

1 **Title:** Small tropical mammals can take the heat- high upper limits of thermoneutrality in a
2 Bornean treeshrew

3

4 **Keywords** – Thermoregulation, thermoneutral zone, endothermy, metabolism, *Tupaia minor*,
5 treeshrew, Scandentia, tropics

6

7 **What is already known**

8 There is limited knowledge on the thermoregulation of small equatorial tropical endotherms and
9 it is generally believed that the upper critical temperatures of the thermoneutral zone in mammals
10 are invariable.

11

12 **What this study adds**

13 We found that the lesser treeshrew possesses a relatively high upper critical temperature of the
14 thermoneutral zone ($>36^{\circ}\text{C}$), and displays flexible body temperature, both characteristics well
15 suited for survival at high ambient temperatures and humidity. Our study provides further
16 insights into the thermoregulatory physiology of tropical endotherms and indication of their
17 potential to respond to anthropogenic changes.

18 **Abstract**

19 Tropical ectotherms are generally believed to be more vulnerable to global heating than
20 temperate species. Currently, however, we have insufficient knowledge of the thermoregulatory
21 physiology of equatorial tropical mammals, and small diurnal mammals in particular, to enable
22 similar predictions. In this study, we measured the resting metabolic rates (via oxygen
23 consumption) of wild-caught lesser treeshrews (*Tupaia minor*, Order Scandentia) over a range of
24 ambient temperatures. We predicted that, similar to other treeshrews, *T. minor* would exhibit
25 more flexibility in body temperature regulation, as well as a wider thermoneutral zone, compared
26 to other small mammals because these thermoregulatory traits provide both energy and water
27 savings at high ambient temperatures. Basal metabolic rate was, on average, 1.03 ± 0.10
28 $\text{m}\ell\text{O}_2\cdot\text{hr}^{-1}\cdot\text{g}^{-1}$, which is within the range predicted for a 65-g mammal. We calculated the lower
29 critical temperature of the thermoneutral zone at 31.0°C (95% CI: $29.3\text{--}32.7^\circ\text{C}$) but, using
30 metabolic rates alone, could not determine the upper critical temperature up to ambient
31 temperatures as high as 36°C . The thermoregulatory characteristics of the lesser treeshrew
32 provide a means of saving energy and water at temperatures well in excess of their current
33 environmental temperatures. Our research highlights the knowledge gaps in our understanding of
34 the energetics of mammals living in high temperature environments, specifically in the equatorial
35 tropics, and questions the purported lack of variance in the upper critical temperatures of the
36 thermoneutral zone in mammals, emphasizing the importance of further research in the tropics.

37 **Abbreviations**

38 BMR = basal metabolic rate, $\dot{V}\text{O}_2$ measured in the TNZ ($\text{m}\ell\text{O}_2\cdot\text{h}^{-1}$)

39 C_{dry} = dry heat transfer coefficient ($\text{W}\cdot^\circ\text{C}^{-1}\cdot\text{cm}^{-2}$)

- 40 C_{wet} = wet thermal conductance ($\text{W}\cdot\text{C}^{-1}$)
- 41 EWL = evaporative water loss ($\text{mg}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$)
- 42 EHL = evaporative heat loss (W)
- 43 MHP = metabolic heat production (W)
- 44 T_a = ambient temperature measured via black box apparatus ($^{\circ}\text{C}$)
- 45 T_{lc} = lower critical temperature of the TNZ ($^{\circ}\text{C}$)
- 46 T_{sub} = subcutaneous body temperature ($^{\circ}\text{C}$)
- 47 T_{uc} = upper critical temperature of the TNZ ($^{\circ}\text{C}$)
- 48 TNZ = thermoneutral zone ($^{\circ}\text{C}$)
- 49 RMR = resting metabolic rate, $\dot{V}O_2$ measured and temperatures outside the TNZ ($\text{m}\ell\text{O}_2\cdot\text{h}^{-1}$)

50 **Introduction**

51 As global environmental temperatures continue to rise and anthropogenic development
52 encroaches on tropical habitats, there is need for a greater understanding of the relationship
53 between temperature and the energetics and performance of animals (Dillon et al. 2010; Huey et
54 al. 2012; IPCC 2014; Urban et al. 2016). Loss of habitat, canopy reduction, and warming
55 temperatures are predicted to have an effect on small endotherms through increases in both
56 energy and water costs (Brodie et al. 2017; McCain and King 2014). Although thermoregulatory
57 adaptations to high environmental temperatures have been extensively studied in ectothermic
58 species, the capability for endothermic species to perform in relatively high temperature
59 environments has received comparatively little attention (Gerson et al. 2019; Huey et al. 2012;
60 Levesque et al. 2016). Our functional knowledge of how endotherms perform in high
61 temperature humid environments, and in the equatorial tropics in particular, is lacking (Alagaili
62 et al. 2017; Lobban et al. 2014; Lovegrove 2003; Mitchell et al. 2018; Welman et al. 2017b).
63 Consequently, many of the assumptions that support current predictions for responses to climate
64 change are based on physiological parameters measured from temperate species (Buckley and
65 Huey 2016; Huey et al. 2012; Khaliq et al. 2014).

