

Temperature explains variation in seasonal temporal activity of *Miniopterus natalensis* more than moonlight or humidity

Mariëtte Pretorius¹, Victor Van Cakenberghe², Hugh Broders³ and Mark Keith^{1*}

ORCID ID's:

MP: 0000-0002-4821-1013

VVC: 0000-0003-1354-2442

HB: 0000-0002-6151-8079

MK: 0000-0001-7179-9989

1 Eugene Marias Chair for Wildlife Management, Mammal Research Institute, Faculty of Natural and Agricultural Sciences, University of Pretoria, Hatfield 0028, South Africa.

2 Functional Morphology Lab, Department of Biology, University of Antwerp, Campus Drie Eiken, Universiteitsplein 1, 2610 Antwerpen, Belgium.

3 Department of Biology, University of Waterloo, 200 University Ave. W, Waterloo, Ontario, N2L 3G1, Canada,

*Corresponding author: mark.keith@up.ac.za

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Abstract

Animals partition their daily activities based on a variety of internal and external factors. For insectivorous bats, the availability of prey, weather conditions, moonlight and reproductive energy demands are proposed as the major influencers of temporal activity. This study investigated the temporal variation in activity of the subtropical cave-dwelling, migratory Natal long-fingered bat, *Miniopterus natalensis*, by temperature, humidity, lunar illumination and the time of moonrise per night. Using echolocation survey data collected 2014 - 2018 near a maternity roost in north-eastern South Africa, differences in activity between the summer maternity (1 September – 28 February) and winter non-breeding (1 March - 31 August) seasons were described. In the non-breeding season, *M. natalensis* exhibited peak activity during the early evening, with decreasing activity throughout the night. In the maternity season, a bimodal activity pattern was observed, probably related to peaks in insect activity and the energy requirements of lactating females. Predictably, temperature had the strongest positive influence on the magnitude of *M. natalensis* activity across both seasons. Humidity also positively affected activity in both seasons to a lesser extent. The time of moonrise did not affect the activity of *M. natalensis* during either of the seasons. Lunar illumination did not affect activity during the maternity season, but activity was diminished on nights with bright moonlight in the non-breeding season. Emergence and return times were not affected by lunar illumination in either season. The need of *M. natalensis* to maximise resource acquisition during the maternity season is likely a strong modulator in the temporal activity of this species and outweighs predation risk in high moonlight conditions. Subsequently, this species exhibits nightly activity behaviours that balance risk factors with intrinsic needs during different seasons.

Keywords: activity, emergence, *Miniopterus*, moonlight, season, temporal

Introduction

The fundamental ecological niche includes variation in all resources and factors in an environment that ultimately influence the survival and reproduction of organisms (Flesch and Steidl 2010). Temporal variation in these resources and factors form an important component of any organism's niche (Halle and Stenseth 2000). To maximise resource acquisition or to avoid agonistic encounters with competitors or predators, animals may partition activities throughout their day (or night), termed temporal activity (Halle and Stenseth 2000; Presley et al. 2009). The organisation of temporal activity is unique to each individual and modulated by a combination of factors (Halle and Stenseth 2000; Refinetti 2008). For insectivorous bats, the major driver of temporal activity is insect availability and abundance (Rydell et al. 1996; Egert-Berg et al. 2018; Halat et al. 2018). Other factors also include moonlight (Saldaña-Vázquez and Munguía-Rosas 2013), air temperature and relative humidity (Lacki 1984), heavy rainfall (Voigt et al. 2011), reproductive energy demands (Wilkinson and Barclay 1997) and interspecific competition (Kunz 1973).

