Seasonal movements of insectivorous bat species in southwestern Madagascar

Stephanie Reher[1], Hajatiana Rabarison[2], Marie Schoroth[1] & Kathrin Dausmann[1]
[1] Functional Ecology, Biocenter Grindel, University of Hamburg, Martin-Luther-King-Platz 3, Hamburg 20146, Germany
E-mail: stephanie.reher@uni-hamburg.de, marieschoroth@googlemail.com, kathrin.dausmann@uni-hamburg.de
[2] Mention Zoologie et Biodiversité Animale, Faculté des Sciences, Université d'Antananarivo, BP 906, Antananarivo 101, Madagascar
E-mail: tianarabari26@gmail.com

Abstract

Seasonal environmental changes can be challenging for animals because they are usually characterized by fluctuations in temperature, considerable decreases in food resources and, in tropical and subtropical regions, water availability. One response to less favorable conditions is migration, which is energetically costly and potentially dangerous. This aspect raises the question of whether there is a critical tipping point where environmental characteristics render residency unfavorable. There is a paucity of information on Malagasy bat habitat requirements and few details are available on migratory species. Here, we aimed to elucidate drivers of seasonal differences in bat species occurrence in the southwest of Madagascar and determine which species are potentially migratory. This region encompasses dry spiny forest with pronounced seasonal fluctuations in ambient temperature and rainfall, conditions that can prompt habitat shifting, among other strategies. During trapping phases in the wet summer and dry winter, we recorded the temporal and spatial occurrence of seven different insectivorous bat species in Tsimanampetsotse National Park. While *Macronycteris commersoni, Triaenops menamena*, *Paratriaenops furculus*, and *Miniopterus mahafaliensis* were present year-round, *M. griffithsi*, *Mormopterus jugularis*, and *Mops leucostigma* were only trapped in the rainy season, suggesting site relocation. Furthermore, this study provides the first record of *Miniopterus griffithsi* and *Mops leucostigma* in Tsimanampetsotse National Park. Although we have no information on where the migrating species reside during the dry season, this study provides data for refining known species distributions and augments information on seasonal variation in the ecological requirements of bats.

Keywords: habitat shift, seasonality, bats, roosting sites, Madagascar

Résumé détaillé

Les changements de conditions environnementales peuvent rendre un habitat difficile à vivre pour les animaux. Les dégradations de l'habitat se produisent par des variations du climat naturel et de l'interaction humaine qui se traduisent par des changements annuel ou saisonnière de l'environnement. Ces variations saisonnières représentent une contrainte environnementale importante pour de nombreux vertébrés et s'accompagnent en général d'un changement de la disponibilité des ressources alimentaires et de la disponibilité de l'eau dans les régions (sub)tropicales. Pour cela, les animaux ont développé alors des adaptations comportementales et physiologiques pour améliorer leur survie. La migration est une approche comportementale adaptative pour faire face aux changements des conditions ambiantes. Une réponse assez complexe qui nécessite une aptitude physique et même physiologique pour bénéficier la sélection de la qualité d'une destination appropriée. Ainsi, cette étude vise à déterminer quelles espèces sont potentiellement migratrices dans le Sud-ouest de Madagascar et de savoir quelles espèces ont préféré quel microhabitat sous différents changements saisonniers favorables à la migration ainsi que la survie de ces espèces migratrices.

Cette étude a été menée dans le Parc National de Tsimanampetsotse à Madagascar. Ce parc, localisé dans la région du Sud-ouest de la Grande île englobe une forêt épineuse sèche comprenant des variations des conditions ambiantes prononcées, favorisant un changement flexible de l'habitat. Entre autres, les informations sur la préférence en habitat des chauves-souris sont encore incomplètes à Madagascar. Il en est de même pour les informations sur les espèces potentiellement migratrices. Lors de