66 The majority of studies on the energetics and thermoregulation of mammals have
67 centered around characterizing the thermal profiles by determining the upper and lower critical
68 temperatures of the thermoneutral zone (TNZ, Scholander et al. 1950b). The TNZ is a range of
69 ambient temperatures (T_a) over which metabolism is maintained at a stable, and minimal level
70 (Scholander et al. 1950b; Withers et al. 2016). Changes in lower critical temperatures of the TNZ
71 (T_{lc}) according to body size, climate and, to a lesser extent phylogeny, have been well studied:
72 colder environmental temperatures and larger body masses are linked with lower temperature

73 thresholds for metabolic heat production (Fristoe et al. 2015; Lovegrove 2005; Riek and Geiser
74 2013; Scholander 1955). The upper limit of thermoneutrality (T_{uc}), however, has been measured
75 in fewer species (93 versus 204 species, Riek and Geiser 2013) and there is some confusion as to
76 whether T_{uc} should be defined as the upper breakpoint in metabolism (Khaliq et al. 2014; Wolf et
77 al. 2017) or the temperature at which evaporative water loss (EWL) increases (IUPS Thermal
78 Commission 2003; Mitchell et al. 2018; Withers et al. 2016), although the former is much more
79 common than the latter (see Supplementary Materials). Moreover, T_{uc} estimates are often
80 believed to be relatively invariant between species, showing little or no relationship to
81 environmental temperatures experienced by the animals (Araújo et al. 2013; Khaliq et al. 2014;
82 Riek and Geiser 2013). The lack of variance in T_{uc} may, in part, however, be the result of a
83 dataset highly skewed towards high latitude as well as nocturnal species, rather than a true
84 biological phenomenon. Existing data from tropical endotherms, including those from the
85 original studies by Scholander *et al.* (1950a; 1950b), often lack estimates of T_{uc} . This represents
86 a significant knowledge gap, as low-latitude species are likely to differ from their high-latitude
87 counterparts – a relationship that has been extensively documented in ectotherms (Deutsch et al.
88 2008; Huey et al. 2009; Tewksbury et al. 2008).

89 Treeshrews (Order Scandentia) are small equatorial mammals that have maintained many
90 of the ancestral placental mammalian characteristics such as insectivory, frugivory, arboreal
91 locomotion, and a relatively simple digestive system (Emmons 1991, 2000; O'Leary et al. 2013).
92 However, they also share a number of apomorphies with their close relatives in the Order
93 Primates, including a predominantly diurnal activity pattern, and a high brain-to-body mass ratio
94 (Aiello and Wheeler 1995; Emmons 2000; Isler and van Schaik 2006). In a previous study we
95 found that the largest diurnal, and most terrestrial, of the Bornean Tupaiidae, the large treeshrew

96 (*Tupaia tana*), which averages 250g, had both a wider TNZ and more variable body temperature
97 than would be predicted for their body mass (Levesque et al. 2018). *T. tana* also had high body
98 temperatures, when compared to other tropical small mammals. We hypothesized, following
99 Crompton (1978), that high body temperatures in diurnal small mammals are beneficial in
100 maintaining a gradient between body and ambient temperature to allow for passive heat
101 dissipation during activity in the hottest times of the day. It remains unclear, however, whether
102 the thermoregulatory phenotype (high body temperature during activity, large daily body
103 temperature amplitudes) observed in our previous study was unique to *T. tana* or whether it
104 represents a broader characteristic of diurnal tropical mammals. We therefore sought to
105 characterize the thermoregulatory physiology of the smallest of the Tupiidae (~65g), the lesser,
106 or pygmy, treeshrew (*Tupaia minor*, Günther, 1876) to see if they had similar phenotypes. *T.*
107 *minor* is diurnal, predominantly arboreal, nests communally, and has a greater population density
108 than its larger conspecifics (Emmons 2000). We predicted that, similar to *T. tana*, *T. minor*
109 would exhibit more flexibility in body temperature regulation, as well as a wider TNZ, compared
110 to other small mammals as these thermoregulatory traits provide both energy and water savings
111 at high ambient temperatures.

112

113 **Materials and Methods**

114 *Study Site and Capture*

115 The study took place intermittently from August, 2014 through June, 2016, at one of two
116 study sites at the base of Mount Singai in Bau District, Sarawak, Malaysia; Kampung Barieng
117 (1.505°N, 110.154°E) and Kampung Tanjong Bowang (1.505°N, 110.178°E). Both forests
118 consist of secondary agroforests that experience moderate to heavy human usage (Tuen et al.

119 2014). Locally-made cage traps were used and baited with fruit (banana, pineapple). Traps were
120 checked at 0:00, 06:00, 12:00, and 18:00. Upon capture, traps containing *Tupaia minor* were
121 covered with a cloth and animals were given an extra banana before transport back to the field
122 station. The animals were weighed to the nearest 0.1g (mean body mass: 65.5 ± 9.3 g, range:
123 49.1- 83.5, n = 17) and morphometric measurements (length of forearm, hind foot, head-body,
124 and tail – Supplementary Material) were taken to confirm the species identification (Payne et al.
125 1985). An ear-tag (Style 1005-3, National Band & Tag Company, Newport, KY) was secured to
126 the right ear. A temperature-sensitive transponder (BioThermo13, Biomark, Boise, ID) was
127 injected into the interscapular region, which provided a means of identifying an individual at
128 recapture and measuring subcutaneous temperature (T_{sub}) during the respirometry measurements.
129 The calibration of the temperature-sensitive transponders was tested by placing five of them in a
130 water bath at temperatures from 20-40°C and compared with a glass mercury thermometer for
131 accurate (to the nearest 0.1°C traceable to a national standard) temperature readings. Similar to
132 other studies (Cory Toussaint and McKechnie 2012; Whitfield et al. 2015), there were no
133 significant differences between the transponders and the mercury thermometer and therefore
134 further calibration was deemed unnecessary. Only non-reproductive, adult individuals were used
135 in the study, all pregnant, lactating, and juvenile animals were released at the location of capture
136 during the following trap check and not used in subsequent respirometry measurements.

