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## Basking African striped mice choose warmer locations to heat up: evidence from a field study

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## ABSTRACT

Basking in the sun is an important energy saving tactic in ectotherm animals. It has also been recognized to be important in several mammal species, especially in arid environments. In particular, small mammals which have a greater surface-to-volume ratio can use basking to reduce metabolic energy expenditure by using external heat to maintain a high body temperature. If basking mainly functions to passively gain heat, animals should choose basking spots that offer a more favorable micro-climate for warming up. We tested this hypothesis in African striped mice (*Rhabdomys pumilio*), a diurnal species that is known to bask. Over 19 months, we displaced 138 individuals from their basking spots and immediately thereafter measured the temperature of the surface ( $T_o$ ) at the spots. We expected that striped mice choose spots for basking that are warmer than random spots, especially in a) the morning, when  $T_o$  is lower compared to afternoon, and b) in the dry season characterized by low food availability in which energy gain due to basking is more beneficial than in the moist season with high food availability. Moreover, we tested whether there are differences in relative safety (measured as available plant cover) at basking spots compared to random spots.  $T_o$  was significantly higher at basking spots than at random spots. However, we did not find any differences in  $\Delta T$  in relation to season, time of the day or in the safety between basking and random spots. In conclusion, our study indicates that striped mice choose basking spots with a favourable microclimate characterized by higher ambient temperature.

Keywords: object temperature, basking, animal behavior, behavioral thermoregulation

## INTRODUCTION

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53

54           Animals inhabiting extreme arid environments display physiological and behavioural  
55 adaptations to harsh thermal conditions and scarce food (Rymer et al 2016). This makes  
56 them also vulnerable to climate change. The most dramatic examples come from Australia  
57 where heat waves caused mass fatalities in birds and bats (McKechnie and Wolf 2009,  
58 Ratnayake et al. 2019). Baseline knowledge on how animals cope with challenging thermal  
59 conditions via physiological and behavioural plasticity is essential to predict future changes in  
60 animal communities in arid ecosystems (Huey et al. 2012, Mitchell et al. 2018).

61           Endothermic animals spend a significant amount of their energy maintaining a  
62 relatively stable and high body temperature. This can be challenging when ambient  
63 temperatures are low and food becomes scarce (Brown and Downs 2005). Thermoregulation  
64 is especially costly for small animals because they have a high surface-to-volume ratio and  
65 high metabolic rate. To cope with these challenges, they use different strategies for energy  
66 saving (Terrien, Perret and Aujard 2011, Cossins, 2012). Some have developed physiological  
67 adaptations such as entering torpor or hibernation (Humphries et al 2002). Others adjust their  
68 behaviour by resting in nests to avoid adverse thermal conditions (Glaster and Lustick 1975,  
69 Morton 1978), huddling with conspecifics to reduce heat loss (Gilbert et al. 2010, Schradin et  
70 al. 2006), intensifying locomotor or foraging activity to produce endogenous heat (Ishii et al.  
71 1996, Brobeck 1948), and basking in the sun to warm up passively (Mzilikazi, Lovegrove and  
72 Ribble 2002, Warnecke and Geiser 2010, Brown and Downs 2007). While basking behaviour  
73 has long been studied in detail in ectotherms, such as insects and reptiles (O'Neill and Rolston  
74 2007, Bennett et al. 2014, Herrera 1995, Row and Blouin-Demers 2006, Webb and Whiting  
75 2005), it only recently received attention as an important tactic in mammals (Mzilikazi et al.  
76 2002, Geiser and Drury 2003, Warnecke and Geiser 2010, Geiser et al. 2017).

77 In mammals, basking has been frequently observed in arid habitats with scarce  
78 vegetation, and where solar radiation is easily accessible and thus provides a reliable source of  
79 energy. Basking in the sun is used by small mammals to save internal energy when arousing  
80 from torpor, as occurs in rock elephant shrews (*Elephantulus myurus*, Mzilikazi et al. 2002)  
81 and in several species of small marsupials (Warnecke et al. 2008 and 2010, Warnecke and  
82 Geiser 2010, Stannard, Fabian and Old 2015, Jastroch et al. 2016). Basking also occurs in  
83 diurnal mammals that do not hibernate or enter into torpor. Several species of small mammals  
84 bask in the morning when ambient temperature ( $T_a$ ) is much lower than their thermoneutral  
85 zone (defined as temperature in which metabolic costs of sustaining constant body temperature  
86 are the lowest; Brown and Downs 2006, Scantlebury et al. 2006) to compensate for heat loss.  
87 Basking is regularly observed in dassie rats (*Petromus typicus*, Rathbun and Rathbun 2006)  
88 and rock hyraxes (*Procavia capensis*, Brown and Downs 2005). Thus, basking is an important  
89 energy saving strategy of many small mammal animal species and we therefore expect that  
90 they choose basking spots that are optimal for energy saving.