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cette étude, les chauves-souris ont été capturées dans deux sites différents du parc : la grotte d'Andranolovy et la grotte de Vintany. Les deux sites possèdent des caractéristiques de microhabitats très différentes. La température et l'humidité restent stables et élevées toutes l'année dans la grotte d'Andranolovy mais par contre fluctuent suivant les saisons dans la grotte de Vintany. La saison sèche et la saison de pluies ont été choisies pour deux sessions de capture d'individus pour chaque site en mai/juin 2016 et février 2017. Une session de capture a consisté à cinq nuits de capture dans un site. Le piège harpe a été utilisé pour capturer les chauves-souris. Ce matériel a été placé à l'entrée pour la grotte d'Andranolovy, tandis qu'il a été placé sur le couloir principal menant à la grotte pour la grotte de Vintany. Au total, 572 individus de *Macronycteris commersoni*, 246 individus de *Triaenops menamena*, 90 individus de *Paratriaenops furculus*, 87 individus de *Miniopterus mahafaliensis*, deux individus de *M. griffithsi*, trois individus de *Mops leucostigma* et trois individus de *Mormopterus jugularis* ont été capturés. Au maximum, 20 individus par espèces ont été choisis pour les mensurations de l'avant-bras et la prise des poids. Ces individus ont été marqués sur leur aile membranaire d'un tatouage à trois chiffres avec une encre non toxique, puis relâchés dans leur milieu d'origine.

Dans la grotte d'Andranolovy, *T. menamena*, *P. furculus* et *Miniopterus mahafaliensis* ont été capturés pendant les deux saisons tandis que *Macronycteris commersoni* n'a été capturé que pendant la saison des pluies avec un nombre important de juvéniles. Dans la grotte de Vintany, *T. menamena* et *Miniopterus mahafaliensis* ont été capturés pendant les deux saisons, tandis que *Macronycteris commersoni*, *Miniopterus griffithsi*, *Mops leucostigma* et *Mormopterus jugularis* ont été capturés pendant la saison des pluies. Cette étude a permis de recenser pour la première fois *Miniopterus griffithsi* et *Mops leucostigma* dans le Parc National de Tsimanampetsotse. *Macronycteris commersoni* accumulait des réserves de graisses nécessaires pour le déplacement de longues distances. Cette espèce a reposé dans la grotte d'Andranolovy et a entré probablement en période de torpeur pour faire face à la saison sèche, ce qui n'a pas permis sa capture pendant la saison sèche. Certaines espèces de chauves-souris reposent régulièrement dans les deux grottes pendant les deux saisons : c'est le cas de *T. menamena* et *Miniopterus mahafaliensis*. Ces deux espèces élargissent leur site de repos à un grand nombre de grottes pendant la saison des pluies mais préfèrent la grotte d'Andranolovy pendant la saison sèche, probablement en raison de conditions microclimatiques chaudes et humides de la grotte. Bien que nous ne disposions d'aucune information sur la provenance de ces espèces, cette étude fournit des données importantes pour étendre et affiner la distribution géographique des espèces, y compris les variations saisonnières des besoins écologiques des chauves-souris.

Mots clés : déplacement d'habitat, saisonnalité, chauves-souris, perchoirs, Madagascar

Introduction

Changes in environmental conditions can be challenging for animals because they have the potential to render a habitat unsuitable or more difficult to occupy (Heldmaier *et al*., 2013; Hill *et al*., 2016). Habitat modification is caused by natural weather variation and human interference, resulting in environments that can change on an annual, seasonal, daily or completely unpredictable basis. The effects of season can be particularly severe as they are relatively long (several months) and accompanied by changes in food availability and, particularly in tropical and subtropical regions, water availability (Janzen & Schoener, 1968; Pinheiro *et al*., 2002). However, unlike other environmental changes such as daily fluctuations and weather extremes, seasonality is predictable and animals have evolved different responses spanning morphological, physiological, and behavioral adaptations.

An adaptive behavioral approach for coping with spatio-temporal shifts in ambient conditions is migration. This is a complex response and requires certain cognitive, physical, and physiological abilities, as well as knowledge (Avgar *et al*., 2014) of the existence, location, and quality of a suitable destination. Awareness of stopover points for fueling the energetic requirements of long-distance movement is also essential (Popa-Lisseanu & Voigt, 2009). Additionally, migration needs preparation such as fat storage and muscle gain (Fleming & Eby, 2003), and is costly in terms of time, invested energy, and management of risks, which include increased mortality during long-term movement owing to predators, sudden food shortages or unpredictable inclement weather (Fleming & Eby, 2003; Newton, 2007; Avgar *et al*., 2014). In markedly seasonal environments, the benefits likely exceed these costs and migratory species profit from travelling to more favorable microclimatic conditions, food that is higher in quantity and/or quality, and, putatively, reduced exposure to parasites and disease (Fryxell & Sinclair, 1988; Fleming & Eby, 2003; Avgar *et al*., 2014).

