The behaviour and activity budgets of two sympatric sloths; *Bradypus variegatus* and *Choloepus hoffmanni*

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It is usually beneficial for species to restrict activity to a particular phase of the 24-hour cycle as this enables the development of morphological and behavioural adaptations to enhance survival under specific biotic and abiotic conditions. Sloth activity patterns are thought to be strongly related to the environmental conditions due to the metabolic consequences of having a low and highly variable core body temperature. Understanding the drivers of sloth activity and their ability to withstand environmental fluctuations is of growing importance for the development of effective conservation measures, particularly when we consider the vulnerability of tropical ecosystems to climate change and the escalating impacts of anthropogenic activities in South and Central America. Unfortunately, the cryptic nature of sloths makes long term observational research difficult and so there is very little existing literature examining the behavioural ecology of wild sloths. Here, we used micro data loggers to continuously record, for the first time, the behaviour of both *Bradypus* and *Choloepus* sloths over periods of days to weeks. We investigate how fluctuations in the environmental conditions affect the activity of sloths inhabiting a lowland rainforest on the Caribbean coast of Costa Rica and examined how this might relate to their low power lifestyle. Both *Bradypus* and *Choloepus* sloths were found to be cathemeral in their activity, with high levels of between-individual and within-individual variation in the amounts of time spent active, and in the temporal distribution of activity over the 24-hour cycle. Daily temperature did not affect activity, although *Bradypus* sloths were found to show increased nocturnal activity on colder nights, and on nights following colder days. Our results demonstrate a distinct lack of synchronicity within the same population, and we suggest that this pattern provides sloths with the flexibility to exploit favourable environmental conditions whilst reducing the threat of predation.

1 **The behaviour and activity budgets of two sympatric sloths;**

2 ***Bradypus variegatus* and *Choloepus hoffmanni***

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19   **ABSTRACT**

20   It is usually beneficial for species to restrict activity to a particular phase of the 24-hour cycle as this

21   enables the development of morphological and behavioural adaptations to enhance survival under

22   specific biotic and abiotic conditions. Sloth activity patterns are thought to be strongly related to the

23   environmental conditions due to the metabolic consequences of having a low and highly variable core

24   body temperature. Understanding the drivers of sloth activity and their ability to withstand

25   environmental fluctuations is of growing importance for the development of effective conservation

26   measures, particularly when we consider the vulnerability of tropical ecosystems to climate change and

27   the escalating impacts of anthropogenic activities in South and Central America. Unfortunately, the

28   cryptic nature of sloths makes long term observational research difficult and so there is very little

29   existing literature examining the behavioural ecology of wild sloths.

30   Here, we used micro data loggers to continuously record, for the first time, the behaviour of both

31   *Bradypus* and *Choloepus* sloths over periods of days to weeks. We investigate how fluctuations in the

32   environmental conditions affect the activity of sloths inhabiting a lowland rainforest on the Caribbean

33   coast of Costa Rica and examined how this might relate to their low power lifestyle. Both *Bradypus* and

34   *Choloepus* sloths were found to be cathemeral in their activity, with high levels of between-individual

35   and within-individual variation in the amounts of time spent active, and in the temporal distribution of

36   activity over the 24-hour cycle. Daily temperature did not affect activity, although *Bradypus* sloths were

37   found to show increased nocturnal activity on colder nights, and on nights following colder days. Our

38   results demonstrate a distinct lack of synchronicity within the same population, and we suggest that this

39   pattern provides sloths with the flexibility to exploit favourable environmental conditions whilst

40   reducing the threat of predation.

41

42

43   **INTRODUCTION**

44   For the majority of animals, time is clearly divided between periods of activity and periods of inactivity

45   (Halle & Stenseth, 2000). During active periods, animals are considered to allocate time to different

46   behaviours judiciously to maximize lifetime reproductive success (Pianka, 1976). All behaviours require

47   energy though, with the combined sum of the power costs of an animal's daily energy budget

48   modulating the animal's field metabolic rate (FMR) (Russell et al., 2015). Successful animals behave so as

49   to minimize energy expenditure and maximize energetic return (maximizing 'net energy gain) (Pyke et

50   al., 1977; Stephens & Krebs, 1986), ultimately investing the gain in resources into reproduction (Alcock,

51   2013).

52   Activity patterns vary greatly across and within taxonomic groups, with different taxa being primarily

53   diurnal, nocturnal, crepuscular or, occasionally, a combination of all these (Ashby, 1972). Species that

54   are able to operate across all diel phases include those animals with multi-modal rhythms of activity

55   (including poly-phasic and ultradian rhythms) (Halle, 2006), and cathemeral species which show

56   significant activity during both the light and dark phases of the 24-hour cycle (Tattersall, 1987). In such

57   species, the temporal distribution of activity is often flexible, being governed by complex interactions

58   that occur between the animals' endogenous rhythms, ecological entrainment mechanisms, and various

59   environmental or ecological factors such as ambient temperature, light, food availability, interspecific

60   competition, and predation risk (Donati & Borgognini-Tarli, 2006; Grignolio et al., 2018; Perea-Rodríguez

61   et al., 2022). It is considered that cathemerality in particular arises as a consequence of an animal's true

62   endogenous rhythm being 'masked' by these external factors (Curtis et al., 2006). Cathemerality can

63   encompass regular activity spanning the 24-hour cycle year-round, or can occur on a more cyclic basis,

64   shifting from nocturnality to diurnality between different days or seasons (Hofmann et al., 2016; Perea-

65   Rodríguez et al., 2022; van der Vinne et al., 2014). However, details of the complex biotic and abiotic

66   factors that govern such flexible activity patterns remain poorly understood (Halle, 2000; Kappeler &

67   Erkert, 2003).

68   Sloths (Genera: *Bradypus* and *Choloepus*) are cryptic canopy mammals that are considered to be

69   cathemeral and nocturnal in their activity patterns, respectively (A. Chiarello, 1998; Gilmore et al., 2001;

70   Giné et al., 2015). However, due to their slow movements (Sunquist et al., 1973), exceptional

71   camouflage (Suutari et al., 2010) and preference for residing high up in the dense rainforest canopy

72   (Montgomery & Sunquist, 1978), there is very little literature documenting the activity patterns of wild

73   sloths. This is particularly the case for sloths in the *Choloepus* genus, for which there is only one set of

74   data from wild animals (Montgomery & Sunquist, 1978; Sunquist et al., 1973). Nevertheless, sloth

75   activity and its determinants are likely to be multifaceted due to their low-calorie folivorous diet (A. G.