91 The thermal microclimate influences the behaviour of heterotherms. For instance, the  
92 space use of Taylor's checkerspot butterflies (*Euphydryas editha taylori*) is shaped by access  
93 to sunlight (Bennett, Betts and Smith 2014). Grasshoppers choose different vegetation levels  
94 depending on time of the day to regulate body temperature (O'Neill and Rolston 2007).  
95 Foraging activity of bees increases significantly with ambient temperature ( $T_a$ ), while basking  
96 frequency decreases (Herrera 1995). Similarly, in reptiles, microhabitat differences in the  
97 thermal environment affect basking opportunities and ultimately behaviour and reproduction  
98 (Aguado and Brana 2014; Schwarzkopf and Shine 2006). Basking spot choice might influence  
99 how effectively individuals are able to save energy. Since basking is a strategy to passively  
100 heat up, the warmer the spot, the faster animals will be able to heat up. Thus, the temperature  
101 of the basking spot could be a crucial factor in its choice. Ambient temperature as well as the

102 object ( $T_0$ ) on which basking occurs can vary significantly within a small spatial scale,  
103 depending on, for example, substrate type, slope, orientation, surrounding vegetation and  
104 humidity (Viles 2005). We therefore predicted that animals might choose basking spots with a  
105 warmer microclimate.

106 Behavioral thermoregulation has been observed in several mammalian species. Yellow  
107 baboons (*Papio cynocephalus*) change their body postures depending on solar radiation and  
108 wind direction (Stelzner and Hausfater 1986). Rock hyraxes adjust their positions while  
109 basking, which was affected not only by the temperature but also by antipredatory vigilance  
110 and social interactions (Brown and Downs 2007). Spotted hyenas (*Crocuta crocuta*) also  
111 account for both safety and thermoregulatory needs while choosing resting spots (Kushata et  
112 al. 2018). However, little is known about how mammals choose basking sites and whether  
113 they purposely choose locations with a warmer microclimate.

114 Our study model is the African striped mice (*Rhabdomys pumilio*), a diurnal semi-arid  
115 resident. The behaviour of striped mice is influenced by basking opportunities, which become  
116 active earlier on sunny days (Schradin et al 2007). Scantlebury et al. (2010) found that within  
117 a metabolic chamber, oxygen consumption of striped mice decreased in direct sunshine  
118 compared with in the shade. This effect occurred independently of the ambient temperature  
119 ( $T_a$ ), indicating that a significant amount of radiant energy was absorbed from the sun. This  
120 previous study thus found that metabolic rate is reduced when i) ambient temperature  
121 increases; and ii) striped mice are directly exposed to radiation (controlling for  $T_a$ ).

122 Here we tested whether African striped mice (*Rhabdomys pumilio*) choose basking  
123 spots that have a higher  $T_0$  (the object used to bask on). than random spots, to assess the  
124 microhabitat preferences of striped mice. Striped mice bask extensively in the morning and in  
125 periods when food availability is low (Schradin et al. 2007), which allows them to reduce  
126 their metabolic rate and save energy (Scantlebury et al. 2010). Thus, we further expected that

127 microhabitat choice is more important when  $T_o$  is low in the morning compared to the  
128 afternoon, when  $T_o$  is higher and close to the thermoneutral zone of striped mice (i.e.,  
129 Scantlebury et al. 2006). Further, we expected striped mice to choose relatively warmer  
130 basking spots in the dry season, when food availability is lower and thus energy saving more  
131 important, than in the food rich moist season (Schradin et al. 2007, Warnecke et al. 2010).  
132 Finally, we also tested whether basking spots might be surrounded with more accessible plant  
133 cover than random spots, which we assumed to be a measure of safety.

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## MATERIAL AND METHODS

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### *Study site and period*

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We collected data for 19 months between February 2016 and August 2017 in Goegap Nature Reserve, Northern Cape, South Africa. Our study site is located at an elevation of 950m above sea level in a sandy, episodic river valley and surrounded by rocky hills. Vegetation is typical for the Succulent Karoo, dominated by ever-green shrub *Zygophyllum retrofractum*, with many species of small succulents and annual plants in spring. The climate is semi-arid, characterized by moist winters and springs (May-November) and dry and hot summers and autumns (December-April). Temperatures at the field site vary between  $-5.0^{\circ}\text{C}$  and  $24^{\circ}\text{C}$  in winter and  $5^{\circ}\text{C}$  and  $44^{\circ}\text{C}$  in summer. The study was conducted during very dry years with an average rainfall of 1.44 mm/month and a maximum value of 10mm/month in June 2017, which was clearly below the average recorded in 2005 – 2017 (13.83 mm/month). We used data from plant surveys to define seasons. Vegetation is a good proxy for denoting the moist season because plant growth depends on more frequent and regular rainfall. High plant availability also affects the onset of reproduction and foraging behaviour of striped mice (Schradin and Pillay 2004). We conducted plant surveys twice a month, determining the number of food plants in 8 monitoring plots of  $4\text{ m}^2$  each. Months with a  $> 5$  average number



152 of vegetating food plant species per month were regarded as moist season, since we know that  
153 at such high food availability there is no physiological indication of food shortage in striped  
154 mice (blood glucose levels are high and blood ketone levels are low; Schradin unpubl. data).