For bats, migration is particularly advantageous because they are small-bodied and lose considerable body heat from their flight membranes when temperatures are low (McNab, 1969), rendering them vulnerable to energetic imbalance in seasonally fluctuating environments. Additionally, they usually live in large aggregations, which can rapidly deplete local resources (Avgar *et al*., 2014), making the relocation to preferred habitat highly beneficial. The main advantage of migration for temperate bats is primarily related to the utilization of roosts with thermal characteristics that benefit metabolism, whereas fluctuations in resource availability and rainfall are the main drivers of bat migration in the tropics (Moreno-Valdez *et al*., 2000; Fleming & Eby, 2003; Rodrigues & Palmeirim, 2008).

Madagascar's highly seasonal dry spiny forest is a challenging environment incorporating the driest and least climatically predictable area of the island (Génin, 2008; Kobbe *et al*., 2014). Such variable environments often encourage flexible habitat shifting or nomadism (Mueller & Fagan, 2008), especially for insectivorous bats, whose prey availability decreases with nighttime temperature in the austral winter (Janzen & Schoener, 1968; Pinheiro *et al*., 2002). However, information on the habitat preferences of Malagasy bats and their general distribution patterns are still incomplete (Goodman & Ramasindrazana, 2013). Because at least one bat species occurring in the spiny forest of southwestern Madagascar is reported to "disappear" during the lean, dry season (Goodman, 2006; Rakotoarivelo *et al*., 2007), we aimed to determine whether there are seasonal differences in insectivorous bat species occurrence and which species are migratory.

Methods

Study site

This study was conducted in Tsimanampetsotse National Park in the extreme southwest. The park is located in the driest and most climatically unpredictable area of the island and receives between 300 and 600 mm of rain each year (Rasoloariniaina *et al*., 2015). Precipitation, ambient temperature, and food resource availability are influenced by season. Rainfall is mainly restricted to the hot rainy season between November and March (austral summer), but the exact timing and amount are highly unpredictable. The dry season, from May to September (austral winter), receives almost no rainfall and is characterized by colder nights (minimum of 6°C in the dry season vs. 15°C in the rainy season; Kobbe *et al*., 2014) and limited resource availability, i.e. plant material and insects. Ambient temperature varies over the course of the year between 6°C and 45°C (Kobbe *et al*., 2014). The region is located on a calcareous plateau covered in dense spiny forest, with numerous different microhabitat types including complex underground cave and stream systems.

We trapped bats at two different sites in the park; Andranolovy Cave (24.04585° S / 043.75396° E) and Vintany Cave (24.04383° S / 043.75519° E). The caves are only 270 m apart but differ in environmental characteristics. Andranolovy Cave is a large, buffered underground system consisting of several connected chambers and a water body covering approximately 25% of the cave floor. Temperature and relative humidity (RH) are stable and high year-round with daily fluctuations less than 1°C and 1% RH, respectively, and were never lower than 29.4°C and 94.8% RH, respectively (Figure 1a, b; recorded for 101 consecutive days per season using Hygrochron iButtons placed at 1.5 m height, Maxim integrated, San Jose, USA). Vintany Cave is smaller, adjoins a former sinkhole and is influenced more by ambient conditions and weather extremes, with daily fluctuations of 7.3 ± 1.5°C (daily mean min – daily mean max: 19.9 – 27.2°C) and 24.3 ± 5.9% RH (55.2 – 79.5%) in the dry season, and 4.7 ± 1.0°C (25.8 – 30.5°C) and 20.3 ± 5.1% RH (63.9 – 84.2%) in the rainy season (Figure 1c, d).