137

138 ***Data Collection***

139 Respirometry measurements were conducted under identical conditions to those
140 described in Levesque et al. (2018), but are summarized briefly below. Treeshrews were fasted
141 prior to the resting metabolic rate measurements, starting at 16:00, and were weighed before and

142 after measurements, which ran from 18:00-07:00. Two different temperatures, randomized
143 between 18°C and 36°C, were tested per night starting with the colder temperature. Exposure to
144 each temperature lasted from 5-6 hrs. The animals were placed into a 3.96ℓ Perspex respirometer
145 (McKechnie and Lovegrove 2001) that was outfitted with two air ports and a raised metal grate,
146 which allowed urine and feces to collect beneath the animal. The animals did not defecate or
147 urinate throughout the measurement period; therefore, the use of mineral oil to absorb liquids
148 was not necessary. In 2014-2015 the respirometer was placed inside an insulated
149 Styrofoam box into which water was pumped from a water bath (Memmert WNE, Schwabach,
150 Germany). In 2016 this system was replaced by a large modified cooler box attached to a PELT5
151 Temperature Controller (Sable Systems, Las Vegas, NV). A mass-flow controlled pump (SS-4
152 sub-sampler, Sable Systems, Las Vegas, NV) pulled ambient air through a column of silica gel
153 and Drierite™, and soda lime to remove incurrent water vapor and CO₂, before being pushed
154 through the respirometer at a flow rate of 400-500 mL/min. Air from the respirometer and from a
155 reference air stream were pushed into manifolds connected to either a RM-8 Flow Multiplexer or
156 BL-2 Baseline Unit (Sable Systems, Las Vegas, NV), which sampled from the reference stream
157 for 10 min out of every 50 min of data collection. Using a field gas analyzer system (FoxBox
158 Field Gas Analysis System, Sable Systems, Las Vegas, NV), a subsample of air (at 150 mL·min⁻¹
159 ¹) was pulled through a relative humidity meter (RH-300 Water Vapor Analyzer, Sable Systems),
160 dried using Drierite™, and then pushed through the CO₂ analyzer. The sample was then
161 scrubbed of CO₂ using soda lime and Drierite™, before entering the O₂ analyzer on the FoxBox.
162 Flow rates were calibrated against a factory calibrated mass-flow meter (MC-10SLPM-D, Alicat
163 Scientific, Tucson, AZ). The respirometer was initially designed for use in a large species, and at
164 the given flow rates the washout times were relatively long (8-10 min), however, only steady

165 state values (20 min averages, see below) were used and the experimental time (~6hrs) was
166 sufficient to compensate for low washout times. Fractional concentrations of O₂, CO₂, water
167 vapor pressure, respirometer flow rate, and barometric pressure were automatically digitally
168 recorded by the Expedata program every five seconds (v 1.1.15, Sable Systems International).
169 The CO₂ gas and water vapor analyzers were calibrated monthly using compressed pure nitrogen
170 gas to set the zero value. The CO₂ span value was set using compressed CO₂ gas of known
171 concentration and the water vapor span values were set by generating humid air of a standard
172 dewpoint using a water bath and a bubbler flask. The O₂ span value was set to 20.95% O₂ (the
173 default for dry, CO₂ free air on the FoxBox) prior to the start of each measurement period and O₂
174 drift was controlled for using the drift correction function in the Expedata program. T_{sub} was
175 recorded every 30s by a Biomark HPR Reader (Biomark, Boise, ID). We monitored T_{as} in the
176 respirometer using temperature data loggers (DS 1922L Thermocron iButtons, Dallas
177 Semiconductor, Dallas, TX) placed in each of the four corners of the respirometer set to record
178 temperature at 1min intervals. In 2016, activity and posture were monitored visually using an
179 infrared USB security camera (ELP, Guangdong, China).

180 ***Data Analysis***

181 Equations modified from Withers (2001) were used to calculate $\dot{V}O_2$, $\dot{V}CO_2$, and
182 evaporative water loss (EWL). $\dot{V}O_2$ was converted to metabolic heat production (MHP in W)
183 using an oxycaloric equivalence calculated from the respiratory quotient ($6.0913 \cdot RQ + 15.439$
184 $J \cdot mlO_2^{-1}$, Withers 1992) and EWL was converted into evaporative cooling (EHL in W) using a
185 latent heat of vaporization value of $T_a \cdot (-2.39) + 2498.42 J \cdot mgH_2O^{-1}$ (Withers 1992). MHP, EHL,
186 and T_{sub} were used to calculate thermal conductance (C_{dry}) following McNab (1980). We also
187 measured dry heat transfer coefficient (in $mW \cdot ^\circ C \cdot cm^{-2}$) using Equation 4 from Dawson and

188 Schmidt-Nielsen (1966). Surface area was estimated assuming a flattened ellipsoid shape
189 (following Marom et al. 2006) for both the body (118.95mm in length, 25mm width, and 20mm
190 for temperatures within the TNZ, and 89.21mm in length below) and the tail (158.67mm, 2mm,
191 2mm). We selected the lowest recorded 20 min section for MHP from each 5-6 hr measurement
192 period as the resting metabolic rate (RMR) for that temperature. Only measurements recorded
193 once the animal had been in the chamber for over two hours were used to ensure that the animal
194 was rested and fully acclimated to the respirometer. T_{sub} values were also used to confirm that
195 the animals were in a steady state. To pinpoint limits of the thermoneutral zone, we used
196 piecewise linear regression analyses implemented using the R package ‘segmented’ (Muggeo
197 2008), with mass as a covariate, to determine the break points in the relationship between MHP
198 and T_a . We ran a preliminary analysis comparing a generalized linear model containing only T_a
199 and mass, to one that also included animal identity (to control for any effects of repeated
200 measures) and found no significant differences between the two models using the ‘anova’
201 function in the ‘nlme’ package ($p=0.999$, Pinheiro et al. 2013). Therefore, running the break
202 point analysis in ‘segmented’, which currently cannot control for repeated measures, was
203 justified. Similarly, the time of the recording was not found to be significant and was therefore
204 omitted from the analyses ($p=0.18$). The break point analysis was repeated for T_{sub} , C_{tot} , C_{dry} ,
205 EHL, and the ratio of MHP to EHL. All statistical analyses were performed in R version 3.3.1 (R
206 Development Core Team 2011).