Weather conditions like temperature, humidity and rainfall affect animal activity patterns by directly influencing physiology (Rebelo et al. 2010). Ambient temperature and rainfall affect the thermoregulatory capabilities of warm-blooded animals like bats, with decreased temperatures and rain resulting in reduced activity (Rebelo et al. 2010; Voigt et al. 2011; Giné et al. 2015; Klüg-Baerwald et al. 2016). Relative humidity may affect the activity of animals by impacting water loss, with animals generally displaying higher activity during higher relative humidity conditions (Ludwig 1945; Hüppop and Hilgerloh 2012; Chaverri and Quirós 2017). The insect prey of bats is also affected by weather conditions, with higher insect

activity at higher temperatures (generally in the early part of the evening) and lower relative humidity (Yela and Holyoak 1997; Meyer et al. 2016; Ruczyński et al. 2020).

Moonlight is an interesting factor suggested to influence the temporal activity of various animal species, including bats (Adams and Hayes 2008). Its effect on bat activity may be variable: some bats alter their emergence and foraging activity patterns to reduce predation risk in bright moonlit conditions (Hecker and Brigham 1999; Saldaña-Vázquez and Munguía-Rosas 2013), but it also affects the availability of insect prey (Lang et al. 2006). One of the effects of moonlight might be a diminished activity, commonly known as "lunar phobia" (Morrison 1978). Alternatively, other studies have not found evidence of an effect of moonlight on the magnitude of activity of bats (Clark et al. 2002; Karlsson et al. 2002; Thies et al. 2006; Holland et al. 2011). Generally, insectivorous bats in temperate zones appear not to alter behaviour with changes in moonlight (Negraeff and Brigham 1995; Karlsson et al. 2002; Halat et al. 2018), whilst lunar phobia appears more common in tropical species including frugivores and fishing bats (Singaravelan and Marimuthu 2002; Börk 2006). Fast-flying, open-air foragers are more agile in evading predators and are not expected to show lunar phobia compared to slow-flying clutter-edge foragers, frugivores, gleaners or aerial fast-hawking bats (Saldaña-Vázquez and Munguía-Rosas 2013), although this hypothesis remains largely untested, particularly for subtropical insectivorous species. The activity of echolocating insectivorous bats should not be directly affected by the amount of moonlight, although increased predation risk from visually navigating nocturnal predators, or the cryptic behaviour of insect prey in brighter moonlit conditions, may suppress bat activity (Negraeff and Brigham 1995).

In addition to the effects of climatic factors, females and males may partition nightly activities in a different way because of differential sensitivity to predation risk and energy

requirements (Brown 1999). For example, lactating females have high energy costs and therefore may modify their nightly activity to increase their nutrient intake by spending more time foraging to provision young regardless of predation risk (Hamel and Côté 2008). In comparison, males may exhibit temporal activity schedules that minimise predation risk by reducing foraging time but maximise long-term survival (Brown and Kotler 2004). The Natal long-fingered bat *Miniopterus natalensis* (A. Smith 1833) (Chiroptera: Miniopteridae) is a cave-dwelling colonial insectivore occurring in southern Africa (ACR 2019), which has a known regional migration route (~ 150 km) between hibernacula caves in the Gauteng Province and the Madimatle maternity cave in the Limpopo Province, South Africa (Van der Merwe 1975). The annual, female-dominated migration to Madimatle occurs October-November each year, with departure during early February (Van der Merwe, 1975; Pretorius et al. 2020). Throughout this spring-summer maternity period, approximately 300,000 individual *M. natalensis* roost in the cave (Van der Merwe 1978). The majority of these individuals are reproductive females (Kearney et al. 2017; Pretorius et al. 2019). A small number of males do not migrate and remain at the cave throughout the autumn and winter months (March - August) (Van der Merwe 1975; Miller-Butterworth et al. 2003). During the December summer period, the sex ratio of individual *M. natalensis* captured at the Madimatle Cave maternity site was 1♂:15♀ (Kearney et al. 2017), whereas during the August winter period, the sex ratio was 17♂:1♀ (Van der Merwe 1975).

