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Microclimate of developing tubular leaves used as roost sites by bats

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Roosts are critical for the reproduction and survival of bats and many species spend a significant portion of their lives in them; thus, individuals should carefully select sites that reduce predation risk while providing ideal microclimatic conditions. Many studies have determined that bats select warmer and more humid roosts in temperate regions, but few studies have determined if roosts selected by tropical species also provide suitable conditions. In this study we compare temperature and humidity within and outside furled tubular leaves of plants in the order Zingiberales, which are used by several tropical species as roost-sites, to determine if these structures provide microclimatic advantages to bats. We found very small differences between the internal and external temperatures of tubular leaves, and the difference further decreased as leaves developed. However, we found large differences in humidity within the tubular leaf compared to external conditions, which were strongly dependent on a leaf's diameter and genus. The internal humidity was often 20% above the external, particularly when leaves were narrower, and tubular leaves in the genus *Heliconia* were more humid than those in the genus *Calathea*. Our findings suggest that, despite being fairly exposed structures, furled tubular leaves provide suitable microclimatic conditions for tropical species.

Key words: disc-winged bats, evaporative water loss, humidity, temperature, thermoregulation

Introduction

Bats use a diversity of roost sites that provide ideal conditions for resting, feeding, and for engaging in many social interactions that include rearing young, copulation, allogrooming, and information transfer. Roosts are also critical for bats' survival as they protect them from predators and harsh environmental conditions (Kunz, 1982; Kunz and Lumsden, 2003; Altringham, 2011). In fact, as bats leave their roosts, they become significantly more vulnerable to predation (Speakman, 1991; Fenton *et al*., 1994; Rodríguez-Durán *et al*., 2010), and thus many species spend a significant portion of their lives in them. By selecting adequate roosts, bats may additionally increase their fitness by spending less energy in thermoregulation and by reducing the rates of evaporative water loss (Webb *et al*., 1995; Speakman and Thomas, 2003). The latter advantages are known as major driving forces of roost-site selection, primarily in temperate regions (Kerth *et al*., 2001; Sedgeley, 2001).

In tropical regions, bats use some of the same roost types available in temperate regions, such as caves and tree cavities. These sites are ideal as they provide stable temperatures and high humidity compared to more exposed conditions (Rodríguez-Durán, 1995; Lundberg and McFarlane, 2015; Maziarz *et al*., 2017). However, in the tropics a large proportion of species also roosts in more exposed sites, such as under modified leaves or inside the developing tubular leaves of several plant species (Kunz and Lumsden, 2003). While generally it is believed that tropical environments do not impose sufficiently detrimental temperature and humidity costs compared with temperate regions, several studies show that tropical species enter torpor during cooler periods (Maloney *et al*., 2002; Czenze and Dunbar, 2017; Welman *et al*., 2017); the latter suggests that even relatively mild environmental conditions can impose significant energetic costs to bats, forcing them to suspend the maintenance of high body temperatures in favour of a less energetically demanding strategy, i.e. reducing metabolic rates with concomitant effects on body temperature (Ruf and Geiser, 2014). Therefore, studying the micro-climatic conditions in more exposed roosts that are readily used by bats in tropical regions is relevant for our understanding of roost-site selection.

There is one study that shows that modified leaves used by tent-making bats as roosts are capable of retaining body heat, and thus provide temperature conditions that facilitate energy savings (Rodríguez-Herrera *et al*., 2016). Another study by Schöner *et al*. (2013) compared internal and external temperature and humidity conditions of aerial pitchers in two species of carnivorous plants of the genus *Nepenthes*; these modified leaves are used as roost-sites by the Bornean woolly bat, *Kerivoula hardwickii* (Payne *et al*., 1985; Grafe *et al*., 2011). Their results indicate that the internal temperature within both species of pitcher plants was always lower than the external temperature; however, they also show that humidity was significantly higher and constant within the pitcher but only for *N. hemsleyana*, which is the species preferred for roosting by *K. hardwickii* (Schöner *et al*., 2013).