207 To compare the breadth of the TNZ obtained in this study to that of other mammals, we
208 used data from a recent compilation of endotherm TNZ parameters (Khaliq et al. 2014). Data
209 selection was heavily edited following Wolf *et al.* (2017) to include only species with confirmed
210 breakpoints in MR at the T_{uc} . These data (95 species) were supplemented with an additional

211 three species from Riek and Geiser (Riek and Geiser 2013) as well additional data from tarsiers
212 (Welman et al. 2017a) and treeshrews (Bradley and Hudson 1974; Levesque et al. 2018). We
213 also recorded whether the studies reported evaporative water loss and if so, at what temperature
214 evaporation increased (Supplementary Materials). As these physiological traits are known to
215 have a large phylogenetic signal (e.g. White et al. 2009) we used phylogenetic independent
216 analyses for the comparative data (Garland et al. 2005). The ‘pgls’ function (for phylogenetic
217 independent generalized least squares) in the R package *caper* (Orme 2013), which uses
218 maximum likelihood to calculate the optimal Pagel’s lambda branch length transformation, and
219 the interpolated mammal super-tree from Hedges *et al.* (2015), were used to determine the
220 relationship between body mass and TNZ breadth for the combined dataset of 101 species
221 (Supplementary Material). Confidence intervals were calculated for the pgls using the ‘pGLS_ci’
222 function in the R package ‘evomap’ (Smaers 2014; Smaers and Rohlf 2016). Using the equations
223 and data provided in the comprehensive phylogenetically independent analysis reported in
224 Genoud *et al.* (2017) %BMR (the amount at which BMR was either higher or lower than
225 predicted) was calculated for the two species of Bornean treeshrews (Table 1).

226 **Results**

227 Respirometry measurements from 17 individuals (13 males and 4 females, Fig 1) were
228 collected. Of the 17 individuals: three individuals (two males, one female) were captured in
229 2014; seven (six males, one female) in 2015; and, seven (five males, two females) in 2016. The
230 T_{lc} , determined using piecewise linear regression, was 31.0°C (95% CI: 29.3-32.7°C). Using
231 metabolic rate alone, no T_{uc} was determined, but there was a measured increase in T_{sub} at T_a
232 30.8°C (95% CI: 27.1-34.5°C), EWL at T_a 29.7°C (95% CI: 27.3-32.2°C), in C_{wet} at 31.9 (95%

233 CI: 31.1-32.7°C) and C_{dry} at 32.8°C (95% CI: 32.1-33.4°C), and in the ratio of MHP to EHL at
234 30.2°C (Fig 1).

235 BMR was calculated as the mean of the mean RMR recorded for each individual for T_{aS}
236 > 31.0°C (n=7), and was $1.03 \pm 0.10 \text{ m}\ell\text{O}_2 \cdot \text{hr}^{-1} \cdot \text{g}^{-1}$ (Table 1, Fig 2). Minimum EWL, calculated
237 as the average EWL recorded for each individual for $T_{\text{aS}} < 32^\circ\text{C}$, was $2.83 \pm 0.18 \text{ mg} \cdot \text{hr}^{-1} \cdot \text{g}^{-1}$.
238 Minimum C_{wet} was $0.0599 \pm 0.0128 \text{ W} \cdot ^\circ\text{C}^{-1}$ and, using an estimate for surface area of 139.30
239 cm^2 for animals measured at temperatures below the TNZ and 155.42 cm^2 within the TNZ,
240 minimum dry heat transfer was $0.286 \pm 0.0314 \text{ mW} \cdot ^\circ\text{C}^{-1} \cdot \text{cm}^{-2}$. At the start of the measurement
241 period, which coincided with the end of the diurnal activity phase (~19:00), T_{sub} ranged from
242 36.7-39.5°C (mean 38.5°C). T_{sub} decreased during the species' rest-phase, reaching a mean low
243 of 35.5°C at 0:00 (lowest 33.3°C), and returning to ~37°C towards the end of the measurement
244 period, around 06:30 (Fig 3). There was also a relationship between T_{a} and T_{sub} in resting
245 animals ($p < 0.0001$, Fig 1) with T_{sub} remaining predominantly below 35.5°C and T_{aS} below the
246 T_{lc} and raising as high as 37.4°C at the higher temperatures.

247 All RMR values were recorded between 21:00 and 6:00 coinciding with the period of
248 time where T_{sub} was at a minimum (Fig 3). We tested for effect of time of experiment (both
249 continuously and as a factor) using linear mixed models, in both cases the effect of time was not
250 significant (df=14, $p=0.193$ df=14, $p=0.206$, respectively). *T. minor* had a TNZ breadth (>6°C)
251 close to that predicted by the pgl's. Of the 101 studies included in our analyses, only 32 measured
252 any form of evaporative water loss, and of those studies, only 24 recorded the EWL breakpoint
253 (Fig 4A). After removing one outlier (*Neotoma lepida*), there was a significant relationship
254 between the break point in metabolic rate and in evaporative water loss ($R^2=0.53$, $p < 0.0001$, Fig

255 4B) with most species showing an increase in water loss rates before an increase in metabolic
256 rates (mean: 1.2°C, range: -0.1 – 10°C).