This study aimed to investigate temporal variation in the nightly activity of *M. natalensis* at the Madimatle cave site in Limpopo, South Africa. The study specifically focused on identifying nightly peaks of *M. natalensis* activity during the summer maternity and winter non-breeding periods and investigating whether humidity, temperature and moonlight conditions affect the temporal activity of this species. We also investigated emergence and

return times to the cave relative to sunrise and sunset and if this was affected by lunar illumination. We made the following predictions: (1) The magnitude of activity will differ between the maternity season and the non-breeding season, reflecting the migratory nature of the species, (2) Warmer temperatures and higher relative humidity would positively influence the magnitude of nightly *M. natalensis* activity during both the maternity and the non-breeding seasons, (3) With *M. natalensis* being a fast-flying, clutter-edge foraging insectivore (Schoeman and Jacobs 2011) and following the prediction by Saldaña-Vázquez and Munguía-Rosas (2013), we did not expect *M. natalensis* to exhibit lunar phobia, (4) We expected the emergence and return times during the maternity season to reflect the needs of reproductive females provisioning young, whereas emergence and return activity during the non-breeding season should reflect the foraging activity of males.

Material & Methods

Study area

This study used four years of echolocation survey data collected from the Madimatle Cave (also known as the Gatkop Cave; 24°37'S 27°39'E), Limpopo, South Africa, which is inhabited year-round by *M. natalensis* bats (Kearney et al. 2017). The area is semi-arid and experiences summer rainfall, with a hot, humid climate during the summer months (October – February) and cool, dry winters (June – August) (WeatherSA 2019). From October to February, *M. natalensis* use the cave for maternity purposes (Van der Merwe 1978). Because of the female-biased sex ratios during the summer season (1 September – 28 February; maternity season), it was assumed that temporal activity patterns would largely reflect behaviour of females. Similarly, because the sex ratio is male-biased during winter (1 March - 31 August;

non-breeding season), we expected activity during this time would largely reflect male behaviour.

Acoustic survey of activity

An SM2-BAT detector (Wildlife Acoustics Inc., Concord, MA, USA) set to zero crossing was deployed 600 meters from the cave next to a concrete water reservoir and recorded continuously throughout each night from March 2014 to March 2018. The bat detector was encased in waterproof housing and the microphone elevated two metres off the ground. All call sequences were passed through a filter developed to identify *M. natalensis* calls (filter smoothness set to 50) in Analoow software version 4.2n (Corben 2017). Free-flying *M. natalensis* occurring in the Limpopo and Gauteng provinces consistently echolocate at a frequency range of 52-56 kHz and calls are unique and distinguishable from sympatric bat species (AfricanBats NPC unpubl. data). An Activity Index (AI) was calculated by summing the number of detected one-minute bat passes following Miller (2001) and the metric was standardised throughout the study by dividing the AI by the number of intervals (i.e., night length in minutes). This standardized AI variable was then categorised according to the summer maternity season and winter non-breeding season.

Weather variables

To evaluate the effects of weather conditions on bat activity, average temperature, relative humidity (percentage of water vapour present in air) and rainfall data were obtained from a Davis Vantage Vue[®] 6250 weather station (Davis Instruments Corporation) deployed from 2014 at the site. These climate variables were averaged for the period of activity monitoring (i.e. nightly averages for readings between 18:00 and 06:00). Due to the semi-arid nature of the study area, only 8% of sample nights recorded rainfall events > 1 mm. Because

of the low prevalence of rainfall and to account for the potential effects of cloud cover, samples with rainfall events during the night (17:00 onwards) > 1 mm were excluded from analyses following Carvalho et al. (2007) and Appel et al. (2017). Only average temperature and relative humidity were therefore retained for statistical models.