155

156 *Measuring  $T_o$  at basking and random spots and  $T_{min}$*

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158 We observed 138 individuals striped mice at their nests during mornings and  
159 afternoons. We waited for individuals to emerge from the nest or return from foraging to bask.  
160 An observer sat still and quiet 5 to 10 meters away from the nest. Such close observations  
161 were possible without disturbing natural behavior of mice, since the population had been  
162 constantly studied for 15 years and striped mice are habituated to the presence of human  
163 observers. We identified individuals by specific dye markings applied to the fur of striped  
164 mice during previous trapping (Schradin and Pillay 2004). We carefully recorded the basking  
165 location of a mouse (using binoculars when necessary) and walked towards the spot (chasing  
166 the mouse away) to measure  $T_o$  of the basking spot.  $T_o$  is the temperature of the object or  
167 surface on which animal was seen basking, such as sand, plants or stones, and can be affected  
168 by factors, such as solar radiation (directly or reflected from the sun), conduction, convection,  
169 evaporation, material composition (Cossins 2012). Due to these factors.  $T_o$  can vary on a  
170 small scale and provide unique thermal conditions to basking animals.

171  $T_o$  was measured with a Powerfix infrared temperature probe (infrared gun;  
172 Kompernass Handels GmbH, Bochum, Germany; Laser class 2, 650nm) with a reported  
173 accuracy of 2%. After the measurement was taken, we took measurements at two random  
174 spots. The first was approximately 20 cm (measured with the length of the infrared gun) to the  
175 right of the basking location (if this was not possible due to impeding vegetation cover, the  
176 measurement was taken to the left). The second random spot was approximately 20 cm in

177 front of the basking spot in the open and away from the shrub. All measurements were taken  
178 in the sun. All procedures needed for behavioural observations were conducted following  
179 protocols approved by the Animal Ethics Screening Committee of the University of the  
180 Witwatersrand (AESC 2012/37/2A, AESC 2014/40/B) and in accordance with Guidelines for  
181 the treatment of animals in behavioural research and teaching (Vitale et al. 2018).

182 Fifty basking spots and their random spots (right and front) were temporarily marked  
183 after temperature measurement was taken. On the following day, all measurements were  
184 repeated at the exact same time but without a mouse being present directly before the  
185 measurement, and this was again compared to random spots. We did this to exclude the  
186 possibility that higher temperatures at basking spots were due to the mouse's body heat  
187 having heated up the spot, rather than due to microclimate differences.

188 Minimum daily temperature ( $T_{\min}$ ) was taken every day at the research station, located  
189 300m away from the study site. We used an electronic thermometer with an accuracy of  
190 0.1°C, and measurements were recorded every morning 10cm above the ground.

191

#### 192 *Plant cover measurements to characterise basking spots*

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194 We marked 61 spots at which we observed mice basking more than once and marked these  
195 locations with small flags. For each of these basking locations, we marked a control spot 20  
196 cm to the right at the same bush. We made sure that these random spots were not used as  
197 basking spots by observing them for a few consecutive days. We measured plant cover at both  
198 spots as a proxy of protection from predators. We created a cover index of 0 to 4 by  
199 considering cover to the left, right, above and behind the marked spot. We summed the score  
200 of plant cover for each spot. Thus, a spot received a score of 4 when it had cover on all four  
201 sides, 3 for cover on three sides and so on.

202

203

*Data analysis*

204

205           In 19 months, we performed 370 observations of 138 individuals. We assigned every  
206 observation to a season (dry or moist) and time of the day (morning or afternoon). 204 of our  
207 observations were conducted in the morning and 166 in the afternoon. 305 observations took  
208 place in dry season and 65 in the much shorter moist season (September-December 2016 and  
209 August 2017); this disproportion is due to the fact that the moist season in the Succulent  
210 Karoo is generally much shorter than the dry season and rainfall during our study period was  
211 especially low.