257 **Discussion**

258 Although equatorial tropical animals are expected to be vulnerable to rising T_a , the lesser
259 treeshrew, *Tupaia minor*, displayed thermoregulatory characteristics indicative of a species that
260 is well equipped for life at high environmental temperatures. Contrary to our predictions, the
261 thermoneutral zone of *T. minor* was not larger than would be predicted for their body mass,
262 mostly due to a relatively high lower critical temperature (31°C, Fig 2). This lower limit is,
263 however, still above the current average daily maximum T_a at the study site (average 27.9°C,
264 range: 24.1-33.9°C, Levesque et al. 2018) indicating an ability to cope with higher ambient
265 temperatures in the future. Although *T. minor* showed no substantial increase in metabolic heat
266 production that would be indicative of an upper critical temperature of the TNZ (at least at the
267 highest temperature measured in this study), evaporative water loss increased at ambient
268 temperature below 32°C. Subcutaneous temperatures also increased at ambient temperatures
269 above 31°C which presumably reduces energy and water costs compared to maintaining strict
270 homeothermy and is therefore highly beneficial in high T_a environments. Using the equation for
271 predicted BMR ($2.382 \cdot \text{mass}^{0.729}$) provided by Genoud *et al.* (2017), we found no evidence that
272 tropical treeshrews have low BMR. Large brain-to-body mass ratios, of which *T. minor* are in the
273 upper 85th percentile for mammals (Boddy et al. 2012), have been shown to correlate with higher
274 metabolic rates due to the high metabolic costs of brain tissue (Isler and van Schaik 2006; White
275 and Kearney 2012).

276 The interactions of a species' BMR, thermal conductance, water loss and T_b shape its
277 thermoneutral zone. The TNZ of *T. minor*, at greater than a 6°C range, is similar in breadth to

278 other species of similar body mass (Fig 2). This is in contrast to other Scandentians which, in
279 general, appear to have wide TNZs that are, on average, larger than 90% of measured
280 mammalian TNZs (Fig 2, Supplementary Materials). It is worth noting, however, that there have
281 been relatively few thermoregulatory studies conducted on mammals from the true tropics with
282 only 25 individual studies on endothermic species found between 10°N and 10°S in latitude
283 (Supplementary Materials). Further, the two largest TNZ reported at >22°C were from tropical
284 primates, however, these values may not be comparable as the authors indicate that lower limits
285 were difficult to pinpoint in these species (Muller et al. 1983).

286 Although *T. minor* showed no substantial increase in MHP that would be indicative of an
287 upper critical limit of the TNZ, EWL increased at $T_{as} > 30^{\circ}\text{C}$. As increases in evaporative water
288 loss rates are indicative of a change in thermoregulatory state, some authors have argued that this
289 should be the upper critical limit, rather than increases in metabolism (IUPS Thermal Commission
290 2003; Mitchell et al. 2018; Withers et al. 2016). In this study, to be comparable to previous meta-
291 analyses, we have based our definition of the T_{uc} on the break points in metabolism, but
292 recognize that either definition is valid, and that characterizing the suite of gradual physiological
293 changes that occur as T_a approaches T_b as a single breakpoint is less than ideal (see Tomlinson
294 2016). Very few of the studies (24/101) reported the temperature at which evaporative water loss
295 increased (Fig 4). In most of these species the break points in rates of evaporative water loss and
296 in metabolism were within 1-2°C of each other (Fig 4B) with the two species of Bornean
297 treeshrews falling outside the 95% confidence intervals of the regression (Fig 4B). The distance
298 between two break point temperatures for the Bornean treeshrews is likely larger than presented
299 here, as in both cases the reported breakpoint in metabolic heat production was not determined
300 and is likely higher than the maximum T_a measured. The only other species in the dataset to have

301 such a large difference between the two break points was the woodrat (*Neotoma lepida*, Nelson
302 and Yousef 1979), and the Cape elephant shrew (*Elephantulus edwardii*, Leon et al. 1983), both
303 arid zone species that also showed similar increases in T_b at higher T_a . However, in the absence
304 of controlled conditions, in particular controlling for differences in chamber humidity between
305 studies, comparisons between species can be difficult and a more standardized means of data
306 collection, such as that used by Gerson *et al.* (2019) should be considered for future studies.
307 Similarly, very few mammal studies that found upper limits of the thermoneutral zone via breaks
308 in metabolic rate report the amount of evaporative cooling in percent of heat production
309 (EWL/MHP). In the current study, the highest percentage recorded for *T. minor* was 40, which
310 was only a 30% increase from the minimum (Fig 1). Comparatively, a study on the jackrabbit
311 (*Lepus alleni*, Dawson and Schmidt-Nielsen 1966) observed a 120% increase. However, in that
312 study rabbits were exposed to ambient temperatures up to 5°C greater than T_b and the
313 contribution of evaporative cooling to overall heat loss increased significantly at the highest T_a .
314 At present, we cannot speculate on whether rates of evaporative heat loss would have shown a
315 similar increase in *T. minor* at higher experimental temperatures. It is interesting to note that
316 most of the studies that reported evaporative water loss were from the 1970s-1990s. We are
317 unsure why measuring water loss fell out of fashion, but we hope that this trend is reversed,
318 particularly as a suite of recent studies on birds have nicely illustrated the effects of different
319 evaporative cooling mechanisms (sweating, panting, gular fluttering) have on the ability for
320 desert birds to stay cool (Gerson et al. 2019; McKechnie et al. 2016; Smit et al. 2018; Whitfield
321 et al. 2015).