76   Chiarello, 1998; Nagy & Montgomery, 1980) and extremely slow rate of digestion (Foley, Engelhardt, et

77   al., 1995; Gilmore et al., 2001; Vendl et al., 2016), which, together, critically limit rates of energy

78   acquisition. In addition, sloths are considered to have an unusually low and variable body temperature

79   compared to typical endothermic homeotherms (Gilmore et al., 2001; Goffart, 1971), so their

80   metabolism (Cliffe et al., 2018), food intake (Cliffe et al., 2015) and consequently all aspects of energy

81   use, are dependent upon the environmental conditions. It is thus expected that fluctuations in ambient

82   temperature, and therefore sloth body temperature, will impose metabolic limitations on activity (Cliffe

83   et al., 2018; Giné et al., 2015) as well as requiring animals to employ behavioural strategies to control

84   rates of heat loss and gain. In line with this, wild sloths have been observed to exhibit thermoregulatory

85   behaviours such as the extension/retraction of limbs while resting and varying their position within the

86   canopy to manipulate levels of sunlight exposure (Gilmore et al., 2001; Urbani & Bosque, 2007).

87   Data available on the activity of *Bradypus* sloths all report great variation, which has been

88   explained by food availability, predator avoidance and climatic differences between study sites (Castro-

89   Vásquez et al., 2010; A. G. Chiarello, 2008; Gilmore et al., 2001; Oliveira Bezerra et al., 2020; Pinder,

90   1985; Queiroz, 1995; Urbani & Bosque, 2007). To date, only two studies have explored the relationship

91   between ambient temperature and sloth activity (Giné et al., 2015; Sunquist et al., 1973). These two

92   studies, along with (Oliveira Bezerra et al., 2020), also represent the only collections of nocturnal data,

93   with other work either ignoring the dark phase entirely, or inferring levels of night-time activity by

94   comparing the distances travelled diurnally to those travelled nocturnally (A. Chiarello, 1998; A. G.

95   Chiarello, 2008). This method likely misses a substantial amount of behaviour as displacement is

96   considered to represent less than 50% of total sloth activity (Castro-Sa et al., 2021), with individual

97   animals showing small bouts of activity before repeatedly returning to the same resting place. Previous

98   work is further limited by the same reoccurring problems, including small sample sizes, a lack of

99   continuous behavioural and/or environmental data, and the obvious difficulties associated with making

100   direct behavioural observations on a cryptic species which has a propensity for living high up in the

101   canopies of dense, remote tropical rainforests (Montgomery & Sunquist, 1978).

102   Based on available data, *Choloepus* sloths are considered to be nocturnal (Sunquist et al., 1973),

103   whereas *Bradypus* sloths show great variation. Some populations appear to show diurnal activity

104   (Oliveira Bezerra et al., 2020; Urbani & Bosque, 2007), while others report nocturnal activity (Castro-

105   Vásquez et al., 2010; Pinder, 1985; Queiroz, 1995), and others still report that they are cathemeral

106   (Castro-Sa et al., 2021; A. Chiarello, 1998; Giné et al., 2015; Sunquist et al., 1973). It has been noted

107   though, that the regions in which higher levels of diurnal activity are observed tend to be climatically

108   cooler due to higher elevations, while warmer lowland areas are associated with an increased frequency

109   of nocturnal movements (A. G. Chiarello, 2008; Giné et al., 2015). However, the influence of ambient

110   temperature on the behavioural ecology of all sloth species is far from being understood, not least

111   perhaps because other important activity modulators of tropical animals, e.g., precipitation and wind

112   speed (Halle, 2000), have not been placed in context with respect to the activity of wild sloths. A pattern

113   that does emerge from the available literature, however, is that there is a high level of inter-individual

114   variation in the amount of time spent active and in the 24-hour temporal distribution of activity,

115   resulting in a distinct lack of synchrony between animals in a population (Castro-Sa et al., 2021; A.

116   Chiarello, 1998; A. G. Chiarello, 2008; Giné et al., 2015; Queiroz, 1995). Individuals appear to operate on

117   their own unique patterns of activity (A. G. Chiarello et al., 2004) which has led to speculation that sloths

118   may entirely lack a circadian rhythm (A. G. Chiarello, 2008; Queiroz, 1995; Sunquist et al., 1973). As

119   sloths have a diverse array of both nocturnal and diurnal predators (including spectacled owls (*Pulsatrix*

120   *perspicillata*) (Voirin et al., 2009), big cats such as jaguars (*Panthera onca*) and ocelots (*Leopardus*

121   *pardalis*), harpy eagles (*Harpia harpyja*) (de Miranda et al., 2020) and tayras (*Eira Barbara*) (Sáenz-

122   Bolaños A et al., 2018), cathemerality and asynchronous activity of individuals within the same

123   population may also function as an effective predator avoidance strategy (i.e., favouring

124   unpredictability) (Richardson et al., 2018).

125   Understanding the temporal activity patterns of sloths and their ability to withstand environmental

126   fluctuations is of growing importance when faced with a dramatically changing world. Climate change

127   alongside with various anthropogenic pressures (land-use change, deforestation, agricultural

128   intensification, and rainforest urbanisation) are threatening sloth populations throughout South and

129   Central America, with both species of sloth in Costa Rica recognised as conservation concerns in the

130   country (Cliffe et al., 2020; Rodriguez-Herrera et al., 2002). In order to develop effective conservation

131   plans, we must first understand how sloths are able to cope with changes in their environment, and how

132   these changes impact the behavioural ecology of the species.

133   Here, we used micro data loggers attached to wild *Bradypus* and *Choloepus* sloths inhabiting a lowland

134   rainforest on the Caribbean coast of Costa Rica to record, for the first time, their behaviour continuously

135   over periods of days to weeks. We examined how environmental conditions impact their activity

136   budgets and how all of these factors might relate to their uniquely low power lifestyle.