212           We analysed data in R version 1.0.136 using basic descriptive statistics with the stats  
213 package and linear mixed models implemented in the lme4 package (lmer function; Bates,  
214 Maechler and Bolker, 2015). To exclude the possibility that basking spots were warmer due to  
215 mouse body heat we compared  $T_a$  with the mouse being present or not present before the  
216 measurement (paired data, Wilcoxon matched-pairs sign rank test), and by comparing  
217 correlation coefficients of 1) temperatures taken at basking spots with a striped mouse being  
218 present and not present before a measurement, and 2) repeated temperature measurements  
219 taken with the mice absent on the following day, using Fisher-Z transformation.

220           We ran 2 separate linear mixed models for morning and afternoon data. Object  
221 temperature was included as the response variable and spot category (basking spot, right and  
222 front random spots), and season (moist or dry) were used as explanatory variables. We also  
223 included individual and nest as random factors.

224           We investigated factors that affected the temperature difference ( $\Delta T$ ) between basking  
225 spots and the right random spot. We chose  $\Delta T$  values based on the right spot as the response  
226 variable in our model because it was taken at the bush, not in the open and thus it had similar

227 thermal properties and plant cover. In addition, the front spot included several outliers and had  
228 greater variation and were not suitable for analyses. We used  $\Delta T$  as a response variable in a  
229 linear mixed model and included time of the day (morning or afternoon), season (dry or  
230 moist) as fixed factors and daily minimum temperature as a continuous factor. Individual and  
231 nest were added as random factors. Finally, we compared the cover index of basking spots  
232 compared to non-basking spots (index of 0-4) using paired Wilcoxon test.

233

234

## RESULTS

235  $T_o$  at basking spots was significantly higher in the afternoon ( $28.2 \pm 5.7^\circ\text{C}$ ,  $\bar{X} \pm \text{SE}$ ) than  
236 in the morning ( $16.1 \pm 4.6^\circ\text{C}$ ;  $t=22.59$ ,  $df=368$ ,  $P<0.001$ , unpaired t-test).  $T_o$  did not differ  
237 between basking spots in the dry ( $21.8 \pm 7.6^\circ\text{C}$ ) and moist season ( $20.1 \pm 9.0^\circ\text{C}$ ;  $t=1.58$ ,  $df=368$   
238  $P=0.11$ , unpaired t-test).

239 There was no significant difference in  $T_o$  when mice were present ( $22.7 \pm 8.3^\circ\text{C}$ ) or  
240 absent ( $24.3 \pm 8.5^\circ\text{C}$ ); Wilcoxon-matched pairs sign rank test:  $V = 1136.5$ ,  $P = 0.4359$ ).  $T_o$   
241 taken after displacing a mouse from a basking spot was significantly and positively correlated  
242 with  $T_o$  at the same basking spots on the next day without a mouse being present (Pearson  
243 correlation,  $r=0.95$ ,  $P<0.001$ ). The second set of measurements comparing 2 temperatures at  
244 basking locations with mice being absent were significantly correlated (Pearson correlation  
245  $r=0.94$ ,  $P<0.001$ ). Fisher-Z transformation revealed no differences between these 2 correlation  
246 coefficients ( $Z=0.5$ ,  $P=0.62$ ).

247 Linear mixed model analyses revealed that  $T_o$  at basking spots was significantly  
248 higher than at the two random spots, both in the morning and in the afternoon (Fig.1).  $T_o$  also  
249 depended on the time of the day and minimum daily temperature, but not on the season (Table  
250 1a and 1b).

251 The temperature difference between basking and random spots ( $\Delta T$ ) did not differ

252 between morning and afternoon ( $P=0.30$ ) nor between moist and dry season ( $P=0.64$ ). There  
253 was no effect of minimum daily temperature on  $\Delta T$  ( $P=0.12$ , see also Table 2).

254 The cover scores at basking spots were  $2.30 \pm 1.15$  and  $2.11 \pm 1.08$  at random spots.  
255 Of the 61 basking spots where we took plant cover measurements, 19 basking spots had  
256 greater cover scores than random spots, 13 basking locations had lower cover scores, and  
257 there was no difference in 22 cases. Overall, we found no difference in cover scores between  
258 basking and random spots (Wilcoxon matched-pairs sign rank test,  $V=306$ ,  $P=0.23$ ).

259

260

## DISCUSSION

261

262 We found that striped mice bask at spots that have a warmer microclimate than  
263 random spots. In contrast, basking spots did not offer more cover from potential predators  
264 than random spots at the same bush. Also,  $\Delta T$  did not differ between seasons and between  
265 morning and afternoon. Striped mice bask to passively heat up and thus save metabolic energy  
266 (Scantlebury et al. 2010). Therefore, choosing basking spots with high  $T_o$  would be adaptive.  
267 Our current results underline the importance of basking for striped mice that seem to  
268 purposely choose warmer basking spots.