Another type of leaf structure, the developing tubular leaves of plants in the order Zingiberales (Fig. 1), are known to be used as roost-sites by several tropical bat species (Kunz and Lumsden, 2003; Pottie *et al*., 2007; McArthur, 2012; Gabadage *et al*., 2018), including one in the Neotropics (*Thyroptera tricolor*) and six in the Paleotropics (*K. hardwickii*, *Myotis bocagii*, *M. mystacinus*, *Murina murina*, *M. muricola*, *Myzopoda aurita*, *Neoromicina nanus*). While this resource is readily available, and studies show that humidity is high within the tubular structure (van der Merwe and Stirnemann, 2009), we still do not know if microclimatic conditions may influence bats' selection of specific plant species and leaf shapes. Studies show that *T. tricolor*, for example, prefer longer leaves in the genus *Heliconia* with a reduced diameter of opening (i.e., between six to eight cm at the apex) presumably as these protect bats from extreme temperatures (Vonhof and Fenton, 2004; Solano-Quesada and Sandoval, 2010; Chaverri and Kunz, 2011). Other species, such as *N. nanus*, roost in leaves with a wider opening (3–24 cm), most likely as the species used (mainly *Musa* spp.) produce longer leaves (Happold and Happold, 1990). However, no studies to date have looked at how a leaf's species and tubular shape may affect its internal temperature and humidity.

In this study we look at the differences in temperature and humidity within and outside furled tubular leaves to determine if these structures provide microclimatic advantages to bats that may use them as roost sites. Beneficial microclimatic conditions would include mean daily temperatures above 25°C but below ca. 33°C, as these are the lower and upper critical temperatures at which many bats, including tropical species, can maintain thermoneutrality (Speakman and Thomas, 2003; Soriano *et al*., 2005; Bonaccorso *et al*., 2006). In addition, if conditions within the leaf are beneficial to bats, we would also expect a constantly higher humidity (> 80%) within the tubular structure compared to the outside, as this would significantly reduce an individual's water loss through evaporation (Webb *et al*., 1995; Baudinette *et al*., 2000). We expect that the difference in temperature and humidity between the leaf's interior and exterior will decrease as the leaf develops (i.e., opens up), which would thereby partly explain why some species select narrow tubular structures.

FIG. 1. Developing tubular leaves in the families Marantaceae (*Calathea lutea*, left) and Heliconiaceae (*Heliconia imbricata*, right)

Materials and Methods

Study Site

This study was carried on between 12–14 January 2019 at Las Cruces Biological Station (Puntarenas, Costa Rica). The site is located at approximately 1,200 m.a.s.l. The temperature ranges between 21–26°C during the day and 15–21°C at night (Daily *et al*., 2001).

Selection of Tubular Sheets

We chose 15 developing tubular leaves from three species that are used as roost-sites by one bat species (i.e., *T. tricolor*): *Heliconia imbricata* (Heliconiaceae), *H. stricta* (Heliconiaceae) and *Calathea* sp. (Marantaceae); five leaves were selected per species. The leaves of *Heliconia* species were found in the Wilson Botanical Garden and *Calathea* sp. was found in the forest of Las Cruces Biological Station. Because *T. tricolor* prefers tubular leaves with a diameter of opening between six and eight cm (Vonhof and Fenton, 2004), we chose leaves with an initial diameter below these values but above four cm so that the centre of the leaf was accessible for measurements of temperature and humidity (next section). While bats were not prevented from entering the leaves, we checked that selected leaves were never occupied when we conducted leaf measurements (next section), since this would have affected our results significantly. As further proof that leaves were never used by bats, we did not observe accumulation of faeces within the tubular structures.