137   Considering the known link between sloth metabolism, digestion, and ambient temperature (Cliffe et al.,

138   2015, 2018), we hypothesised that sloths would favour nocturnal movements and show increased

139   activity on cooler days in our study location (a hot lowland rainforest). As sloths rely on behavioural

140   crypsis as their primary method of predator evasion, we also hypothesised that sloth movement would

141   be positively correlated with wind speed due to an increased ability to blend in with swaying rainforest

142   branches in windy conditions.

143

144   **MATERIALS AND METHODS**

145   **Ethics**

146   This research was approved by the Swansea University Animal Welfare & Ethical Review Process

147   Group (AWERP), and the Costa Rican government and associated departments (MINAE, SINAC, ACLAC)

148   permit number; R-033-2015

149

150   **Sample**

151   Data was collected over a 17-month period from April 2014 until August 2015 from eight free-living

152   adult *Bradypus variegatus* sloths (seven male, one female) and four adult *Choloepus hoffmanni* sloths

153   (all female) (Table 1). The exact ages of these animals were not known due to the difficulty of

154   approximating age in wild sloths (Peery & Pauli, 2014). However, all body weight measurements fell

155   within the expected adult range for these species (Gilmore et al., 2001).

156   **Study area**

157   All sloths were from the same region of secondary forest surrounding the Sloth Sanctuary of Costa Rica

158   (N 09°47'56.47", W 082°54'47.20"). This forest is protected from development and has a high level of

159   canopy connectivity, however there are some anthropogenic stressors present in the area including

160   human settlements, domestic dogs, and a major highway. There is a variety of other species present in

161   the area including other arboreal folivores such as howler monkeys (*Alouatta caraya*), and predators

162   including tayras (*Eira barbara*), spectacled owls (*Pulsatrix perspicillata*), boas *(Boa constrictor)*, and

163   ocelots (*Leopardus pardalis*). Notably, the sloth's primary diurnal predator, the harpy eagle (*Harpia*

164   *harpyja*) is extinct in the region.

165   The study region maintains high and stable temperatures year-round with high levels of humidity and

166   rainfall. Although there is minimal seasonal variation in temperature, four *Bradypus* and one *Choloepus*

167   sloth were repeatedly tagged at different times of the year to investigate whether any seasonal

168   variations in activity patterns could be identified (Table 1).

169

170   **Capture and tagging procedure**

171   All *Bradypus* sloths were caught opportunistically by hand and equipped with tags (see below) without

172   anaesthesia. *Choloepus* sloths were anaesthetised during capture using 1 mg/kg of ketamine (Ketamina

173   50®, Holliday Scott) and 0.008 mg/kg of dexmedetomidine (Dexdomitor®, Zoetis) administered

174   intramuscularly. Anaesthesia was reversed prior to release using 0.008 mg/kg of anti-sedante

175   (atipamezol; Antisedan®, Zoetis). Body mass measurements were taken for each individual at capture (E-

176   PRANCE® Portable Hanging Scale (±0.01 g)).

177   Sloths were equipped with pre-calibrated Daily Diary (DD) data loggers (R. Wilson et al., 2008),

178   programmed to record 9 parameters (barometric pressure (mbar), external temperature (ºC), relative

179   humidity (%), tri-axial magnetometry (gauss), and tri-axial acceleration (g)) at a rate of 40 Hz. The data

180   loggers were held within non-lubricated condoms containing 0.5 g silica gel desiccant to protect the

181   electronics from moisture damage. DDs were combined with Very High Frequency (VHF) radio

182   transmitters (Biotrack PIP3 VHF tag) within 3D-printed housings and attached *via* elastic, backpack-style

183   harnesses, positioning the devices firmly on the upper back (Fig. S1) (Cliffe et al., 2014). The total weight

184   of the backpack was 90 g.

185

186   **Post-release monitoring**

187   After being equipped with a backpack, all sloths were released in the same location they were originally

188   found. Backpacks were retrieved manually when the sloth was in an appropriate position for recapture

189   close to the ground following daily checks. Due to the difficulty of recapturing *Choloepus* sloths, a small

190   link of dissolvable film (Aquatics ROMEO) was braided into the harness of these animals which allowed

191   the backpack to fall off when exposed to heavy rain.

192

193   **Weather data**

194   Corresponding weather data was recorded for 997 hours of *Bradypus* sloth data and 176 hours of

195   *Choloepus* sloth data to coincide with tag deployment periods. Ambient temperature (ºC), humidity (%),

196   wind speed (m/s), maximum gust speed (m/s) and rainfall (mm/15 min) were recorded every 15 minutes

197   by a weather station (Davis Vantage Vue) mounted 17 meters above the ground on the edge of the

198 study site. Light intensity was measured using a HOBO Pendant® UA-002-64 - Temperature/Light Data

199 Logger (64K) mounted adjacent to the weather station.

200

201 **Data Analysis**

202 DD data were analysed using the computer software program DDMT

203 (http://www.wildbytetechnologies.com/software.html). Standard metrics for looking at animal

204 behaviour (Grundy et al., 2009; Shepard et al., 2008) involving static and dynamic acceleration

205 derivatives are difficult to apply to sloth data because these animals have very little dynamism in their

206 movement (see later) although careful examination of the data from all channels indicated clear

207 patterns from various behaviour categories. To ascertain this, and to provide a behaviour identification

208 key, Daily Diary tags were attached to captive sloths and extensive observation undertaken which

209 allowed us to equate sensor signals with 6 primary behaviours. These were: locomotion (climbing),

210 climbing upwards, climbing downwards, grooming, resting, and sleeping (Figs. S2 & S3). Sensor signals of

211 value included slow changes in the static acceleration and magnetometry signals combined with the

212 pressure rate of change. Feeding could not be distinguished from resting due to leaf mastication

213 generating no distinguishable body movements. Behaviours were broadly categorized into 'active'

214 (including grooming and all climbing – Fig. S2) and 'inactive' (including sleeping and resting - Fig. S3)

215 based on the Vector of the Dynamic Body Acceleration (VeDBA), a proxy for energy expenditure, (Gleiss

216 et al., 2011; R. P. Wilson et al., 2006, 2020), with inactive behaviours typically producing a signal less

217 than 0.03 g.