269 We found that African striped mice use basking spots with higher temperature than  
270 random spots. Basking spots were warmer than random spots at the shrubs and in the open.  
271 Our data indicate that areas close to the shrubs had a warmer microclimate than those away  
272 from a shrub (the random spot to the right of a shrub was significantly warmer than the one in  
273 front), although they did not differ in terms of safety, indicating that between 2 spots with  
274 similar safety, mice chose the one with higher  $T_o$ . Basking spots also had higher  $T_o$  than  
275 random locations measured the following day without a mouse being present, indicating that  
276 it was not the presence of the basking mouse that would have heated up the basking spot.

277 Thus, our results indicate that the temperature is a crucial factor affecting basking spot choice  
278 in African striped mouse.

279 Even though mice chose warmer basking spots, we did not find clear patterns between  
280  $\Delta T$  and minimum daily temperature or season. Our results indicate that mice prefer warmer  
281 spots for basking, but the difference between selected spots and random was rather subtle  
282 (average difference between basking spots and random spots was lower than 2°C). African  
283 striped mice usually bask in front of the nest in which they spent the night (Schradin et al.  
284 2007). It is possible that under natural conditions the access to optimal thermal locations for  
285 basking is very limited, and thus it is energetically not worth traveling longer distances in  
286 search of a warmer location. Instead animals pick the most favourable spots around their  
287 nests.

288 Basking at exposed spots probably increases predation risk since it exposes striped  
289 mice to visual predators, such as shrikes, birds of prey, wildcats and jackals, all of which are  
290 known to prey frequently on striped mice in our study population (Schradin, unpubl. data).  
291 The trade-off between basking and safety was previously described in reptiles (Carrascal et al.  
292 1992, Carter, Goldizen and Tromp 2010, Meek et al. 2008, Web and Whiting 2005). Striped  
293 mice chose basking locations that are warmer and also offered adequate protection against  
294 potential predators, since these were directly at shrubs. While basking spots offer the  
295 option to quickly withdraw into the safety of the shrub should a predator approach, basking  
296 spots did not offer more cover than random spots at the same shrubs. Thus, we did not find  
297 that striped mice chose particularly safe basking spots, possibly because all spots at a shrub  
298 offer sufficient cover to quickly hide in case of a predation event.

299 The selection of basking sites might be based not only on object temperature but also  
300 on whether they adequately camouflage the basking animal. For example, Aegean wall lizards  
301 (*Podarcis erhardii*) selected basking sites in which their dorsal surface better matched the

302 background surface, providing camouflage against avian predators (Marshall et al. 2016).  
303 Whether striped mice similarly selected basking sites that offered camouflage is currently  
304 unknown; the stripes might have a dazzle effect creating confusion (Schradin  
305 *ENCYCLOPEDIA!*, Stevens 2007). Moreover, mice also stay still (freeze) while basking  
306 which is a common antipredatory behaviour in many species, protecting them from being  
307 spotted by predators sensitive to visual motion (Bolles 1970, Stevens 2007). Basking in the  
308 open is occasionally observed in striped mice but it is rather uncommon behaviour (Schradin,  
309 unpubl. data). Therefore, with the relative safety provided by near a bush, it was more  
310 important for animals to choose a spot with higher  $T_o$ .

311 It has only recently been recognized that basking is an important energy saving  
312 strategy in mammals. Here we present one of the first studies demonstrating that mammals,  
313 similar to reptiles or invertebrates, choose basking spots with a favourable microclimate for  
314 basking. Several other factors might also influence basking spot choice such as proximity to  
315 the nest or social factors (Brown and Downs 2007), and particularly predator avoidance and  
316 ability to camouflage (Marshall et al. 2016). Striped mice bask at safe spots, from where they  
317 can withdraw quickly into the safety of a shrub. However, while basking spots did not differ  
318 in cover providing safety compared to random spots, they were warmer. This indicates that  
319 basking spots are chosen in a way to maximize energy savings due to passively heating up  
320 while being in a relatively safe location, which would represent an adaptive choice of basking  
321 spots.

322 Our findings provide important insight into thermoregulatory behaviours of African  
323 striped mice. This semi-desert species is known for its behavioural, physiological and social  
324 adaptations that help it cope with harsh environmental conditions (Mallarino, Pillay, Hoekstra,  
325 and Schradin 2018). However, the species is facing temporary size and population viability  
326 declines due to more frequent droughts in the Succulent Karoo region (Nater et al. 2018).

327 Temperature rise and droughts may also affect basking patterns in this and other arid species.

328 It is essential to understand the mechanisms shaping these thermoregulatory behaviours

329 predict future responses of species to challenges of climate change.