Moonlight variables

The lunar illumination (percentage of moon illuminated), sunrise (top edge of the sun appears above the horizon, morning civil twilight ends), sunset (top edge of sun disappears below the horizon, evening civil twilight starts), moonrise (top edge of the moon appears above the horizon), the start of the night (evening nautical twilight starts), start of dawn (morning nautical twilight ends, morning civil twilight starts) and night lengths (number of hours between sunset and sunrise) was calculated using the R package ‘suncalc’ (Thieurmel and Elmarhraoui 2019). Calculated times were offset by + 2 hours to convert Coordinated Universal Time (UTC) time data to South African Standard Time (SAST). Following Appel et al. (2019), the night type was classified by lunar illumination as either dark nights (0 - 39%), bright nights (70 - 100%) and added a ‘moderate’ category for intermediate illumination levels (40 - 69%). Additionally, we investigated whether the time of moonrise affected *M. natalensis* activity by classifying the time that the moon appeared above the horizon each evening (early evening: 18:00 - 20:59, late evening: 21:00 - 23:59, early morning: 00:00 - 02:59 and late morning: 03:00 - 05:59) to equalise the number of observations in each group (Bowden 1973).

Effects of weather and moonlight on activity

All statistical analyses were conducted using R (The R Foundation for Statistical Computing 2013) in RStudio Desktop Software Version 1.1.383, with all graphing conducted using the package *ggplot2* (Wickham 2009). The influence of the night type, moonrise time,

average temperature and relative humidity on *M. natalensis* activity in the maternity and non-breeding seasons were investigated using general linear models (GLMs). To determine which of the variables best predicted *M. natalensis* activity, variable selection was first performed using variance inflation factors (VIFs) using the R *car* package (Fox and Weisberg 2011). All VIFs were > 5 , indicating no collinearity between covariates. Because of the migratory nature of *M. natalensis*, separate GLM analyses were constructed for the maternity and non-breeding seasons using the *lme4* package (Bolker et al. 2009; Bates et al. 2016). In addition to lunar illumination, hours of moonlight per night may also affect animal activity (Appel et al. 2017). Therefore, to test for an effect of time of moonrise per type of night on activity, we first ran the global models using an interaction effect. The interaction effect was non-significant for both the summer maternity period ($p = 0.57$) and the winter non-breeding period ($p = 0.26$) and was therefore excluded from subsequent models. The best candidate GLM model for each season was then selected using Akaike Information Criterion (AIC) and delta Akaike (Δ AIC) with the *MuMIn* package (Bartoń 2019). Estimates of the most parsimonious models were visualised using *sjPlot* (Lüdtke 2019).

Emergence and return times

Emergence and return times to the cave were also determined. To investigate emergence times, we filtered the echolocation survey datasheet to extract the first call detection for each night. Because the detector was not stationed directly at the cave entrance, call times were subtracted from sunset times each night and detections up to 60 minutes after sunset were also included in the analyses, as this is indicative of emergence activity of bats roosting in the vicinity (Menard 2001). Similarly, the times of the last call detection in the mornings were investigated as an indication of when the bats return to the roost. For this, we calculated how many minutes before or after sunrise the last call was recorded for each night sample. We then

compared whether these emergence and return times varied between the seasons using Kruskal-Wallis H-tests (`kruskal.test`) with pair-wise post-hoc tests (`kruskalmc` in the *pgirmess* package (Giraudoux 2019)).

Results

Acoustic survey of activity

From March 2014 to March 2018, excluding evenings with rainfall > 1 mm, 199,851 detector minutes were sampled over 1,282 nights of continuous recording and 174,355 identifiable *M. natalensis* call sequences were recorded. *Miniopterus natalensis* activity was higher during the summer maternity season (mean AI \pm SE, 204.42 ± 2.11) than the non-breeding season (26.99 ± 0.34) ($H_{(1)} = 193.11$, $p < 0.001$). Different trends of temporal activity were observed. The length of the nocturnal activity period ranged between 0 and 644 minutes for the maternity season and 0 and 750 minutes for the non-breeding season. On average, *M. natalensis* activity was bimodal during the maternity season with peaks at 18 ± 6.07 minutes after sunset and 576 ± 1.50 minutes after sunset (Figure 1A). During the non-breeding season, average activity peaked 26 ± 3.12 minutes after sunset and showed a decreasing trend throughout the night (Figure 1B).