218

219 **Statistical Analysis**

220   All data were classified using 'expert' observers. The observers were trained using the calibration

221   datasets and then given unknown samples from a calibration dataset to ascertain those behaviours were

222   being correctly classified. Observers worked within DDMT (in-house software), specifically designed to

223   enhance manual identification of Daily Diary datasets. Data from all sensors within a single tag and

224   derivatives (VeDBA and rate of change metrics) were displayed as time-based parallel traces that were

225   inspected over both time- and sensor resolution scales.

226   To determine overall activity budgets, the total percent time allocated to different behaviours was

227   calculated for each dataset.

228

229   **Activity budgets**

230   To ascertain whether *Bradypus* and *Choloepus* sloths differed in their overall levels of activity, the mean

231   hourly percent time spent active was calculated and compared using a Wilcoxon rank-sum test. The

232   significance of between-individual variation in the mean hourly percent time spent active was calculated

233   using Kruskal-Wallis tests.

234   The significance of the difference in the total amount of time spent climbing upwards vs climbing

235   downwards for all sloths combined was determined using a Welch's two-sample t-test. The total time

236   spent climbing downwards (for all sloths combined) was compared across different times of the day

237   using an analysis of variance (ANOVA) followed by a Tukey Honestly Significant Differences (Tukey's

238   HSD) test. This was repeated for the total time spent climbing upwards. For these tests, the 24-hour day

239   was broken down into 4 bins: morning (06:00-12:00), afternoon (12:00-18:00), evening (18:00-00:00)

240   and night (00:00-06:00). The significance of the relationship between climbing upwards and light

241   intensity was tested by using a point bi-serial correlation case of the Pearson's product-moment

242   coefficient (as "climbing up" is a Boolean variable).

243

244 **Activity patterns and effect of the environmental conditions**

245 To determine the effect of the environmental conditions, the mean hourly percent times spent active,

246 mean hourly ambient temperatures, and mean hourly maximum wind speeds were calculated. Using

247 this data, and assuming diurnal hours to be between 05:00 and 17:00, and nocturnal hours to be

248 between 17:00 and 05:00, the daily percent times spent active diurnally and nocturnally were calculated

249 for each sloth for each day that had corresponding weather data (4 individuals totalling 29 days for

250 *Bradypus* sloths and 4 individuals totalling 11 days for *Choloepus* sloths). Corresponding daytime and

251 night-time ambient temperatures were also calculated.

252 The significance of the relationships between the percent time spent diurnally active and the mean

253 diurnal temperature for both *Bradypus* and *Choloepus* sloths were determined using Spearman's Rank

254 correlations. The significance of the relationships between the mean percent time spent nocturnally

255 active and the mean daily and nightly ambient temperatures were determined using general linear

256 models (GLM) using normal data that was centred and box-cox transformed (power transformation of

257 0.3608). The significance of the relationships between maximum wind speed and the mean percent time

258 spent active for the day and night were tested using Spearman's Rank correlations.

259 In order to determine the significance of the difference in percent time spent active between different

260 periods of the day for each sloth, the 24-hour day was again broken down into 4 bins: dawn (04:00-

261 07:00), day (07:00-16:00), dusk (16:00-19:00) and night (19:00-04:00). The percent times spent active

262 during each bin were compared using a Kruskal Wallis test with a significance threshold of α = 0.05,

263 followed by a Dunn's *post hoc* test to identify which periods of the day differed from each other. Based

264 on the significance level, sloths are identified as either nocturnal (significantly higher activity during the

265   night compared to the day), diurnal (significantly higher activity during the day compared to the night)

266   or cathemeral (no significant difference in activity throughout the day according to a Kruskal Wallis test).

267

268   **Results**

269   **Activity budgets**

270   A total of 2,356 hours of behavioural data was collected for *Bradypus* sloths and 206 hours for

271   *Choloepus* sloths. *Bradypus* sloths were inactive for a total of 85.5% of time, comprising 62.7% and

272   22.8% of time spent sleeping and resting, respectively. There was significant between-individual

273   variation in their mean hourly percent time spent active ($\chi2$ = 57.1, df = 7, p-value < 0.001), with total

274   time spent in inactive behaviours ranging from 49.3 – 97.1% (Fig. 1 & Tables S1 – S2).

275   *Choloepus* sloths spent a total of 72.6% of their time inactive, comprising 56.4% and 16.2% of their time

276   sleeping and resting. There was no significant difference in the mean hourly percent time spent active

277   between *Choloepus* and *Bradypus* (W = 8742.5, N = 288, P = 0.433), however *Choloepus* sloths also

278   demonstrated significant between-individual variation ($\chi2$ = 25.0, df = 3, p-value < 0.001), with total time

279   spent in inactive behaviours ranging from 37.8 – 95.2% (Fig. 1 & Tables S1 – S2).

280   Both *Bradypus* and *Choloepus* sloths spent a significantly higher proportion of total percent time

281   climbing upwards (1.5% and 3.2% of time, respectively) compared to climbing downwards, where the

282   equivalent values were (0.1% and 1.2% of time, respectively) (p-value = 0.044). Sloths spent more time

283   making vertical movements within the canopy during nocturnal hours. This included significantly more

284   time spent climbing downwards during the night compared either to the morning or afternoon (p-values

285   = 0.001 and 0.039, respectively). Similarly, sloths spent a significantly higher proportion of total active

286   time climbing upwards at night compared to the morning, afternoon, or evening (p-values = 0.02, 0.004,

287   and 0.012, respectively). There was no significant correlation between the occurrence of upwards climbs

288   and light intensity for all sloths (r = -0.015, p-value = 0.508).

289

290   **Activity patterns and the effect of environmental conditions**

291   The mean and standard deviation in ambient temperature during the study period was of 26.3 ± 3.0°C,

292   ranging from an overall recorded minimum of 20.5°C to an overall recorded maximum of 32.8°C. There

293   was no significant difference in the amount of time spent diurnally active and the mean ambient

294   temperature during daytime hours (05:00-17:00) for *Bradypus* or *Choloepus* sloths (r = 0.011, df = 27, p-

295   value = 0.956 and r = 0.329, df = 9, p-value = 0.323, respectively). However, *Bradypus* did spend

296   significantly more time active nocturnally (17:00-05:00) on days which had cooler ambient daytime

297   temperatures (05:00-17:00) ($\chi 2$ = 2.672, df = 24,3, p-value = 0.018), with individuals differing

298   significantly in their response to this. Overall, there was also a strong significant negative relationship

299   between the percent time *Bradypus* sloths spent nocturnally active and the ambient night-time

300   temperature (17:00-05:00) ($\chi 2$ = 4.233, df = 24,3, p-value <0.001), with increased activity on colder

301   nights (R squared = 0.731).