322 Regardless of their potential capacity to tolerate T_a higher than T_b , it is clear that *T.*
323 *minor*, like the other *Tupaia* species measured to date (Table 1), is capable of withstanding T_{as}

324 close to T_b with little to no thermoregulatory costs. Changes in dry thermal conductance (Fig 1)
325 were not apparent until $\sim 33^\circ\text{C}$, after increases in T_b (starting near 30°C) had already been
326 observed. *T. minor* have a large number of eccrine and apocrine glands along their skin and an
327 abundance of capillaries surrounding the palms of the hands and soles of the feet, indicative of
328 multiple means of evaporative heat loss (Montagna et al., 1962). However, evaporation is less
329 efficient in the high humidity environments inhabited by this species (Gerson et al. 2014;
330 Weathers 1997; Withers and Cooper 2014). During experimentation at the higher $T_{a,s}$ ($>34^\circ\text{C}$),
331 the animals were often observed sprawled on their back, exhibiting the bare underside of their
332 tails. Potential avenues for dry heat loss, such as the tail, are equally, if not more, important
333 (Tattersall et al., 2012). As the highest temperature measured in our study (35.6°C) was below
334 the T_b of *T. minor*, it is impossible to determine if evaporative cooling would have increased at
335 higher T_a .

336 A better understanding of the link between high $T_{a,s}$ and endotherm performance is
337 needed, yet there is still much to be understood about mammal thermoregulation (Huey et al.
338 2012; Mitchell et al. 2018). Future studies of small tropical endotherms should focus on these
339 responses to higher $T_{a,s}$, both in resting and in active animals, to understand how they may adjust
340 to a warming climate. The lack of increase in metabolic rate, as well as minimal increases in
341 evaporation, at increasingly high $T_{a,s}$ in this study indicates that lesser treeshrews can likely
342 manage $T_{a,s}$ much higher than they experience in their environment (where the maximum daily
343 T_a is usually less than 31°C , Levesque et al. 2018). The collection of more realistic
344 thermoregulatory measurements, such as field metabolic rates, of small tropical endotherms
345 should be prioritized as this will garner a more robust understanding of the relationship between
346 thermoregulatory physiology and T_a . Unlike tropical ectotherms, which are known to be more

347 sensitive to changes in T_a than their temperate counterparts, tropical endotherms may be less
348 climate-sensitive than previously thought. Yet, conclusions from our work on treeshrews stand in
349 sharp contrast to previous studies on small nocturnal tropical mammals, basoendotherms (*sensu*
350 Lovegrove 2012), that are likely to be at a higher risk of adverse effects due to climate change as
351 their body temperatures are already close to current ambient temperatures (Lovegrove et al.
352 2014; Welman et al. 2017a). Our data suggests that some tropical mammals have the ability to
353 cope with rising T_a better than others, and a more complete knowledge of the different
354 thermoregulatory phenotypes of small mammals are necessary for accurate predictions of a
355 species' sensitivity to rising temperatures.

356

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- 540

541 **Table 1** Known parameters for the thermoneutral zone of Scandentians.

	Mass (g)	T _{lc} (°C)	T _{uc} (°C)	Mean T _b at T _{lc} (°C)	Mean T _b at T _a max (°C)	BMR (mLO ₂ ·hr ⁻¹ ·g ⁻¹)	%BMR*	Origin	Source
<i>Tupaia minor</i>	65.2	31.0	> 36	35.7 (T _{sub})	37.1 (T _{sub} , n=3)	1.03 ± 0.10	135	Wild- Malaysian Borneo	This study
<i>Tupaia tana</i>	246.9	25.5	>37	35.5 (T _{sub} =35.7)	37.9 (T _{sub} =38.0)	0.75 ± 0.10	140	Wild- Malaysian Borneo	Levesque <i>et al.</i> (2018)
<i>Tupaia belangeri</i>	186	27.5	35			0.68	118	Captive- Unknown	Weigold (1979) <i>in</i> Genoud <i>et al.</i> (2017)
<i>Tupaia glis</i>	123	30	> 37	37 (T _a not specified)		0.76 ± 0.07	118	Captive- Unknown (purchased)	Bradley and Hudson (1974)
<i>Ptilocercus lowii</i> (nocturnal)	57.5	-	-	35.7 (T _a not specified)		0.75	94	Wild- Malaysia	Whittow and Gould (1976)
<i>Urogale everetti</i>	264	-	-			0.87 ± 0.02	166	Philippines	Nelson and Asling (1962)

542 *%BMR was calculated using the values predicted for mass BMR = 2.382*mass^{0.729} Genoud *et al.* (2017) and reflects whether the BMR is
 543 higher (>100%) or lower than predicted for the a given body mass. All parameters are presented as the mean (± 1 s.d. if known) for each
 544 species

545 **Figure Captions**

546 **Figure 1** Thermoregulatory parameters of *Tupaia minor* measured during the rest-phase of their
547 activity cycle. Individuals were captured from the wild in Malaysian Borneo and kept overnight
548 for measurements. The ambient temperature at which the physiological character of interest
549 increased or decreased significantly, as calculated using segmented regression analysis, is
550 represented by the solid vertical line with the dashed line indicating the 95% confidence interval
551 of the break point analysis.