Trapping and handling

Each trapping period consisted of five consecutive nights per site in May/June 2016 (dry season) and February 2017 (rainy season). A harp trap was placed at the entrance of Andranolovy Cave and the main approaching corridor at Vintany Cave. To capture bats emerging from their roosts for their first evening foraging flight, the trap was opened approximately half an hour before sunset at 18:00 (dry season) and 19:00 (rainy season) and closed at 21:30, and checked every 15-20 min. At each site, a maximum of 20 adult individuals of each species were randomly chosen for the measurements of body mass and forearm length, and for sex determination. Individuals were aged based on wing bone and joint ossification (Brunet-Rossinni & Wilkinson, 2009). To avoid pseudoreplication, these bats were individually marked with a 3-digit wing membrane

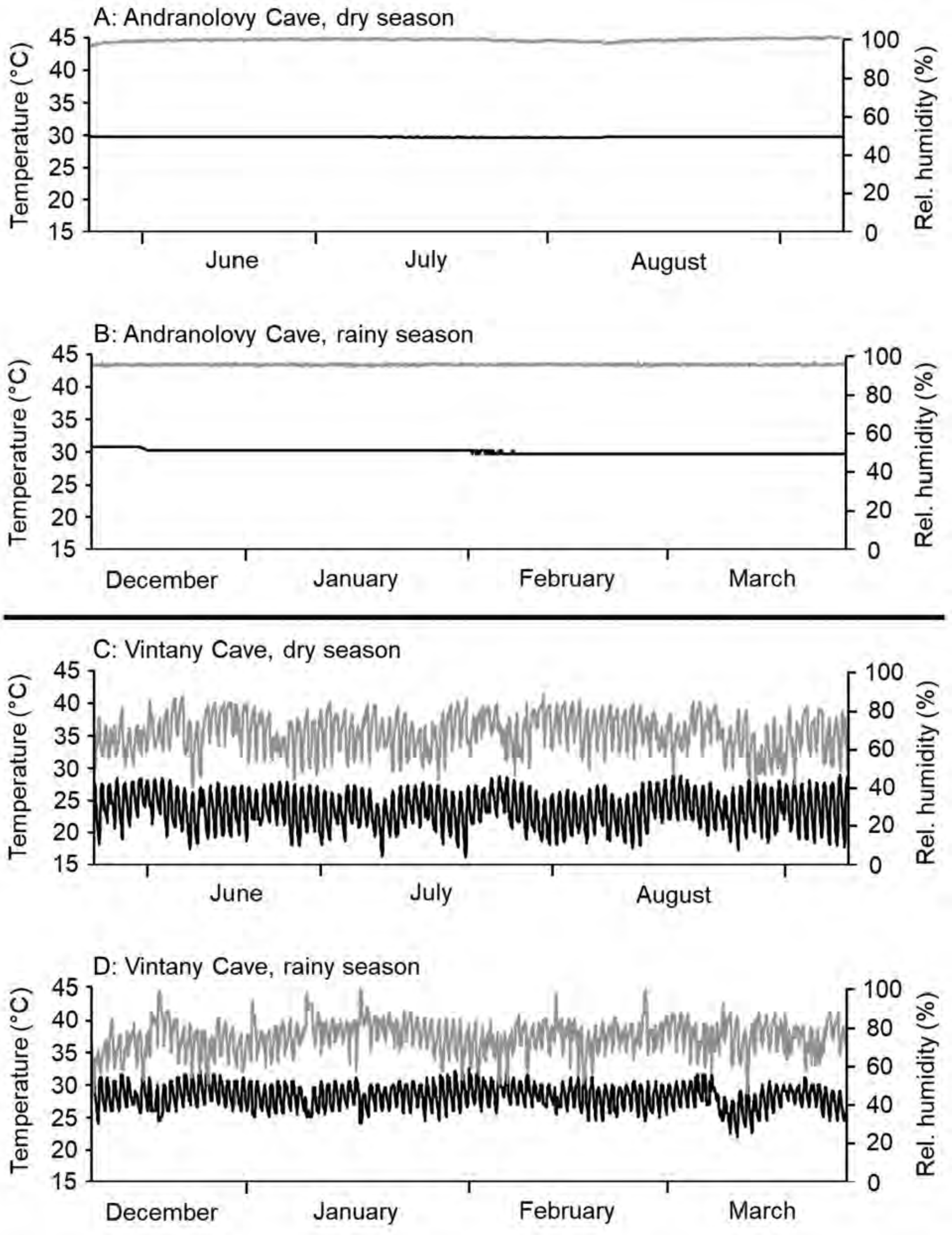

Figure 1. Ambient temperature (black line) and relative humidity (grey line) in two different caves, Andranolovy (A, B) and Vintany (C, D), in Tsimanampetsotse National Park in the dry (A, C) and rainy (B, D) seasons. Data were recorded once per hour for 101 consecutive days.