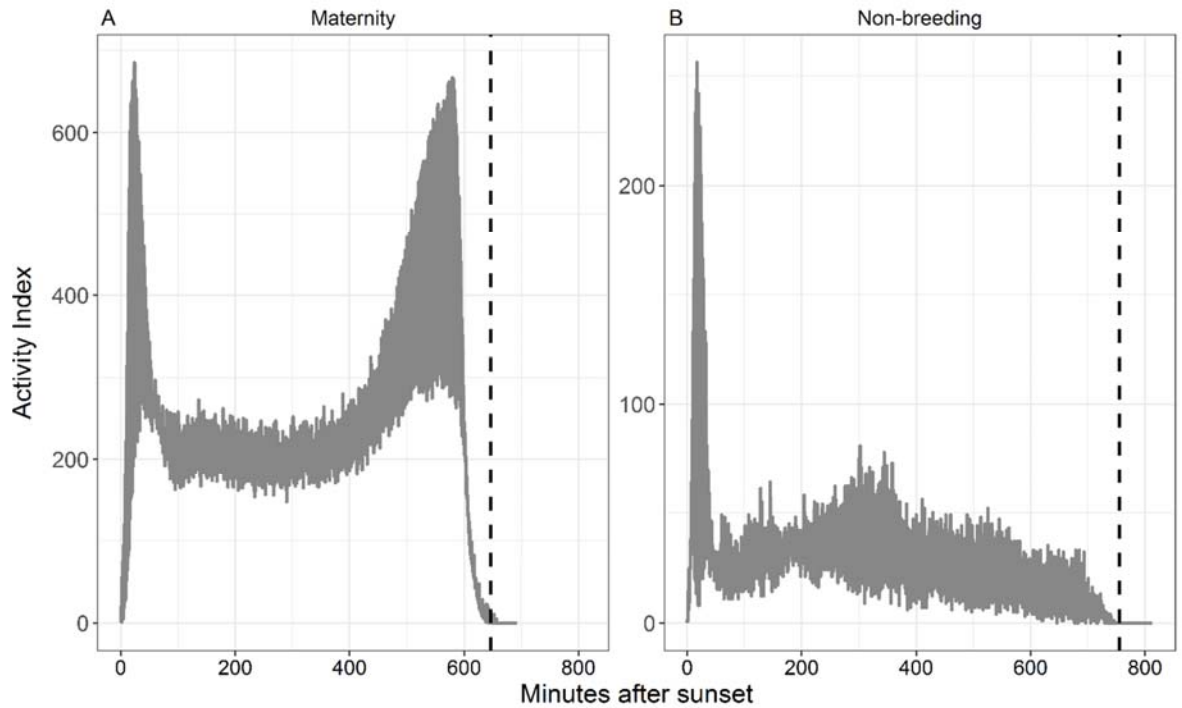


Figure 1 Nightly temporal Activity Index (as the sum of detected one-minute bat passes per night) of *Miniopterus natalensis* by minutes after sunset during the A) maternity and B) non-breeding season. The vertical dashed line indicates the average time of sunrise. Echolocation calls were recorded throughout each night from March 2014 to March 2018 at the Meletse Bat Research Conservation and Training Centre, Limpopo, South Africa. Note the different scales on the Y-axis of each season indicating variable activity levels

Effects of weather and moonlight

Night temperatures averaged 23.10 ± 0.12 °C during the maternity season and 15.38 ± 0.17 °C during the non-breeding season. Relative humidity averaged 53.64 ± 0.77 % during the maternity season and 60.06 ± 0.63 % during the non-breeding season. Night type, moonrise time, average temperature and relative humidity showed different levels of importance between the maternity and the non-breeding season (Table 1). In the maternity season, model results suggested that average temperature and relative humidity explained variation in *M. natalensis* activity, but neither moonrise time nor night type (Table 2). Contrastingly, night type, along with average nightly temperature and relative humidity, were important predictors of *M.*