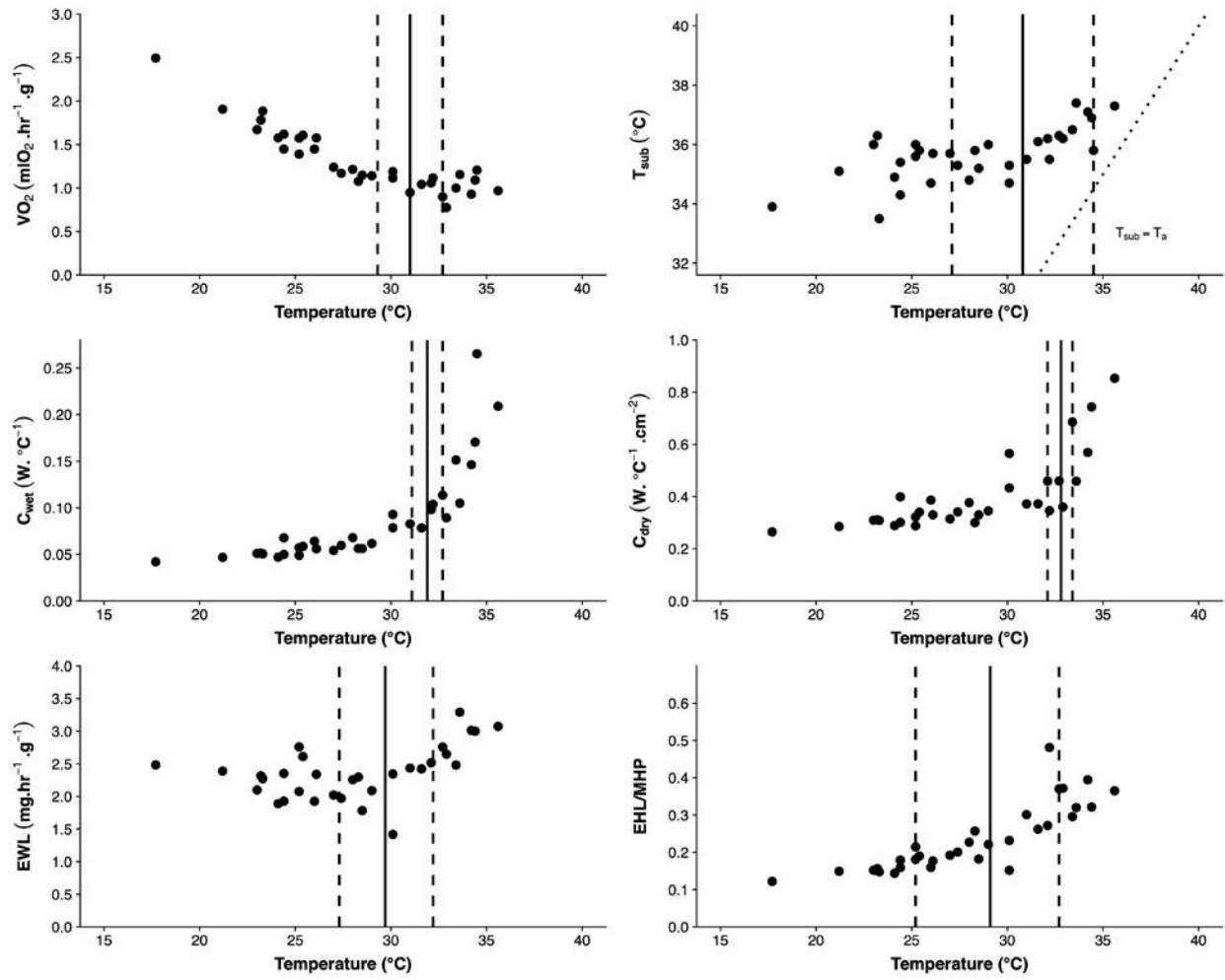
552
553 **Figure 2** The width of the TNZ, and the BMR of a number of mammal species. Treeshrews from
554 Borneo (*Tupaia minor* and *Tupaia tana*) are represented by the blue squares, other Scandentians
555 by the yellow triangles. The dashed lined are the regression lines determined using ordinary least
556 squares and the solid black lines by phylogenetic generalized least squares (pgls, see text), the
557 grey indicate the 95% confidence intervals of the pgls analysis. All BMR data from Genoud *et al*
558 (2017) were used to calculate the confidence intervals but only species less than 1kg are pictured
559 for visual clarity.

560
561 **Figure 3** Subcutaneous temperature (T_{sub}) of *Tupaia minor*, from Sarawak, Malaysia during the
562 resting metabolic rate measurement periods. T_{sub} reflected the species strict diurnal activity
563 pattern, dropping each evening around sunset, and re-warming before sunrise. Individual data are
564 presented with the average for all individuals, at all temperatures illustrated by the blue line.

565
566 **Figure 4 A.** The ambient temperature at which there was a marked increase (break point) in
567 metabolic rate (RMR) or evaporative water loss (EWL) for 101, and 24 species of mammal

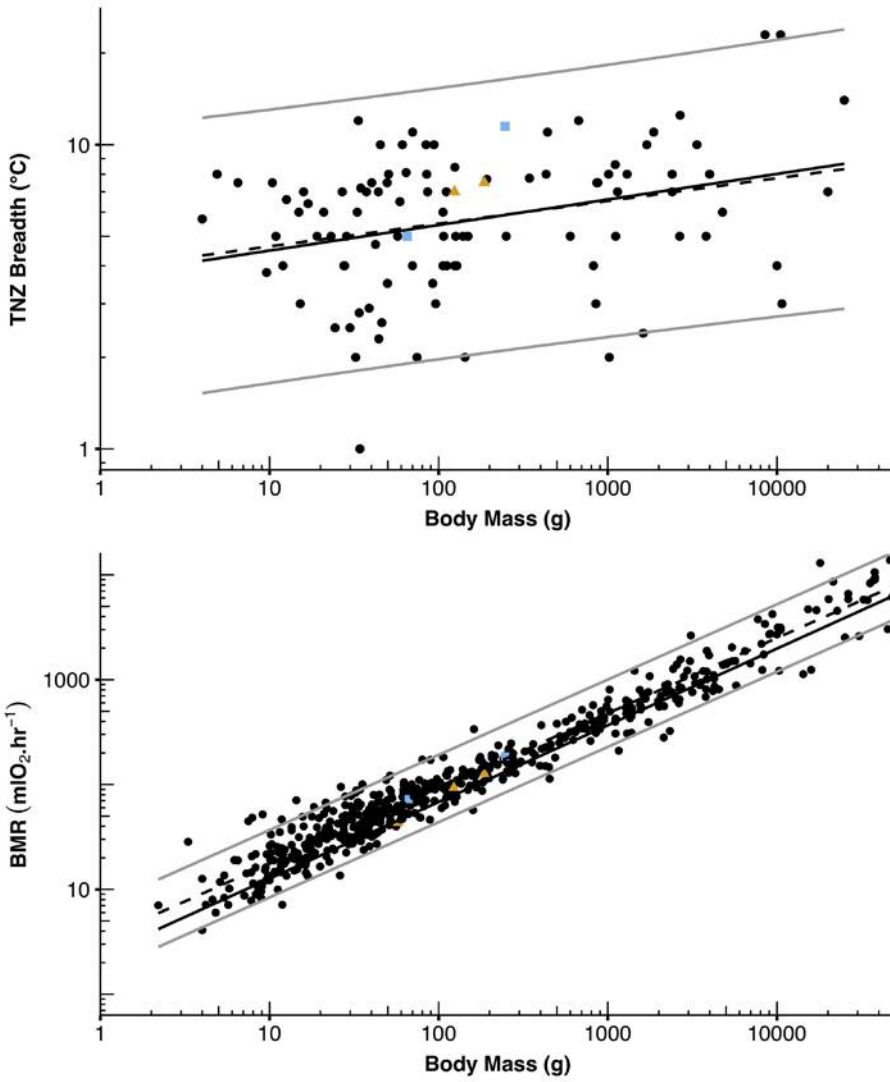
568 respectively (see Supplementary Material). **B.** The break point of evaporative water loss that of
569 evaporative water loss for 22 species of mammals (black) plus two species of treeshrews (blue)
570 from Borneo, *Tupaia minor* (this study) and *T. tana* (Levesque et al. 2018), for these species
571 there was no break point in metabolism and so the number is that of the highest temperature
572 measured in the experiment. The dashed line indicates when the two breakpoints are equal to one
573 another, the solid line the regression line and the grey shading indicates the 95% confidence
574 interval of the regression.
575