tattoo using non-toxic ink (Hauptner-Herberholz, Solingen, Germany) after local anesthesia (EMLA, AstraZeneca, Wedel, Germany).

Analysis

We only compared forearm length and body mass of adult *Triaenops menamena* and *Miniopterus mahafaliensis* between seasons and caves, owing to the small sample sizes of the other species (Table 1). After testing for normality using the Shapiro-Wilk test, data were further analyzed using unpaired samples t-tests or Mann-Whitney-U tests. IBM SPSS v24 was used for all analyses.

Results

Species composition differed temporally and spatially between the two cave systems (Table 1). At Andranolovy Cave we captured four different bat species. The most frequent species was *Macronycteris commersoni* with 566 individuals; however, it was only trapped in the rainy season, and 92% of individuals were juveniles. *Paratriaenops furculus* was also trapped more often in the rainy season than the dry season. *Triaenops menamena* and *Miniopterus mahafaliensis* were trapped in both seasons, each with about twice as many individuals in the dry season as the rainy season. *Triaenops menamena* trapped in the dry season had smaller forearm lengths than those in the rainy season (Z = -3.078, P = 0.002, N = 21; Table 1) and *M. mahafaliensis* were heavier in the rainy season (Z = -2.188, P = 0.029, N = 20; Table 1). *Paratriaenops furculus* was only trapped at Andranolovy Cave.

At Vintany Cave, six species were captured. Similar to at Andranolovy Cave, *T. menamena* and *M. mahafaliensis* were trapped in both seasons while *Macronycteris commersoni*, *Miniopterus griffithsi*, *Mops leucostigma,* and *Mormopterus jugularis* were trapped exclusively in the rainy season and with few individuals (Table 1; N = 2-6). In contrast to the trapping success at Andranolovy Cave, the number of trapped *T. menamena* and *Miniopterus mahafaliensis* was higher in the rainy season than in the dry season and we did not find any difference in forearm length (*T. menamena*: t_{18} = -0.399, P = 0.695, N = 20; *M. mahafaliensis*: Z = -1.845, P = 0.065, N = 15) or body mass (*T. menamena*: t_{18} = -0.257, P = 0.800, N = 20; *M. mahafaliensis*: t_{13} = -0.511, P = 0.618, N = 15) between seasons. *Miniopterus griffithsi*, *Mops leucostigma*, and *Mormopterus jugularis* were only trapped at Vintany Cave.

A direct comparison of the two roosting sites revealed that only individuals from *T. menamena* were smaller at Vintany Cave than Andranolovy Cave and only in the rainy season (Z = -2.360, P = 0.018, N = 21; Table 1).

Table 1. Total number (#) as well as body mass (BM, g) and forearm length (FA, mm) of a subsample of individuals (N) of trapped bat species at two different caves, Andranolovy and Vintany, in Tsimanampetsotse National Park in the dry (DS) and rainy season (RS). Each trapping period consisted of five consecutive nights per site. Only adults were included in BM and FL measurements. For statistical details, see text. * including 92% juveniles, $^{\Delta}$ including 51% juveniles, † this species also uses a second entrance.