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332

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342

343

## REFERENCES

344

345 Aguado S., Brana F., 2014. Thermoregulation in a cold-adapted species (Cyren's rock lizard  
346 *Iberolacerta cyreni*): influence of thermal environment and associated costs. Canadian Journal  
347 of Zoology 92:955-964. DOI:10.1139/cjz-2014-0096  
348 Bates D., Maechler M., Bolker B., Walker S., 2015. Fitting Linear Mixed-Effects Models  
349 Using lme4. Journal of Statistical Software, 67(1), 1 -48. DOI:10.18637/jss.v067.i01  
350 Bennett V.J., Betts M.G., Smith W.P. 2014. Influence of thermal conditions on habitat use by a  
351 rare spring-emerging butterfly *Euphydryas editha taylori*, Journal of Applied Entomology,  
352 138:623-634. DOI:10.1111/jen.12137  
353 Bristow, K. L. 1998. Measurement of thermal properties and water content of unsaturated  
354 sandy soil using dual-probe heat-pulse probes. Agricultural and Forest  
355 Meteorology, 89(2):75-84. DOI:10.1016/S0168-1923(97)00065-8

356

357 Brown, K. J., Downs, C. T. 2006. Seasonal patterns in body temperature of free-living rock  
358 hyrax (*Procavia capensis*). *Comparative Biochemistry and Physiology Part A: Molecular and*  
359 *Integrative Physiology*, 143(1):42-49. DOI: 10.1016/j.cbpa.2005.10.020

360 Brown, K. J., Downs, C. T. 2007. Basking behaviour in the rock hyrax (*Procavia capensis*)  
361 during winter. *African Zoology*, 42(1):70-79. DOI: 10.1080/15627020.2007.11407379

362 Carrascal, L. M., López, P., Martín, J., Salvador, A. 1992. Basking and antipredator behaviour  
363 in a high altitude lizard: implications of heat exchange rate. *Ethology*, 92(2):143-154. DOI:  
364 10.1111/j.1439-0310.1992.tb00955.x

365 Carter, A. J., Goldizen, A. W., Tromp, S. A. 2010. Agamas exhibit behavioral syndromes:  
366 bolder males bask and feed more but may suffer higher predation. *Behavioral Ecology*,  
367 21:655-661. DOI: 10.1093/beheco/arq036

368

369 **Chown, S. L., Hoffmann, A. A., Kristensen, T. N., Angilletta Jr, M. J., Stenseth, N. C.,**  
370 **Pertoldi, C., 2010. Adapting to climate change: a perspective from evolutionary**  
371 **physiology.** *Climate Research*, 43(1-2), 3-15. DOI: 10.3354/cr00879

372 Cossins. A., Bowler, K., 2012. *Temperature biology of animals.* Chapman and Hall, London,  
373 United Kingdom.

374

375 Geiser F., Drury R.L., 2003. Radiant heat affects thermoregulation and energy expenditure  
376 during rewarming from torpor. *Journal of Comparative Physiology B*, 173:55-60. DOI:  
377 10.1007/s00360-002-0311-y

378

379 Geiser, F., Stawski, C., Wacker, C. B., Nowack, J. 2017. Phoenix from the Ashes: Fire, Torpor,  
380 and the Evolution of Mammalian Endothermy. *Frontiers in Physiology*, 8:842. DOI:

381 10.3389/fphys.2017.00842

382

383 Gilbert C., McCafferty D., Le Maho Y., Martrette J.-M., Giroud S., Blanc S., Ancel A. 2010.

384 One for all and all for one: the energetic benefits of huddling in endotherms, *Biological*

385 *Revisions* 85:545-569. DOI: 10.1111/j.1469-185X.2009.00115.x.

386

387 Glaster H., Lustick S. 1975. Energetics and nesting behavior of northern white-footed mouse

388 (*Peromyscus leocopus-noveboracensis*). *Physiological Zoology* 48(2):105-113. DOI:

389 10.1086/physzool.48.2.30155644

390

391 Vitale A., Calisi R., Carere C., Carter T., Ha J. C., Hubrecht R., Jennings D., Metcalfe A.,

392 Ophir G., Ratcliffe J. M., Roth T. C., Smith A., Sneddon L. 2018. Guidelines for the Use of

393 Animals. Guidelines for the treatment of animals in behavioural research and teaching 2018.

394 *Animal Behaviour* 135(2018):I-X. DOI:

395

396

397 Herrera C.M., 1995. Floral biology. Microclimate and pollination by ectothermic bees in an

398 early-blooming herb. *Ecology* 76:218-228. DOI: 10.2307/1940644

399

400 Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A., Jess, M., & Williams, S. E.,

401 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology

402 and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*,

403 367(1596), 1665-1679

404

405 Humphries M. M., Thomas D. W., Speakman J. R. 2002. Climate-mediated energetic

406 constraints on the distribution of hibernating mammals. *Nature*. 418(6895):313-316. DOI:  
407 10.1038/nature00828  
408