Measurement of Variables

Using iButtons (DS1923, Maxim Integrated, San Jose, CA, USA) we measured the temperature and humidity in each tubular leaf selected every 10 minutes. We placed two iButtons per leaf, one at the apex of the leaf over the adaxial surface and right above the opening of the tubular structure (Fig. 2), to monitor the external conditions; another iButton was placed inside the tubular structure, at the midpoint. We defined the midpoint of the sheet by measuring the total length of the sheet and placing the iButton at half the total length. In addition, in the same areas where the sensors were placed, we measured the diameter of the tubular leaf's opening (Fig. 2) every two hours using a digital vernier (± 0.03 mm). All leaves were measured to the highest possible opening point, because after a period of slow change in the leaf's diameter, they opened quickly and after that, they are not used by bats (Vonhof and Fenton, 2004).

Data Analysis

We generated linear mixed-effects models to test the relationship between the difference of external and internal temperature and humidity and diameter of a leaf's opening. We also estimated the leaf's opening rate as the final diameter minus the initial diameter divided by the time needed for the leaf to open up. With these data we used an ANOVA to evaluate if there are any differences in opening rates among the three species. Finally, we performed a linear model to test the relationship between the leaf's opening rate and its length. All analyses were performed using the R programming language version 3.5.1 (R Core Team, 2017) with the package 'nlme' (Pinheiro *et al*., 2019).

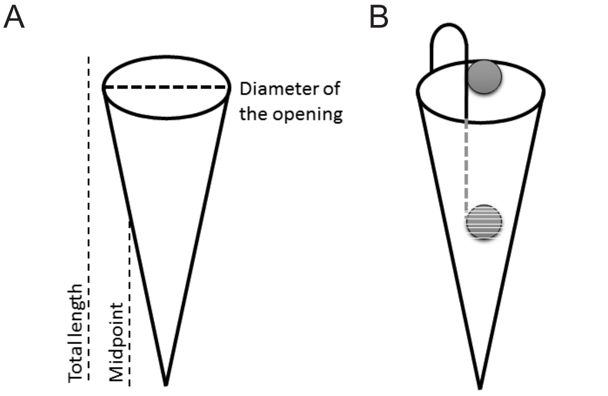

Fig. 2. Some measurements taken from each tubular leaf (A), and the position of the iButtons and their attachment from the leaf (B). The dashed line and dashed iButton indicate that they are positioned inside the tubular structure

Results

We found a negative relationship between the difference in the external and internal temperature and the opening diameter in *Calathea* sp., and a positive relationship for the two *Heliconia* species (diameter * genus: $\chi^2 = 3.84$, $P < 0.05$). For *Calathea*, the internal temperature was lower than the external when leaves were narrower, but the difference disappeared as the leaves unfurled. For *Heliconia* leaves, the internal temperature was just slightly greater than the external for narrower tubular leaves, and again, the difference disappeared as leaves unfurled (Fig. 3).

We found also that the leaf's diameter and its genus affect its internal humidity (diameter: $\chi^2 = 4.59$, $P < 0.05$; genus: $\chi^2 = 32.42$, $P < 0.001$; in all cases

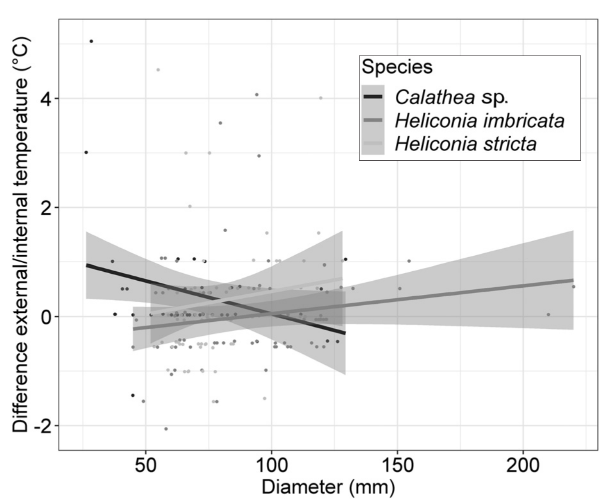

Fig. 3. Relationship between a leaf's opening rate and the difference of external and internal temperature of the tubular sheet in the three plant species

d.f. = 1 — Fig. 4). Narrower leaves have a significantly higher internal humidity and the difference disappears as leaves unfurl. For all leaf diameters, *Heliconia* leaves had significantly higher internal humidity than *Calathea*.