		Andranolovy				Vintany			
	Season	**#**	**BM [g]**	**FA [mm]**	**N**	**#**	**BM [g]**	**FA [mm]**	**N**
Hipposideridae									
Macronycteris commersoni	DS	0				0			
	RS	566*	47.5 ± 11.7	84.4 ± 4.7	20	6	41.3 ± 3.8	81.5 ± 2.3	3
Rhinonycteridae									
Triaenops menamena	DS	121	8.9 ± 1.1	48.1 ± 1.1	10	34	9.3 ± 0.9	48.8 ± 1.5	10
	RS	51	9.5 ± 1.3	50.5 ± 2.8	11	40	9.1 ± 1.5	48.6 ± 1.8	10
Paratriaenops furculus	DS	5	6.3 ± 0.6	44.7 ± 1.4	4	0			
	RS	35$^{\Delta}$	6.8 ± 1.1	45.2 ± 1.6	12	0			
Miniopteridae									
Miniopterus mahafaliensis	DS	28†	4.7 ± 0.5	37.5 ± 0.8	10	17	4.7 ± 0.4	38.1 ± 0.8	10
	RS	13†	5.0 ± 0.6	36.8 ± 1.3	10	29	4.9 ± 1.0	37.4 ± 0.6	5
Miniopterus griffithsi	DS	0				0			
	RS	0				2	25.3 ± 1.1	46.8 ± 0.7	2
Molossidae									
Mops leucostigma	DS	0				0			
	RS	0				3	22.5 ± 0.7	43.6 ± 0.4	3
Mormopterus jugularis	DS	0				0			
	RS	0				3	12.7 ± 1.5	36.4 ± 0.7	3

Discussion

We found seasonal differences in bat species occurrence in Tsimanampetsotse National Park that imply spatial relocation or torpor as strategies to cope with the extreme seasonal environment. Additionally, this study provides the first record of *Miniopterus griffithsi* and *Mops leucostigma* in this protected area.

Miniopterus griffithsi was only described about a decade ago (Goodman *et al*., 2009) and little information on its distribution and ecology are known (Goodman & Ramasindrazana, 2013). Our observation at Vintany Cave is the most northern record for this species, but this is in a location similar to those of previous studies in the extreme southeast near Ranopiso, and the southwest near Itampolo (Goodman *et al*., 2009; ~70.3 km from our record). The vegetation at these previous trapping sites ranged from spiny forest and coastal bushland to disturbed gallery forest and all locations had caves or rock shelters (Goodman *et al*., 2009). Interestingly, both trapped individuals were about twice as heavy (25.3 ± 1.1 g, N = 2) as previously captured *M. griffithsi* (13.6 ± 1.2 g, N = 6; Goodman *et al*., 2009), which were trapped at the end of the rainy season (late February) and in May. The two individuals trapped in May had accumulated considerable amounts of subcutaneous fat (body mass = 15.5 and 16.5 g; Goodman *et al*., 2009) but still weighed much less than the bats we trapped. Thus, the new listing in Tsimanampetsotse National Park may either provide information on the species' morphological variation (i.e. expanding the range in body mass) and distribution.

Mops leucostigma is widely distributed across different habitats on Madagascar but had not been reported for Tsimanampetsotse National Park (Ramasindrazana & Goodman, 2012; Ramasindrazana *et al.*, 2012). Current distribution estimations include southwestern spiny bush, western dry deciduous forest, and eastern humid forest (Ratrimomanarivo *et al*., 2008). Furthermore, this is the first record of this species roosting in a cave (Goodman, 2011). *Mormopterus jugularis* is also known to have a broad distribution throughout varying bioclimatic zones, ranging from the driest to the most humid regions in Madagascar and up to 1750 m in altitude (Goodman *et al*., 2005; Ratrimomanarivo *et al*., 2009). Along with *Mops leucostigma*, *Mormopterus jugularis* has been found to share synanthropic day roosts (Goodman & Cardiff, 2004; Ratrimomanarivo *et al*., 2008). Both species are hunted for food in Madagascar (Goodman, 2006; Monadjem *et al*., 2017). Although no reliable human consumption rates are available for either species, studies on *Macronycteris commersoni* revealed that exploitation of these bats is unsustainable (Goodman, 2006). This makes information on exact distribution ranges and suitable habitat types of both species crucially for assessing the availability of possible refugia.

