloepus hoffmanni and Bradypus variegatus: a comparison study
  - 1. Research Ethics Application Form

Action Required on Form	Status	Review Reference	Date Modified
No	Approved	4 2024 10948 10355	16/09/2024 08:53

III.   Health and Safety: Risk Assessment

Risk Assessment			
College/PSU	Swansea University, Singleton Park Campus	Assessment Date	20/06/23
Location	Wallace Building, SLAM	Assessor	Amelia Symeou
Activity	Computer work	Review Date (if applicable)	NA
Associated documents	NA		

Part 1. Risk Assessment

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/No

Slips and trips	Staff, students and visitors	may be injured if they trip over objects or slip on spillages	Area is well lit, floor is kept clear and is well maintained, general housekeeping is carried out by students and staff, trailing leads. Cables are moved/protected	No	NA	NA	NA
Display screen equipment e.g. computers, laptops.	Staff, students and visitors	posture problems and pain, discomfort or injuries e.g. to their hands/ arms, from overuse or improper use or from poorly designed workstations or work environments. Headaches or sore eyes can also occur, e.g. if the lighting is poor.	Daily work is planned to include regular breaks or change of activity.	No	NA	NA	NA

Electrical	Staff, students and visitors	electrical shocks or burns from using faulty electrical equipment	Electrical appliances are PAT tested before use in SLAM	No	NA	NA	NA
Fire	Staff, students and visitors	If trapped, could suffer fatal injuries from smoke inhalation/ burns.	Fire escape route is clearly marked, fire alarms are tested regularly by the University	No	NA	NA	NA

Part 2. Actions arising from risk assessment

Actions	Lead	Target Date	Done Yes/No
NA	NA	NA	NA

IV.   Statement of contributions

Contributor Role	Role Definition
Conceptualization	AS, ES, RW, LB, RC
Data Curation	RC MH
Formal Analysis	AS ES MH EL
Funding Acquisition	AS
Investigation	RC
Methodology	AS ES EL LB RC
Project Administration	AS ES RC
Resources	RC
Software	MH
Supervision	ES, RW, LB
Validation	AS, ES
Visualization	AS, ES
Writing – Original Draft Preparation	AS, ES
Writing – Review & Editing	ES, RW