When looking at conditions throughout the day and night, we found that temperature and humidity in *Calathea* sp. were similar inside the tube until its opening (Figs. 5 and 6). For both *Heliconia* species we found that the leaf's internal temperature is similar to the external (Fig. 5). However, humidity remains relatively high and constant inside the *Heliconia* leaves, particularly during daytime and more significantly at noon when the external humidity drops to below ca. 50% while staying above ca. 75% inside the tubular structure (Fig. 6).

Finally, we found that *Calathea* sp. has a faster opening rate than the two species of *Heliconia*, but no differences in the rates of opening were found between the latter ($F_{2, 12} = 10.92$, $P < 0.001$ — Fig. 7). The opening rate of the leaves, in all species, did not depend on their length ($F_{1, 13} = 1.79$, $P = 0.20$).

Discussion

The results of our study suggest that developing tubular leaves may provide microclimatic advantages to tropical species that readily use them as roost sites. These tubular leaves may protect bats from extreme temperatures, as our results show slightly greater average internal temperatures when leaves have a narrower opening, but only for *Heliconia* leaves. However, as leaves develop the internal and external conditions start to resemble one another, and thus the benefits of thermal isolation may begin to weaken. The latter could explain why bats tend to prefer narrower tubular structures (Solano-Quesada and Sandoval, 2010), although it is possible that the advantages of using such leaves could be also, or primarily, explained by a reduction in conspicuousness to predators that move above the understory.

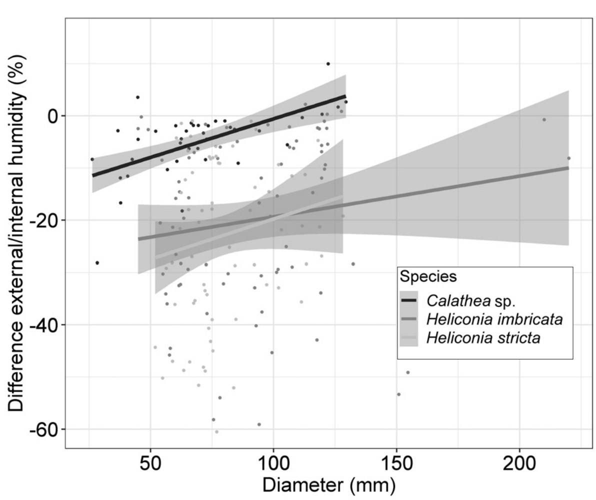

Fig. 4. Relationship between a leaf's opening rate and the difference of external and internal humidity of the tubular sheet in the three plant species

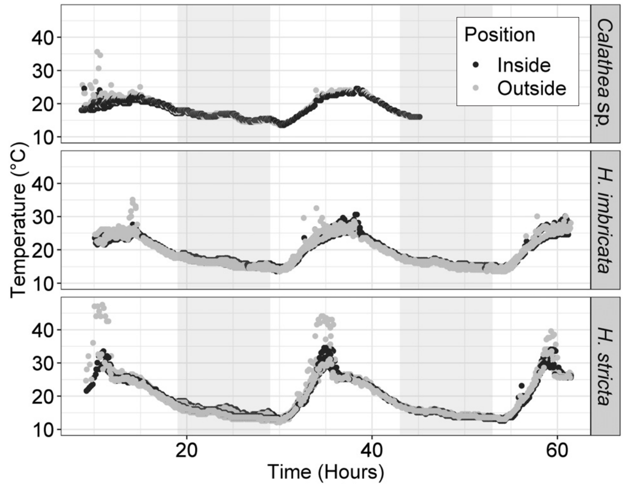

Fig. 5. Variation of temperature inside and outside the tubular leaf throughout the sampling hours. The grey area represents the hours of the night, spanning from 7 p.m. to 5 a.m.