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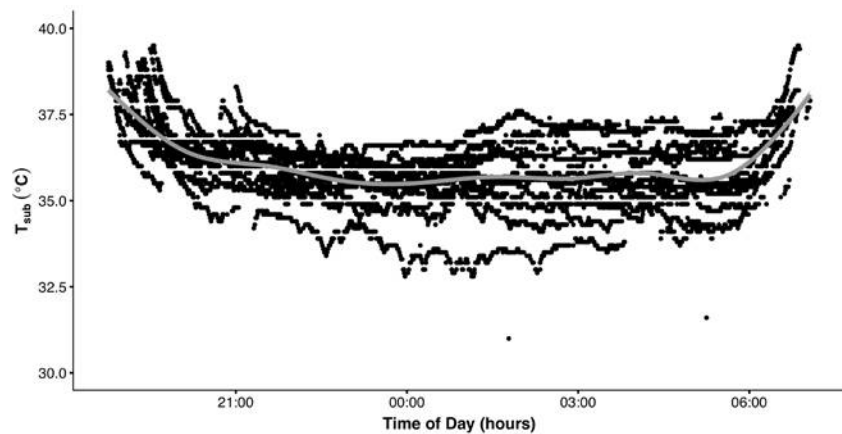
577

578 **Figure 1**



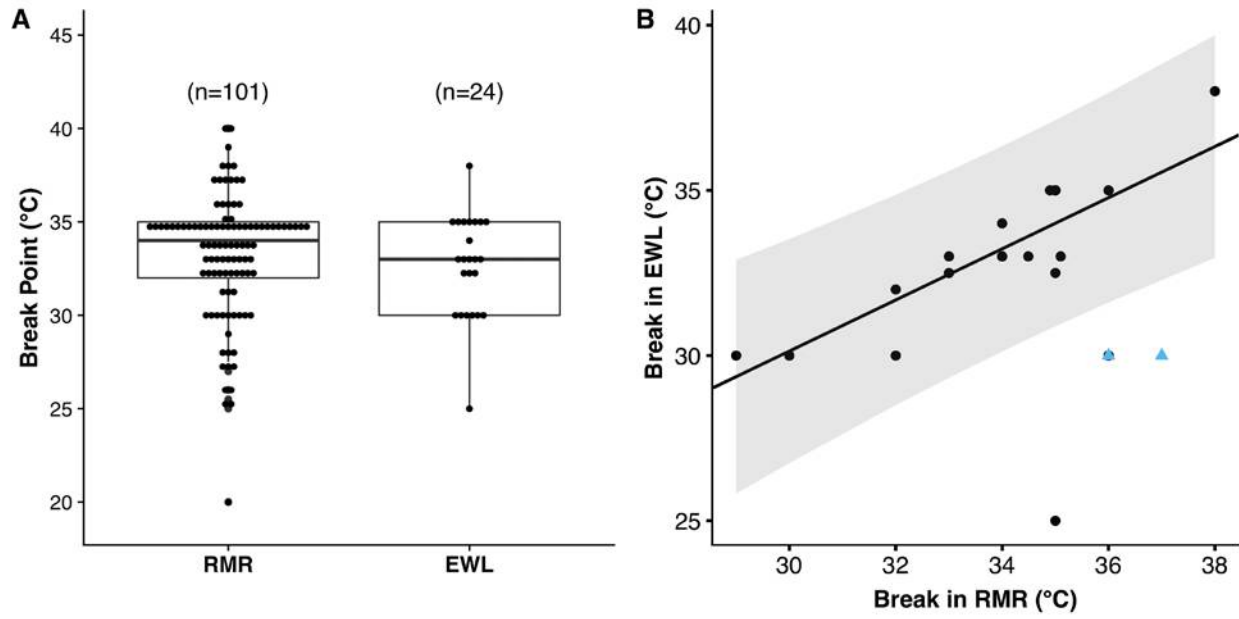
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580 **Figure 2**



581

582 **Figure 3**



583

584 **Figure 4**