302   Maximum wind speed did not significantly affect the amount of time spent active for either *Choloepus*

303   or *Bradypus* during either the day or the night.

304   Actograms reveal that all sloths were typically active in frequent small bursts lasting on average 5.52 ±

305   8.55 minutes, interspersed by longer resting and/or sleeping periods (Table S3 & Figs. S4 - S15). When

306   data for all 8 individuals was considered together, *Bradypus* sloths were significantly more active during

307   both the daytime ($\chi 2$ = 113.57, df = 3, p-value < 0.001) and at night ($\chi 2$ = -5.69, df = 3, p-value < 0.001)

308   compared to at dawn, and they were significantly more active during the day than they were at dusk ($\chi 2$

309   = 3.86, df = 3, p-value < 0.001). However, there was significant variation in the periodicity of activity

310   between individuals (Table S4); some sloths significantly favoured nocturnal activity, some favoured

311   diurnal activity, and some favoured a cathemeral pattern, with peaks of activity occurring during both

312   the day and night (Figs. 2 & S4 – S11). *Choloepus* sloths were cathemeral in their activity patterns

313   overall, with no significant difference in the amount of time spent active between dawn, day, dusk, and

314   night (Table S4). Only one individual (ch3) displayed a significant reduction in activity at dawn, with

315   activity remaining equal throughout the rest of the diel (Figs. 2 & S12 – S15).

316

317   **DISCUSSION**

318   The activity budgets of both *Bradypus* and *Choloepus* sloths observed in this study are broadly similar to

319   those previously reported for wild sloths in terms of percent time allocated for different behaviours and

320   overall activity, and levels of variation between individuals in activity (Castro-Vásquez et al., 2010; A.

321   Chiarello, 1998; Giné et al., 2015; Oliveira Bezerra et al., 2020; Sunquist et al., 1973; Urbani & Bosque,

322   2007). The overall levels of sloth activity are also comparable to those observed in other, similar sized

323   arboreal folivores, including the brown howler monkey (*Alouatta guariba*) (A. G. Chiarello, 1993) and

324   koala (*Phascolarctos cinereus*) (Ryan et al., 2013). While observers could not accurately distinguish

325   feeding from resting, feeding is thought to account for only a small portion of the sloth's daily activity

326   budget (A. Chiarello, 1998; Giné et al., 2015; Urbani & Bosque, 2007) and incurs little movement or

327   energetic cost (as also indicated by our VeDBA data). The overall low levels of activity displayed by both

328   *Bradypus* and *Choloepus* sloths are consistent with those expected for a folivorous mammal with a low

329   metabolic rate (McNab, 1978, 1982; Nagy & Montgomery, 1980; Vendl et al., 2016).

330   All sloths were found to spend more time climbing upwards than downwards, suggesting that it may

331   take a longer "period" to cover the same distance when climbing upwards due to the added effort of

332   moving against gravity. This is particularly pertinent in sloths, with their low power usage, because the

333   biomechanical power invested for climbing upwards is given by the rate of change of potential energy

334   (where PE = mgh; m = mass, g = gravitational constant and h is the height difference) so that power

335   usage is directly proportional to speed. Sloths were also found to spend more time making vertical

336   movements within the canopy during the night than they did during the day, although overall levels of

337   activity did not differ within nychthemeral cycle. This may represent an increased tendency to descend

338   to the ground during the night, although this would seem surprising considering the increased threat of

339   predation from nocturnally active large cats (Harmsen et al., 2011; Huck et al., 2017). Alternatively, it

340   may represent a slower rate of movement during the night. The reason for this is unknown, however it

341   is unlikely to be a consequence of reduced visual capabilities considering sloth eyes are only functional

342   in extremely low light conditions (Emerling & Springer, 2014).

343   While *Choloepus* sloths were previously considered to be strictly nocturnal (Sunquist et al., 1973), the

344   sloths in this study were cathemeral in their activity patterns, with only one individual showing a marked

345   decrease in activity at dawn. Our ability to be definitive about the activity patterns of *Choloepus* sloths is

346   limited by our small sample size, but given the backdrop of almost no literature at all on the behavioural

347   ecology of wild two-fingered sloths, our data represent a substantial contribution to current knowledge

348   (Alvarez et al., 2004; A. G. Chiarello, 2008; Sunquist et al., 1973).

349   *Bradypus* sloths were cathemeral in their activity patterns when all individuals were considered

350   together, with a curious marked depression in activity at both dawn and dusk (Sunquist et al., 1973).

351   Within this broad classification, however, there was significant variation in the temporal distribution of

352   activity between individuals, with some clearly favouring nocturnality, and some favouring diurnality

353   (Fig. 2). High levels of inter-individual variation in patterns of activity for sloths inhabiting the same

354   portion of forest, at the same time, demonstrate a distinct lack of synchronicity within the same

355   population. While the different ages or physiological states of the "studied" animals (which we could not

356   determine) may have influenced activity, this pattern is in accord with the existing literature and

357   suggests that the reported variation in the periodicity of activity between different regions may not be

358   entirely due to climatic differences, and rather could simply reflect the high levels of variation that exist

359   between all sloths anyway (Castro-Sa et al., 2021; Castro-Vásquez et al., 2010; A. Chiarello, 1998; A. G.

