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

M. Zduniak, Neville Pillay, Carsten Schradin

► To cite this version:

M. Zduniak, Neville Pillay, Carsten Schradin. Basking African striped mice choose warmer locations to heat up: evidence from a field study. *Journal of Zoology*, 2019, 309 (2), pp.133-139. 10.1111/jzo.12687 . hal-02169446

HAL Id: hal-02169446

<https://hal.science/hal-02169446>

Submitted on 20 Jul 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Short title: Basking spot preferences of African striped mouse

**Title: Basking African striped mice choose warmer locations to heat up:
evidence from the field study.**

Published as

Zduniak, M., Pillay, N. & **Schradin, C.** 2019. Basking African striped mice choose warmer locations to heat up: evidence from a field study. *Journal of Zoology*, **309**, 133-139.

Milena Zduniak, Neville Pillay, Carsten Schradin

Adam Mickiewicz University, Department of Systematic Zoology, Umultowska 89, 61-614

Poznań, Poland (MZ)

University of the Witwatersrand, School of Animal, Plant and Environmental Sciences,

Private Bag 3, WITS 2050, Johannesburg, South Africa (MZ, NP, CS)

IPHC, UNISTRA, CNRS, 23 rue du Loess, 67200 Strasbourg, France (CS)

Corresponding author : Milena Zduniak, zdun@amu.edu.pl

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 ΔT 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

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

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

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

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

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

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

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

MATERIAL AND METHODS

Study site and period

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°C and 24°C in winter and 5°C and 44°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 m^2 each. Months with a > 5 average number

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

Measuring T_o at basking and random spots and T_{min}

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

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

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

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

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

Plant cover measurements to characterise basking spots

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

Data analysis

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

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

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

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

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

RESULTS

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 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 between basking spots in the dry ($21.8 \pm 7.6^\circ\text{C}$) and moist season ($20.1 \pm 9.0^\circ\text{C}$; $t=1.58$, $df=368$, $P=0.11$, unpaired t-test).

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

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

The temperature difference between basking and random spots (ΔT) did not differ

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

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

DISCUSSION

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

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

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

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

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

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

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

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

Our findings provide important insight into thermoregulatory behaviours of African striped mice. This semi-desert species is known for its behavioural, physiological and social adaptations that help it cope with harsh environmental conditions (Mallarino, Pillay, Hoekstra, and Schradin 2018). However, the species is facing temporary size and population viability 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.

330

ACKNOWLEDGEMENTS

We would like to thank all the people involved in data collection, Jessica Mulvey and Dominik Schüßler for discussions and their input in the study design. We would also like to thank Rafał Zwolak for his advice with statistical analyses. This study was made possible with the support of the Succulent Karoo Research Station (registered South African NPO 122-134) and Goegap Nature Reserve. This study was supported by the University of the Witwatersrand and the CNRS. Animals were captured and handled following protocols approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC 2012/37/2A extended until December 2019, AESC 2014/40/B).

REFERENCES

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

10.3389/fphys.2017.00842

Gilbert C., McCafferty D., Le Maho Y., Martrette J.-M., Giroud S., Blanc S., Ancel A. 2010.
One for all and all for one: the energetic benefits of huddling in endotherms, Biological
Revisions 85:545-569. DOI: 10.1111/j.1469-185X.2009.00115.x.

Glaster H., Lustick S. 1975. Energetics and nesting behavior of northern white-footed mouse
(*Peromyscus leocopus-noveboracensis*). Physiological Zoology 48(2):105-113. DOI:
10.1086/physzool.48.2.30155644

Vitale A., Calisi R., Carere C., Carter T., Ha J. C., Hubrecht R., Jennings D., Metcalfe A.,
Ophir G., Ratcliffe J. M., Roth T. C., Smith A., Sneddon L. 2018. Guidelines for the Use of
Animals. Guidelines for the treatment of animals in behavioural research and teaching 2018.
Animal Behaviour 135(2018):I-X. DOI:

Herrera C.M., 1995. Floral biology. Microclimate and pollination by ectothermic bees in an
early-blooming herb. Ecology 76:218-228. DOI: 10.2307/1940644

Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A., Jess, M., & Williams, S. E.,
2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology
and adaptation. Philosophical Transactions of the Royal Society B: Biological Sciences,
367(1596), 1665-1679

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Ratnayake, H. U., Kearney, M. R., Govekar, P., Karoly, D., & Welbergen, J. A., 2019.
 Forecasting wildlife die-offs from extreme heat events. *Animal Conservation*. Online first
<https://doi.org/10.1111/acv.12476>

Row J.R., Blouin-Demers G., 2006. Thermal quality influences effectiveness of
 thermoregulation, habitat use, and behaviour in milk snakes. *Oecologia* 148:1-11. DOI:
[10.1007/s00442-005-0350-7](https://doi.org/10.1007/s00442-005-0350-7)

Scantlebury M., Krackow S. Pillay N., Bennett N., Schradin C., 2010. Basking is affected by
 season and influences oxygen consumption in desert-living striped mice. *Journal of Zoology*
 281:132-139. DOI: [10.1111/j.1469-7998.2010.00687.x](https://doi.org/10.1111/j.1469-7998.2010.00687.x)

Schradin, C., Pillay, N., 2004. The Striped Mouse (*Rhabdomys pumilio*) from the succulent
 karoo, South Africa: a territorial group-living solitary forager with communal breeding and
 helpers at the nest. *Journal of Comparative Psychology*, 118(1):37-47. DOI: [10.1037/0735-7036.118.1.37](https://doi.org/10.1037/0735-7036.118.1.37)

Schradin C., Krackow S., Schubert M., Keller C., Schradin B., Pillay N., 2007. Regulation of
 activity in desert-living striped mice: the importance of basking. *Ethology* 113:606-614. DOI:
[10.1111/j.1439-0310.2007.01361.x](https://doi.org/10.1111/j.1439-0310.2007.01361.x)

Schwarzkopf, L., Shine, R., 1991. Thermal biology of reproduction in viviparous skinks,
Eulamprus tympanum: why do gravid females bask more? *Oecologia*, 88(4):562-569. DOI:
[10.1007/BF00344607](https://doi.org/10.1007/BF00344607)

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

499

500

501

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

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

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

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
Intercept	27.30	0.96	28.38	<0.001
Front	-1.99	0.19	-10.66	<0.001
Right	-1.06	0.19	-5.71	<0.001
Season (moist)	2.14	1.33	1.61	0.11
Minimum daily temperature	0.45	0.09	5.10	<0.001

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

Response variable = ΔT	Estimate	SE	t	P
Intercept	1.51	0.37	4.14	<0.001
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

522