Interestingly, during the dry season *M. commersoni* was never trapped, and *P. furculus* rarely trapped, even though both species were found in large numbers roosting in Andranolovy Cave during both seasons. Individuals observed in the dry season were generally less responsive than in the rainy season, suggesting that these species entered torpor to cope with the lean dry season (Reher *et al*., 2018). *Triaenops menamena* and *Miniopterus mahafaliensis* still foraged regularly during this season. Both species and *P. furculus* have a diet primary consisting of Lepidoptera, which, especially in the dry season, is supplemented by Coleoptera and, in the case of *M. mahafaliensis*, Hymenoptera (Ramasindrazana *et al.*, 2012). *Macronycteris commersoni* however prefers Coleoptera year-round (Ramasindrazana *et al.*, 2012). Thus, the habitat offers sufficient insect abundance for *T. menamena* and *Miniopterus mahafaliensis* to allow activity in both seasons, while *Macronycteris commersoni* and *P. furculus* reduced activity to cope with the leaner dry season. Nevertheless, all four species are residents in Tsimanampetsotse National Park, indicating that the region offers them suitable environmental conditions year-round. *Triaenops menamena* and *M. mahafaliensis* were the only two species that regularly roosted in both caves during the two seasons. Interestingly, we trapped more individuals from each of these two species at Andranolovy Cave in the dry season than in the rainy season, but the opposite at Vintany Cave. Consequently, both species appeared to have broadened their roosting preferences to a wider range of caves in the rainy season, but to prefer Andranolovy Cave for the harsh dry season, probably owing to stable humid and warm microclimatic conditions (Figure 1). Because seasonal fluctuations in ambient conditions in tropical areas are often small, negating the need for long distance movement, a local shift in microhabitat preference may be enough to ensure survival (Popa-Lisseanu & Voigt, 2009). Therefore, a slight relocation to a more constant roosting environment probably allows *T. menamena* and *M. mahafaliensis* to remain in the park. Indeed, our data indicate that more bats use Andranolovy Cave, with stable conditions, than the fluctuating microclimate of Vintany Cave. These results are in particular interesting as bats are captured by villagers in Andranolovy Cave. We found several traps from villagers in each chamber of the cave but no signs of hunting in Vintany Cave. Thus, our results suggest that the stable microclimatic conditions in Andranolovy Cave were more favorable regardless of hunting pressure, probably because the high temperature makes energetically costly active thermoregulation unnecessary (Reher *et al*., 2018).

The complete absence of *M. griffithsi*, *Mormopterus jugularis*, and *Mops leucostigma* during the dry season suggests a seasonal habitat shift in response to the highly fluctuating environment of Vintany Cave. All three species were trapped in small numbers and only late in the rainy season (late February), indicating that they may have been passing through Tsimanampetsotse National Park. Bats inhabiting tropical and subtropical regions that undergo seasonal pressures and bottlenecks in resource availability often migrate (Fleming & Eby, 2003), although they tend to move shorter distances than temperate migrants (Popa-Lisseanu & Voigt, 2009). This habitat shifting, or regional migration, is more likely to be found in forest dwelling than cave roosting bats, and more likely in nectar and fruit feeding bats than in insectivorous species (Bonaccorso, 1979; Fleming & Eby, 2003; Popa-Lisseanu & Voigt, 2009). However, in regions like Madagascar's southwest, where seasonality strongly influences ambient temperature and precipitation, the advantage of shifting habitat also increases for insectivorous bats, because insect activity and availability decreases sharply during the dry season (Janzen & Schoener, 1968; Pinheiro *et al*., 2002). This likely also affected the three potentially migratory species in our study (*Miniopterus griffithsi*, *Mormopterus jugularis*, and *Mops leucostigma*), which presumably tracked their food resources rather than roosting opportunities.

We acknowledge the limitations of our presence/absence data. Nevertheless, the information presented herein improves knowledge of habitat preferences for certain bats species under varying seasonal and environmental pressures, and for better understanding the critical tipping point at which habitat becomes unsuitable, making spatial shifts necessary. We found clear seasonal spatial and temporal dynamics in bat species composition in Tsimanampetsotse National Park. While some species remained in the region year-round, others clearly had a lower tolerance for seasonal environmental pressures. Although we have no data as to where the migrating species relocated to, or the scale of their movements, this study provides important data for correcting and refining what is known of the distribution of certain taxa and improves awareness of the seasonal variation in their ecological requirements.

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