Despite our observation of greater internal temperatures in narrower *Heliconia* structures, overall our results do not point to substantial thermal benefits of roosting in tubular leaves. In fact, the mean temperature within these structures was less than 1°C above external temperatures. However, as has been demonstrated in several other species that use other types of roosting resources (Willis and Brigham, 2007; Russo *et al*., 2017), bats that roost in developing tubular leaves may be able to reduce the energetic cost of thermoregulation not by selecting hotter roosts, but through huddling (i.e., social thermoregulation). Of the seven species that roost inside developing tubular leaves, at least five are known to form groups (*M. bocagii*, *M. muricola*, *M. aurita*, *N. nanus*, *T. tricolor* — Brosset, 1976; Wilson and Findley, 1977; Happold and Happold, 1990; Pottie *et al*., 2007; Ralisata *et al*., 2010); thus, these species may reduce the energy required to maintain elevated and stable body temperatures through social thermoregulation. Other solitary species that roost in tubular leaves may alternatively enter torpor to reduce energetic expenditure (Schöner *et al*., 2013); notwithstanding, torpor entails a reduction of important physiological functions, such as protein synthesis, brain function, and immune responses, and may render individuals susceptible to predation because of a significant decrease in sensory and motor capabilities (reviewed in Humphries *et al*., 2003).

While we were unable to find substantial thermal benefits of tubular leaves, we did find that these structures are able to maintain a high and stable internal humidity regardless of external conditions. In fact, humidity remained high and stable within the tubular structures throughout the day (Fig. 6), often well above 20% that of external conditions and even as the leaf unfurls (Fig. 4). This has also been observed for similar structures, specifically the tubular leaves of *Musa acuminata* used by *N. nanus*, and the pitchers preferred by *K. hardwickii* (van der Merwe and Stirnemann, 2009; Schöner *et al*., 2013). Bats are critically prone to evaporative water loss given their high lung surface area-to-body mass ratio (Studier, 1970), and thus selecting roosting structures that provide a constantly high humidity not only reduces water loss, but the energetic investment necessary to maintain homeostasis (Davies, 1970; Thomas and Cloutier, 1992). It is possible that a high humidity is caused by the leaf's transpiration (Happold and Happold, 1990), and is subsequently maintained by its long and narrow structure being protected from desiccation from the wind (Schöner *et al*., 2013). This, however, would not explain the differences we observed between *Calathea* and *Heliconia* plants. Therefore, the factors that increase humidity within certain tubular structures and not others remain to be determined.

In conclusion, our study shows that developing tubular leaves, which are used by many bat species as roost-sites, maintain a substantially more humid environment compared to external conditions. These findings add further evidence that furled leaves, and other homologous structures, provide adequate environmental conditions for bats despite being relatively exposed roosts. Notwithstanding, of the three species of plants selected for this study, only two (i.e., *Heliconia* spp.) maintained very high internal humidity, and this might explain why bats often prefer to roost in these species. *Heliconia* leaves also develop significantly more slowly (Fig. 7), and thus bats may additionally gain from remaining in a roost with more stable microclimatic conditions for longer periods of time. This study did not address how the shape of tubular structures may allow bats to avoid detection by predators, nor whether leaf choice may also be influenced by acoustic properties that facilitate communication among group members (Chaverri and Gillam, 2013); further studies on these and related topics would allow us to understand the roosting ecology of a fascinating group of bats.