natalensis activity during the non-breeding season, but not moonrise time. Average temperature and relative humidity had significant positive effects on *M. natalensis* activity during both the maternity and the non-breeding season and temperature had a stronger and more significant positive effect than relative humidity (Figure 2). Moonrise time suppressed *M. natalensis* activity during the maternity season, but the effect was not statistically significant. Moonrise time did not affect activity during the non-breeding season. Night type had a significant but small negative effect on *M. natalensis* activity during the non-breeding season and a negative but non-significant effect during the maternity season. Parameter estimates of the most parsimonious models are presented in the supplementary material Table S1.

Table 1 Ranked Akaike Information Criterion (AIC) general linear models investigating the effects of moonlight (night type and moonrise time) and weather (average temperature and relative humidity) on the nightly activity of *Miniopterus natalensis* during the maternity and non-breeding season at the Madimatle Cave, Limpopo, South Africa. The most parsimonious models are shown in bold. The night type was determined by the amount of moonlight during the night: dark nights (0 - 39%), moderate nights (40 - 69%) and bright nights (70 - 100%) and moonrise denotes the time when the moon appears above the horizon (early evening: 18:00 - 20:59, late evening: 21:00 - 23:59, early morning: 00:00 - 02:59 and late morning: 03:00 - 06:00 respectively)

Season	Model	df	AIC	Δ AIC	Weight
Maternity	Moonrise + average temp + humidity	7	4999.1	0.00	0.68
	Average temp + humidity	9	5002.1	2.90	0.16
	Night type + moonrise + average temp + humidity	11	5002.1	2.97	0.15
	Humidity	2	5047.8	47.00	0.00
	Night type + moonrise + average temp + humidity	5	5061.0	60.13	0.00
Non-breeding	Night type + average temp + humidity	6	3493.7	0.00	0.87
	Night type + moonrise + average temp + humidity	9	3499.6	3.87	0.12
	Night type + moonrise + average temp	7	3517.6	19.97	0.00
	Average temp	3	3525.0	27.38	0.00
	Humidity	3	3590.0	92.43	0.00

Table 2 Mean emergence and return times in minutes \pm Standard Deviation (SD) of *Miniopterus natalensis* bats during the maternity and non-breeding season, calculated using echolocation calls recorded nightly near the Madimatle Cave, Limpopo Province, South Africa from March 2014 to March 2018. Calculated time of sunset and sunrise for the area is shown as hours: minutes (hh:mm) \pm SD. Means in second and fourth columns followed by the same letter in bold are not significantly different ($p < 0.05$) according to Kruskal-Wallis pairwise posthoc tests

Season	Time of sunset (hh:mm) \pm SD (mm:ss)	Emergence (mean minutes after sunset \pm SD)	Time of sunrise (hh:mm) \pm SD (mm:ss)	Return (mean minutes before sunrise \pm SD)
Maternity	18:45 \pm 00:19	11.65 \pm 0.18 a	05:29 \pm 00:21	36.06 \pm 0.22 a
Non-breeding	17:58 \pm 00:15	23.56 \pm 0.14 b	06:28 \pm 00:19	86.37 \pm 0.35 b