360   Chiarello, 2008; A. G. Chiarello et al., 2004; Gilmore et al., 2001; Giné et al., 2015; Sunquist et al., 1973;

361   Urbani & Bosque, 2007). Actograms reveal a high level of intra-individual variation in the total percent

362   time spent active by the same *Bradypus* sloths on different days, demonstrating what appears to be a

363   lack of any regular activity pattern within individuals as well as between individuals. Some of the

364   variation in individual levels of nocturnal activity can be related to differences in ambient temperature,

365   with sloths showing increased levels of activity during both colder nights and nights that followed colder

366   days. Additionally, the sporadic patterns of day-to-day activity may also reflect the individual animal's

367   requirement to thermoregulate or travel to find food or a mate. Sloths have highly specific feeding

368   preferences for young leaves, encompassing approximately 7-19 tree species based on the secondary

369   metabolites present in the leaves (A. G. Chiarello, 1998, 2008). This preference is passed down from

370   mother to infant and subsequently differs substantially between individuals (A. G. Chiarello et al., 2004;

371   Montgomery & Sunquist, 1978). *Bradypus* sloths move between preferred feeding or 'modal' trees in a

372   cyclic rotation, often spending consecutive days in the same tree before moving to the next. It may be

373   that sloths are more active on the days which involve changing tree; however more work would be

374   required in order to test this hypothesis.

375   It is possible that sex and reproductive-related differences may contribute to the observed high levels of

376   inter-individual variation in activity, however the uneven sex-distribution of our sample limits our ability

377   to account for this. The oestrus cycle for female three-fingered sloths is still unknown, and there is much

378   speculation as to the presence of a mating season to ensure birth coincides with favourable climatic

379   conditions; however, there are many conflicting arguments over this (Gilmore et al., 2000; Lara-Ruiz &

380   Chiarello, 2005; Martins Bezerra et al., 2008). It seems likely that reproductive seasonality may differ by

381 region based on phenological and climatic differences (Dias et al., 2008). From what we know about

382 sloths in the study region (personal observation, R. Cliffe, 2009-2022) there is no reproductive season -

383 probably due to the absence of any significant wet and/or dry seasons - and both *Bradypus* and

384 *Choloepus* sloths are thought to reproduce year-round.

385 While there is still much to learn about the drivers of sloth activity, it appears that the irregular

386 observed patterns are a consequence of complex interactions between their natural endogenous

387 rhythms (such as exist), their physiology, and the environmental conditions. Inter-individual differences

388 in activity have historically been ignored or considered to be of little scientific value, however such

389 variances likely form an adaptive flexibility of substantial biological importance (Slater, 1981).

390 Although uncommon, cathemeral activity patterns with high levels of individual variation have been

391 previously observed in other mammals and in some cases are thought to be an effective method of

392 evading or confusing predators (Pepin & Cargnelutti, 1994). Avoiding detection by predators is likely to

393 be a factor of high importance for sloths as, due to their low metabolic rate, they lack the ability to run

394 away or defend themselves if detected (Voirin et al., 2009). Another common benefit of cathemeral

395 activity patterns in mammals is the avoidance of competition (Curtis et al., 2006). While male *Bradypus*

396 sloths are known to engage in territorial disputes over access to females (Greene, 1989; Pauli et al.,

397 2012), it seems that there is no competition over access to resources since there are few vertebrates

398 that subsist primarily on leaves. Multiple sloths are often observed residing in the same tree, and large

399 overlaps in home ranges are common (Pauli et al., 2012). This is likely feasible due to an abundance of

400 food, high levels of individual specificity in diet choice (A. G. Chiarello, 1998; A. G. Chiarello et al., 2004),

401 and low levels of food consumption due to a slow digestive rate (Cliffe et al., 2015; Foley, Engelhardt, et

402 al., 1995; Montgomery & Sunquist, 1975; Nagy & Montgomery, 1980). In line with this, any potential

403 benefits relating to metabolic demands, or the temporal distribution of food are unlikely. There is no

404 seasonal variability in the availability of food, and the feeding trees favoured by sloths tend to be

405   asynchronous in the production of new leaves, thereby ensuring a constant supply of new leaves year-

406   round (A. G. Chiarello, 2008).

407   It would therefore seem that the primary benefit of a cathemeral activity pattern for sloths is the

408   flexibility to exploit favourable environmental conditions, without any added risk of predation. This

409   would also provide a reasonable explanation for the substantial day-to-day variation in activity within

410   individuals. Sloths, having at least partially sacrificed their capacity for adaptive thermogenesis, have a

411   body temperature and metabolic rate which fluctuate widely (by mammalian standards) based on the

412   ambient conditions (Cliffe et al., 2018; Irving et al., 1942; Nagy & Montgomery, 1980). This, combined

413   with a low caloric diet, means that sloths have very little energy at their disposal. In order to maximise

414   their energy budget and considering their need for movement is based on factors which are rarely time-

415   limited, it would therefore seem beneficial to delay activity until the environmental conditions are at

416   their most favourable.

417   Flexible activity patterns in response to abiotic factors have also been observed in other members of the

418   Xenarthra magnorder, including the giant anteater (*Myrmecophaga tridactyla*) (di Blanco et al., 2017)

419   and the nine-banded armadillo (*Dasypus novemcinctus*) (Norris et al., 2010), as well as in other

420   sedentary arboreal mammals such as the koala (*Phascolarctos cinereus*) (Ryan et al., 2013). However, it

421   does seem surprising that the *Bradypus* sloths in this study were significantly more active on colder

422   nights, especially considering the depressing effect that low temperatures have on sloth metabolic rate

423   (Cliffe et al., 2018). It has been previously theorised that sloths may increase nocturnal activity in

424   warmer regions (A. G. Chiarello, 1993; Giné et al., 2015; Oliveira Bezerra et al., 2020), and so the

425   observed pattern may be related to the comparatively warmer climate of this study region(Giné et al.,

426   2015).

427   Why then, is there a tendency for *Bradypus* sloths to reduce activity at dawn and dusk? Predatory

428   animals including medium and large cats often display crepuscular patterns of activity in order to exploit

429   the vulnerability of early-starting nocturnal (or diurnal) prey species that are operating at their visual

430   limits in terms of light intensity (Daly et al., 1992; Foster et al., 2013; Harmsen et al., 2011; Helfman,

431   1986). It would therefore seem beneficial for a species such as the sloth to minimise movement during

432   the twilight hours when a large proportion of its predators may be at their most active (the predator-

433   avoidance hypothesis) (Carrillo et al., 2009; Shamoon et al., 2018; Sih & McCarthy, 2002).