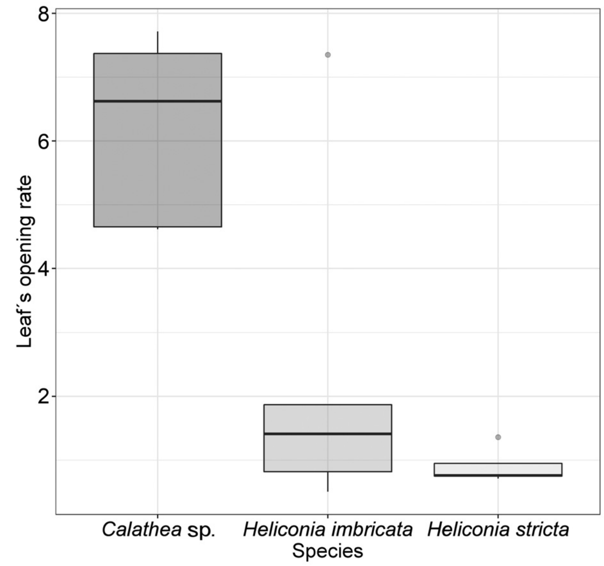

FIG. 7. Leaf's opening rate for the three study species, which corresponds to the change in diameter at the leaf's opening over time

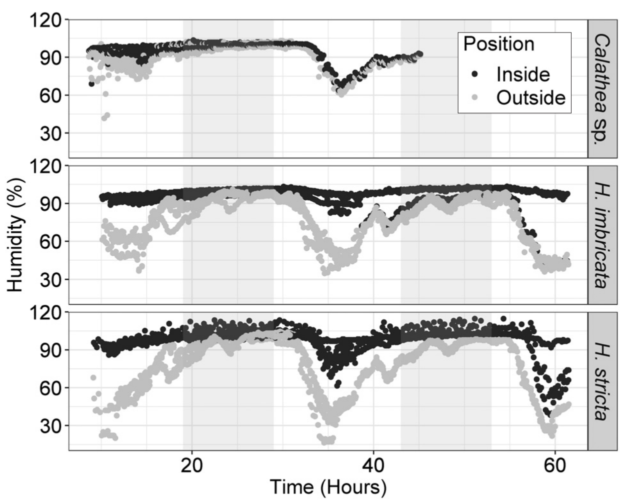

FIG. 6. Variation of humidity inside and outside of tubular sheet throughout the sampling hours. The grey area represents the hours of the night, spanning from 7 p.m. to 5 a.m.

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LITERATURE CITED

ALTRINGHAM, J. D. 2011. Bats: from evolution to conservation. Oxford University Press, Oxford, UK, xv + 324 pp.

Baudinette, R. V., S. K. Churchill, K. A. Christian, J. E. Nelson, and P. J. Hudson. 2000. Energy, water balance and the roost microenvironment in three Australian cave-dwelling bats (Microchiroptera). Journal of Comparative Physiology, 170B: 439–446.

Bonaccorso, F. J., T. Morton, A. Arends, D. Cantoni, and M. Genoud. 2006. Thermal ecology of moustached and ghost-faced bats (Mormoopidae) in Venezuela. Journal of Mammalogy, 73: 365–378.

Brosset, A. 1976. Social organization in the African bat, *Myotis boccagei*. Zeitschrift für Tierpsychologie, 42: 50–56.

Chaverri, G., and E. H. Gillam. 2013. Sound amplification by means of a horn-like roosting structure in Spix's disc-winged bat. Proceedings of the Royal Society, 280: 20132362.

Chaverri, G., and T. H. Kunz. 2011. Response of a specialist bat to the loss of a critical resource. PLoS ONE, 6: e28821.

Czenze, Z. J., and M. B. Dunbar. 2017. Hot bats go cold: heterothermy in neotropical bats. Canadian Journal of Zoology, 95: 909–912.

Daily, G. C., P. R. Ehrlich, and G. A. Sánchez-Azofeifa. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. Ecological Applications, 11: 1–13.