409 Ishii K., Kuwahara K., Tsubone H., Sugano S. 1996. The telemetric monitoring of heart rate,  
410 locomotor activity and body temperature in mice and voles (*Microtus arvalis*) during ambient  
411 temperature changes. *Laboratory Animals*, (1):7-12. DOI: 10.1258/002367796780744992  
412

413 Jastroch M., Giroud S., Barrett P., Geiser F., Heldmaier G., Herwig A. 2016. Seasonal control  
414 of mammalian energy balance: recent advances in the understanding of daily torpor and  
415 hibernation. *Journal of Neuroendocrinology*, 28(11). DOI: 10.1111/jne.12437  
416

417 Kushata J. N. T., Périquet S., Tarakini T., Muzamba M., Mafuwa B., Loveridge A. J., Valeix  
418 M., 2018. Drivers of diurnal rest site selection by spotted hyaenas. *Journal of Zoology*,  
419 304(2). DOI: 10.1111/jzo.12504.  
420

421 Marshall, K.L., Philpot, K.E. and Stevens, M., 2016. Microhabitat choice in island lizards  
422 enhances camouflage against avian predators. *Scientific Reports*, 6, p.19815.  
423

424 McKechnie, A. E., & Wolf, B. O. (2009). Climate change increases the likelihood of  
425 catastrophic avian mortality events during extreme heat waves. *Biology letters*, 6(2), 253-256  
426

427 Meek R., Avery R.A., 2008. Basking in the Australian water dragon *Physignathus lesueurii*;  
428 why do alpha males not respond to operative temperatures in the same way as adults and sub-  
429 adults? *Amphibia-Reptilia*, 29, 257-262. DOI: 10.1163/156853808784125009  
430

431 Mitchell, D., Snelling, E. P., Hetem, R. S., Maloney, S. K., Strauss, W. M., & Fuller, A.  
432 (2018). Revisiting concepts of thermal physiology: Predicting responses of mammals to  
433 climate change. *Journal of Animal Ecology*, 87(4), 956-973.

434

435 Morton S. R., 1978. Torpor and nest sharing in free-living *Sminthopsis crassicaudata*  
436 (Marsupialia) and *Mus musculus* (Rodentia). *Journal of Mammalogy* 59(3):569-575. DOI:  
437 10.2307/1380234

438

439 Mzilikazi M., Lovegrove B.G., Ribble D.O., 2002. Exogenous passive heating during torpor  
440 arousal in free-ranging rock elephant shrews *Elephantulus myurus*. *Oecologia* 133. DOI:  
441 10.1007/s00442-002-1052-z

442

443 O'Neill K.M., Rolston M.G., 2007. Short-term dynamics of behavioral thermoregulation by  
444 adults of the grasshopper *Melanoplus sanguinipes*. *Journal of Insect Science* 7. DOI:  
445 10.1673/031.007.2701

446

447 O'Shea, T. J., Cryan, P. M., Hayman, D. T., Plowright, R. K., & Streicker, D. G. (2016).  
448 Multiple mortality events in bats: a global review. *Mammal Review*, 46(3), 175-190

449

450 Porter, K., 1982. Basking behaviour in larvae of the butterfly *Euphydryas aurinia*. *Oikos*,  
451 38:308-312. DOI: 10.2307/3544670

452

453 Rathbun G.B., Rathbun C.D., 2006. Sheltering, basking and petrophily in the noki or dassie-  
454 rat (*Petromus typicus*) in Namibia. *Mammalia* 70(3-4):269-275. DOI:  
455 10.1515/MAMM.2006.038

456 Ratnayake, H. U., Kearney, M. R., Govekar, P., Karoly, D., & Welbergen, J. A., 2019.  
457 Forecasting wildlife die-offs from extreme heat events. *Animal Conservation*. Online first  
458 <https://doi.org/10.1111/acv.12476>  
459  
460 Row J.R., Blouin-Demers G., 2006. Thermal quality influences effectiveness of  
461 thermoregulation, habitat use, and behaviour in milk snakes. *Oecologia* 148:1-11. DOI:  
462 10.1007/s00442-005-0350-7  
463  
464 Scantlebury M., Krackow S. Pillay N., Bennett N., Schradin C., 2010. Basking is affected by  
465 season and influences oxygen consumption in desert-living striped mice. *Journal of Zoology*  
466 281:132-139. DOI: 10.1111/j.1469-7998.2010.00687.x  
467  
468 Schradin, C., Pillay, N., 2004. The Striped Mouse (*Rhabdomys pumilio*) from the succulent  
469 karoo, South Africa: a territorial group-living solitary forager with communal breeding and  
470 helpers at the nest. *Journal of Comparative Psychology*, 118(1):37-47. DOI: 10.1037/0735-  
471 7036.118.1.37  
472  
473 Schradin C., Krackow S., Schubert M., Keller C., Schradin B., Pillay N., 2007. Regulation of  
474 activity in desert-living striped mice: the importance of basking. *Ethology* 113:606-614. DOI:  
475 10.1111/j.1439-0310.2007.01361.x  
476  
477 Schwarzkopf, L., Shine, R., 1991. Thermal biology of reproduction in viviparous skinks,  
478 *Eulamprus tympanum*: why do gravid females bask more? *Oecologia*, 88(4):562-569. DOI:  
479  
480 Stannard H.J., Fabian M., Old J.M., 2015. To bask or not to bask: Behavioural