434   Due to the extreme range of light intensities experienced by cathemeral animals, the sensory systems of

435   these species are exposed to different selection pressures compared to those that restrict activity to

436   nocturnal or diurnal periods. For example, while diurnal mammals tend to have morphological

437   adaptations of the eye to maximise visual acuity, and nocturnal mammals to maximise visual sensitivity,

438   cathemeral mammals typically maintain a compromise between the two extremes (Peichl et al., 2019;

439   Veilleux & Lewis, 2011). Sloths are rod monochromats (completely lacking cone cells in the retina)

440   (Emerling & Springer, 2014) and so appear more specialised to exploit the nocturnal conditions than the

441   typical cathemeral mammal. This condition results in total colour blindness and represents an extreme

442   adaptation to dim light conditions. Sloths consequently have very poor visual acuity when light levels are

443   low and are completely blind when exposed to bright light, so that they probably only use vision at

444   dawn, dusk, and during the night. Regardless, with their slow and deliberate style of locomotion, sloths

445   have little need for high levels of visual acuity. In fact, they have little need for any level of high-speed

446   processing, and as such, have a basal pattern of neural organisation and slow neuromuscular responses

447   (Espírito Santo Saraiva & Magalha˜es-Castro, 1975; Gilmore et al., 2000; Toole & Bullock, 1973).

448   Considering that the metabolic cost of neural processing is high (Laughlin et al., 1998), and the sloth

449   lifestyle has little requirement for well-developed sensory or reactive abilities, a reduction in neural

450   processing would therefore substantially aid in reducing energetic demands. With the sloths'

451   dependence on sensory and neural function minimised, the selective pressures exerted by circadian

452   differences in light intensity become insignificant and cathemeral activity patterns are thus a feasible

453   option.

454

455   **CONCLUSIONS**

456   This study represents the first continual collection of behavioural data for both *Bradypus* and *Choloepus*

457   sloths and shows them both to be cathemeral in their activity, with high levels of between-individual

458   and within-individual variation in the amounts of time spent active, and in the temporal distribution of

459   activity over the 24-hour cycle. *Choloepus* sloths were previously considered to be exclusively nocturnal

460   and so the results of this study represent a substantial contribution to current knowledge on the activity

461   of this species. *Bradypus* sloths were found to show increased nocturnal activity on colder nights and on

462   nights following colder days, which may be due to the comparatively warmer climate of this study region

463   (Giné et al., 2015). Our results further demonstrate a distinct lack of synchronicity between sloths within

464   the same population, and we suggest that the previously reported variation in sloth activity patterns

465   between different regions may not be exclusively due to climatic differences and could also reflect the

466   high levels of variation that exist between all sloths anyway. Finally, we hypothesise that cathemerality

467   with high levels of between-individual and within-individual variation in activity provides sloths with the

468   flexibility to exploit favourable environmental conditions whilst also reducing the threat of predation.

469

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473

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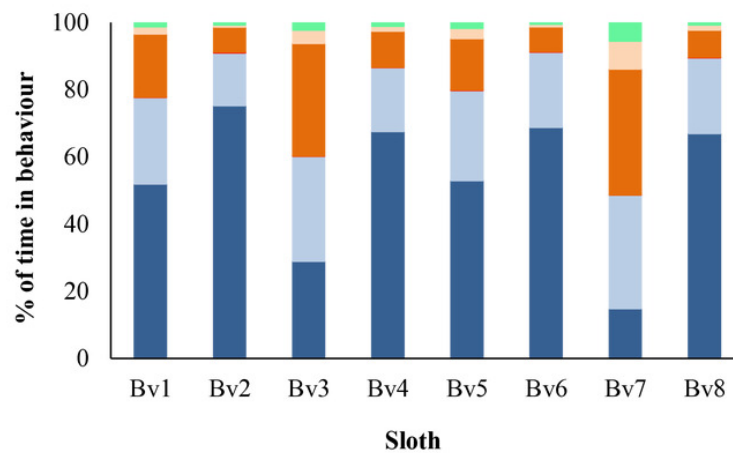
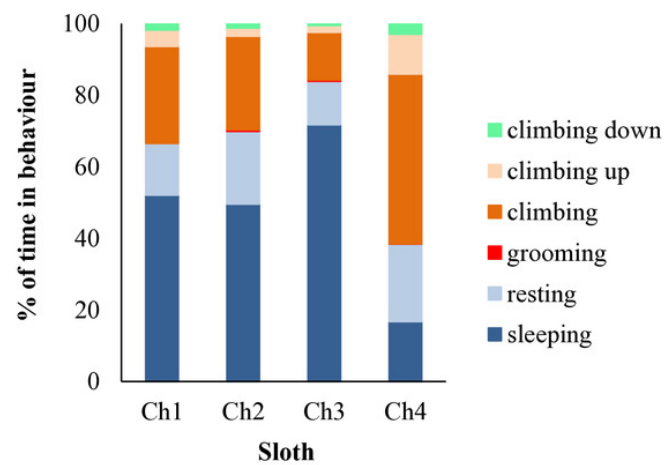
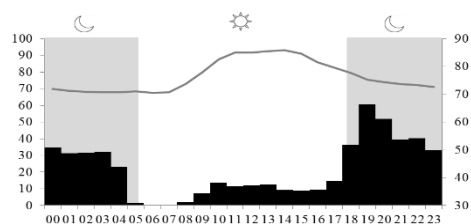
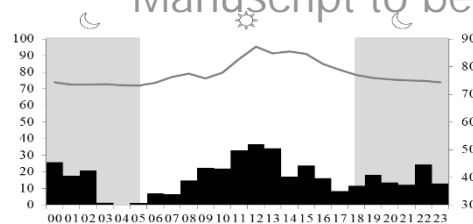
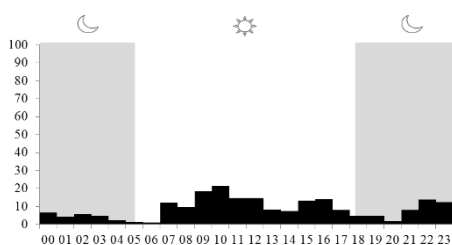
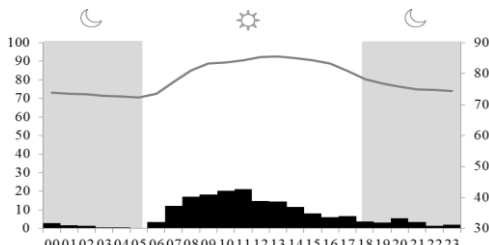
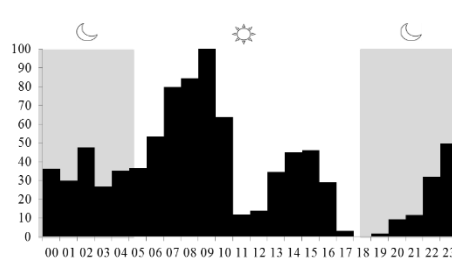
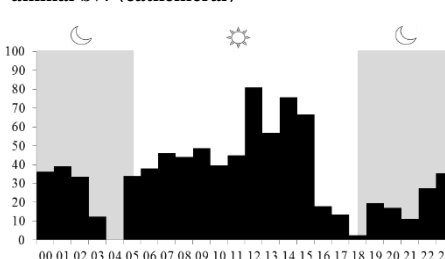
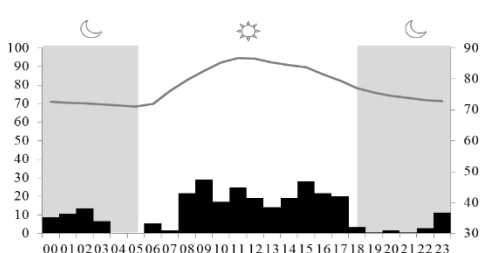
Figure 1