Davies, W. H. 1970. Hibernation: ecology end physiological ecology. Pp. 265–300, *in* Biology of bats. Volume 1 (W. A. Wimsatt, ed.). Academic Press, New York, xii + 418 pp.

Fenton, M. B., I. L. Rautenbach, S. E. Smith, C. M. Swanepoel, J. Grosell, and J. Van Jaarsveld. 1994. Raptors and bats: threats and opportunities. Animal Behaviour, 48: 9–18.

Gabadage, D., S. Karunarathna, T. Surasinghe, G. Edirisinghe, K. Perera, and M. Botejue. 2018. A new record of *Kerivoula hardwickii* (Horsefield, 1824) (Mammalia: Chiroptera: Vespertilionidae) after 23 years from a lowland rainforests of Sri Lanka. Journal of Threatened Taxa, 10: 12344–12349.

Grafe, T. U., C. R. Schöner, G. Kerth, A. Junaidi, and M. G. Schöner. 2011. A novel resource-service mutualism between bats and pitcher plants. Biology Letters, 7: 436–439.

Happold, D. C. D., and M. Happold. 1990. The domiciles, reproduction, social organisation and sex ratios of the banana bat *Pipistrellus nanus* (Chiroptera, Vespertilionidae) in Malawi, Central Africa. Zeitschrift für Saugetierkunde, 55: 145–160.

Humphries, M. M., D. W. Thomas, and D. L. Kramer. 2003. The role of energy availability in mammalian hibernation: a cost-benefit approach. Physiological and Biochemical Zoology, 76: 165–179.

Kerth, G., K. Weissmann, and B. Konig. 2001. Day roost selection in female Bechstein's bats (*Myotis bechsteinii*): a field experiment to determine the influence of roost temperature. Oecologia, 126: 1–9.

Kunz, T. H. 1982. Roosting ecology of bats. Pp. 1–50, *in* Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York, 425 pp.

Kunz, T. H., and L. F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pp. 3–87, *in* Bat ecology (T. H. Kunz and M. B. Fenton, eds.). University Of Chicago Press, Chicago, 779 pp.

Lundberg, J., and D. A. Mcfarlane. 2015. Microclimate and niche constructionism in tropical bat caves: a case study from Mount Elgon, Kenya. The Geological Society of America Special Paper, 516: 211–229.

Maloney, S. K., G. N. Bronner, and R. Buffenstein. 2002. Thermoregulation in the Angolan free-tailed bat *Mops condylurus*: a small mammal that uses hot roosts. Physiological and Biochemical Zoology, 72: 385–396.

Maziarz, M., R. K. Broughton, and T. Wesołowski. 2017. Microclimate in tree cavities and nest-boxes: implications for hole-nesting birds. Forest Ecology and Management, 389: 306–313.

McArthur, E. 2012. New records of bats from Gunung Mulu World Heritage Area, Sarawak, Malaysian Borneo. Malayan Nature Journal, 64: 141–151.

Payne, J., C. Francis, and K. Phillipps. 1985. A field guide to the mammals of Borneo. Sabah Society, World Wildlife Fund Malaysia, Kota Kinabalu, Malaysia, 332 pp.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2019. nlme: linear and nonlinear mixed effects models. R package version 3.1-141. Available at https://CRAN.R-project.org/package=nlme.

Pottie, S. A., D. J. W. Lane, T. Kingston, and B. P. Y.-H. Lee. 2007. The microchiropteran bat fauna of Singapore. Acta Chiropterologica, 7: 237–247.

Ralisata, M., F. R. Andriamboavonjy, D. Rakotondravony, O. R. Ravoahangimalala, F. H. Randrianandrianina, and P. A. Racey. 2010. Monastic *Myzopoda*: the foraging and roosting ecology of a sexually segregated Malagasy endemic bat. Journal of Zoology (London), 282: 130–139.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at www.r-project.org.

Rodríguez-Durán, A. 1995. Metabolic rates and thermal conductance in four species of Neotropical bats roosting in hot caves. Comparative Biochemistry and Physiology, 110A: 347–355.