481 thermoregulation in two species of dasyurid. *Phascogale calura* and *Antechinomys laniger*.  
482 Journal of Thermal Biology 53:66-71. DOI: 10.1007/BF00317720.  
483  
484 Stelzner, J. K., Hausfater, G., 1986. Posture, microclimate, and thermoregulation in yellow  
485 baboons. Primates, 27(4):449-463.  
486  
487 Stevens, M. (2007). Predator perception and the interrelation between different forms of  
488 protective coloration. Proceedings of the Royal Society B: Biological Sciences, 274(1617),  
489 1457-1464. DOI: [10.1098/rspb.2007.0220](https://doi.org/10.1098/rspb.2007.0220)  
490 Terrien J., Perret M., Aujard F., 2011. Behavioral thermoregulation in mammals: a  
491 review. Frontiers in Biosciences, 16:1428-1444. DOI: 10.2741/3797  
492  
493 Webb, J. K., Whiting, M. J., 2005. Why don't small snakes bask? Juvenile broad-headed  
494 snakes trade thermal benefits for safety. Oikos, 110(3):515-522. DOI: 10.1111/j.0030-  
495 1299.2005.13722.x  
496  
497 Viles, H. A., 2005. Microclimate and weathering in the central Namib Desert, Namibia.  
498 Geomorphology, 67(1-2):189-209. DOI: 10.1016/j.geomorph.2004.04.006

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502 Figure 1. Temperatures at basking spots and two random locations, 20cm away at the same  
503 bush as a basking spot and 20cm away to the front of a basking spot. Values represent mean  
504 temperatures  $\pm$ SE in the morning (AM) and afternoon (PM).

505



506 Table 1a. The statistical output of the temperature of basking and random spots in the  
 507 morning depending on the season (dry or moist) and minimum daily temperature. Intercept is  
 508 temperature at basking spot in the in the dry season. Significant variables are shown in bold.

	Estimate	SE	t	P
<b>Intercept</b>	<b>16.17</b>	<b>0.59</b>	<b>27.25</b>	<b>&lt;0.001</b>
<b>Front</b>	<b>-1.93</b>	<b>0.14</b>	<b>-13.82</b>	<b>&lt;0.001</b>
<b>Right</b>	<b>-1.09</b>	<b>0.14</b>	<b>-7.77</b>	<b>&lt;0.001</b>
Season (moist)	-0.08	0.69	-0.12	0.90
<b>Minimum daily temperature</b>	<b>0.52</b>	<b>0.05</b>	<b>10.39</b>	<b>&lt;0.001</b>

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511

512 Table 1b. The statistical output of the temperature of basking spots and random spots  
 513 in the afternoon depending on the season (dry or moist) and minimum daily temperature.  
 514 Intercept is temperature at basking spot in the in the dry season. Significant variables are  
 515 shown in bold.  
 516

	Estimate	SE	t	P
<b>Intercept</b>	<b>27.30</b>	<b>0.96</b>	<b>28.38</b>	<b>&lt;0.001</b>
<b>Front</b>	<b>-1.99</b>	<b>0.19</b>	<b>-10.66</b>	<b>&lt;0.001</b>
<b>Right</b>	<b>-1.06</b>	<b>0.19</b>	<b>-5.71</b>	<b>&lt;0.001</b>
Season (moist)	2.14	1.33	1.61	0.11
<b>Minimum daily temperature</b>	<b>0.45</b>	<b>0.09</b>	<b>5.10</b>	<b>&lt;0.001</b>

517 Table 2. The statistical output of the difference between basking spots and right control  
 518 ttemperature ( $\Delta T$ ) depending by season (dry or moist), minimum daily temperature and time  
 519 of the day: morning (am) or afternoon (pm). Intercept is  $\Delta T$  in the morning (am) in the dry  
 520 season.  
 521

Response variable = $\Delta T$	Estimate	SE	t	P
<b>Intercept</b>	<b>1.51</b>	<b>0.37</b>	<b>4.14</b>	<b>&lt;0.001</b>
Minimum daily temperature	-0.04	0.02	-1.56	0.12
Season (moist)	-0.24	0.22	-1.06	0.29
Time (pm)	0.16	0.34	0.49	0.62

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