Variation in the percent of time spent in different behaviors for 8 wild Bradypus (a) and 4 wild Choloepus (b) sloths.

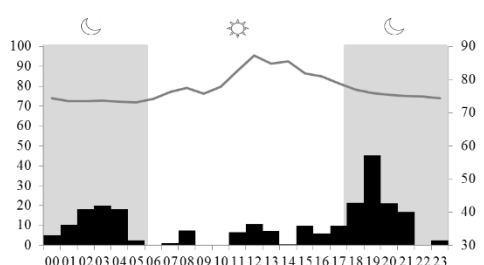
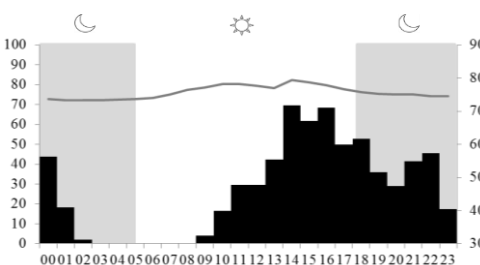
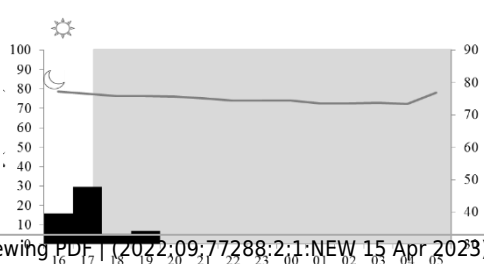
Each behaviour is denoted by a different colour.

Variation in the periodicity of activity and ambient temperature over 24 hours for (a) Bradypus sloths and (b) 4 Choloepus sloths in Costa Rica to illustrate inter-individual variation.

Dark phases are shown by grey shading. Because of the number of 0's in the data, the interquartile range varies between 0 – 93.3 and is not shown in the figure.

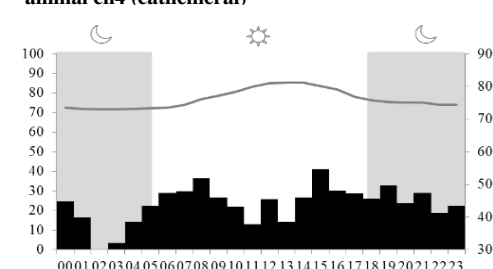
a). *Bradypus*

animal bv1 (nocturnal)

animal bv5 (cathemeral)

animal bv2 (diurnal)

animal bv6 (diurnal)

animal bv3 (cathemeral)

animal bv7 (cathemeral)

animal bv4 (diurnal)

animal bv8 (diurnal)

b). *Choloepus*

animal ch1 (cathemeral)

animal ch3 (cathemeral)

animal ch4 (insufficient data)

animal ch4 (cathemeral)

Activity (% of time)

Ambient temperature (°C)

Time (hour)

List of sloths sampled

Includes species, sex, body weight, date of release following tagging with a Daily Diary logger (DD) and the total duration of the resultant dataset

Dataset #	Sloth	Species	Sex	Weight (Kg)	Date released	DD data (hh:mm:ss)
1	Bojangles	*B.variegatus*	M	2.20	20/2/2015	91:52:16
2	(bv1)			2.50	04/3/2015	102:39:37
3				3.20	09/7/2015	156:55:23
4				3.20	25/7/2015	180:44:19
5	Burrito	*B.variegatus*	M	4.80	24/4/2014	179:18:16
6	(bv2)			4.70	07/8/2015	92:50:13
7	Guillermo (bv3)	*B.variegatus*	M	3.45	04/8/2015	55:10:21
8	Quatro (bv4)	*B.variegatus*	M	4.30	27/3/2015	184:38:12
9	Spock (bv5)	*B.variegatus*	M	3.90	15/4/2015	156:46:17
10	Star (bv6)	*B.variegatus*	F	3.80	20/11/2014	116:53:50
11				4.00	11/2/2015	124:28:59
12				3.90	17/2/2015	181:29:28
13				3.90	09/5/2015	187:26:52
14				4.00	18/5/2015	30:21:08
15				3.90	06/6/2015	201:04:03
16	Steve (bv7)	*B.variegatus*	M	4.25	18/7/2015	32:50:39
17	Valentino	*B.variegatus*	M	5.00	08/9/2014	169:51:41
18	(bv8)			5.00	26/7/2015	54:53:55
19				5.00	03/8/2015	55:46:44
	Total					2356:02:13
20	Beckett	*C.hoffmanni*	F	8.20	16/11/2014	29:56:35
21	(ch1)		F	8.25	15/4/2015	46:37:35
22	Lizz (ch2)	*C.hoffmanni*	F	5.40	15/4/2015	11:59:53
23	Walda (ch3)	*C.hoffmanni*	F	7.30	10/3/2015	43:10:31
24	Willa (ch4)	*C.hoffmanni*	F	6.90	10/3/2015	74:20:01
	Total					206:04:35