Rodríguez-Durán, A., J. Pérez, M. A. Montalbán, and J. M. Sandoval. 2010. Predation by free-roaming cats on an insular population of bats. Acta Chiropterologica, 12: 359–362.

Rodríguez-Herrera, B., L. Víquez-R, E. Cordero-Schmidt, J. M. Sandoval, and A. Rodríguez-Durán. 2016. Energetics of tent roosting in bats: the case of *Ectophylla alba* and *Uroderma bilobatum* (Chiroptera: Phyllostomidae). Journal of Mammalogy, 97: 246–252.

Ruf, T., and F. Geiser. 2014. Daily torpor and hibernation in birds and mammals. Biological Reviews, 90: 891–926.

Russo, D., L. Cistrone, I. Budinski, G. Console, M. Della Corte, C. Milighetti, I. di Salvo, V. Nardone, R. M. Brigham, and L. Ancillotto. 2017. Sociality influences thermoregulation and roost switching in a forest bat using ephemeral roosts. Ecology and Evolution, 7: 5310–5321.

Schöner, C. R., M. G. Schöner, G. Kerth, and T. U. Grafe. 2013. Supply determines demand: influence of partner quality and quantity on the interactions between bats and pitcher plants. Oecologia, 173: 191–202.

Sedgeley, J. A. 2001. Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. Journal of Applied Ecology, 38: 425–438.

Solano-Quesada, M. G., and L. Sandoval. 2010. Requirements of the roost used by spix's disk-winged bat (*Thyroptera tricolor*). Chiroptera Neotropical, 16: 786–788.

Soriano, P. J., A. Ruiz, and A. Arends. 2005. Physiological responses to ambient temperature manipulation by three species of bats from Andean could forests. Journal of Mammalogy, 83: 445–457.

SPEAKMAN, J. R. 1991. Why do insectivorous bats in Britain not fly in daylight more frequently? Functional Ecology, 5: 518–524.

SPEAKMAN, J. R., and D. W. THOMAS. 2003. Physiological ecology and energetics of bats. Pp. 430–490, *in* Bat ecology (T. H. KUNZ and M. B. FENTON, eds.). Chicago University Press, Chicago, xix + 779 pp.

STUDIER, E. H. 1970. Evaporative water loss in bats. Comparative Biochemistry and Physiology, 35: 935–943.

THOMAS, D. W., and D. CLOUTIER. 1992. Evaporative water loss by hibernating little brown bats, *Myotis lucifugus*. Physiological Zoology, 65: 443–456.

VAN DER MERWE, M., and R. L. STIRNEMANN. 2009. Group composition and social events of the banana bat, *Neoromicia nanus*, in Mpumalanga, South Africa. South African Journal of Wildlife Research, 39: 48–56.

VONHOF, M. J., and M. B. FENTON. 2004. Roost availability and population size of *Thyroptera tricolor*, a leaf-roosting bat, in north-eastern Costa Rica. Journal of Tropical Ecology, 20: 291–305.

WEBB, P. I., J. R. SPEAKMAN, and P. A. RACEY. 1995. Evaporative water-loss in 2 sympatric species of vespertilionid bat, *Plecotus auritus* and *Myotis daubentoni* — relation to foraging mode and implications for roost site selection. Journal of Zoology (London), 235: 269–278.

WELMAN, S., A. TUEN, and B. LOVEGROVE. 2017. Using thermoregulatory profiles to assess climate change vulnerability in an arboreal tropical bat: heterothermy may be a pre-adaptive advantage. Climate Research, 74: 161–170.

WILLIS, C. K. R., and R. M. BRIGHAM. 2007. Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. Behavioral Ecology and Sociobiology, 62: 97–108.

WILSON, D. E., and J. S. FINDLEY. 1977. Thyroptera tricolor. Mammalian Species, 71: 1–3.

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