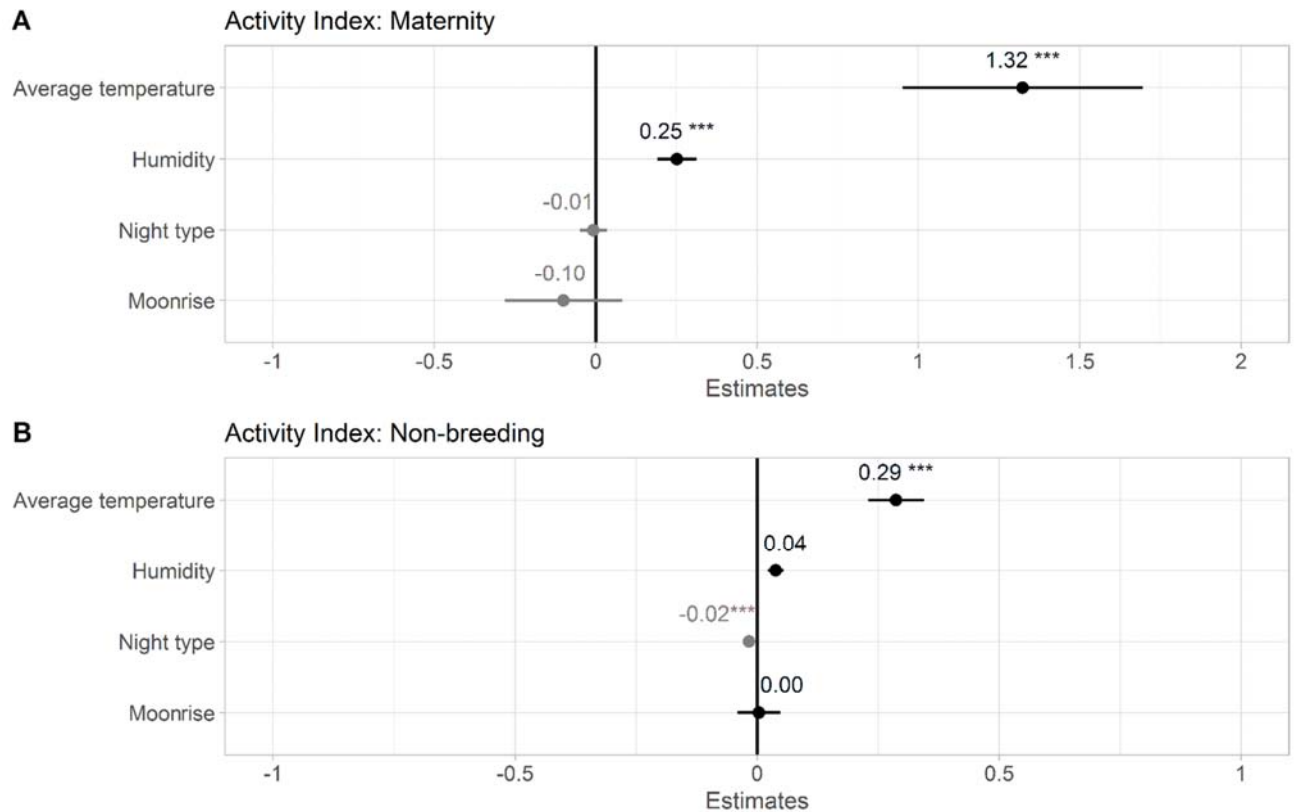


Figure 2 Plotted estimates of climatic predictors (average temperature, relative humidity, night type and moonrise time) from the candidate general linear regression models assessing their effect on the Activity Index (the sum of detected one-minute bat passes per night) of *Miniopterus natalensis* in the summer maternity (A: 1 September – 28 February) and winter non-breeding (B: 1 March - 31 August) seasons. Dots are labelled with their corresponding estimate values and 95% Confidence Intervals (CI - horizontal bars). Black dots represent positive effects and grey dots represent negative effects. Dots with CIs falling on the vertical line indicate a zero effect. Asterisks indicate significance levels of p-values (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

Night type had no effect on *M. natalensis* activity during the maternity season ($H_{(2)} = 3.61$, $p = 0.16$), with similar average activity across dark (245.72 ± 9.23), moderate (223.32 ± 13.53) and bright (222.86 ± 10.35) nights (Figure 3A). Night type significantly affected *M. natalensis* activity during the non-breeding season ($H_{(2)} = 10.93$, $p < 0.01$). Average *M. natalensis* activity was similar during nights of dark (49.97 ± 2.64) and moderate (50.57 ± 4.44) lunar illuminations. Activity during bright nights (38 ± 2.71) was significantly lower when compared to dark nights (Figure 3B).

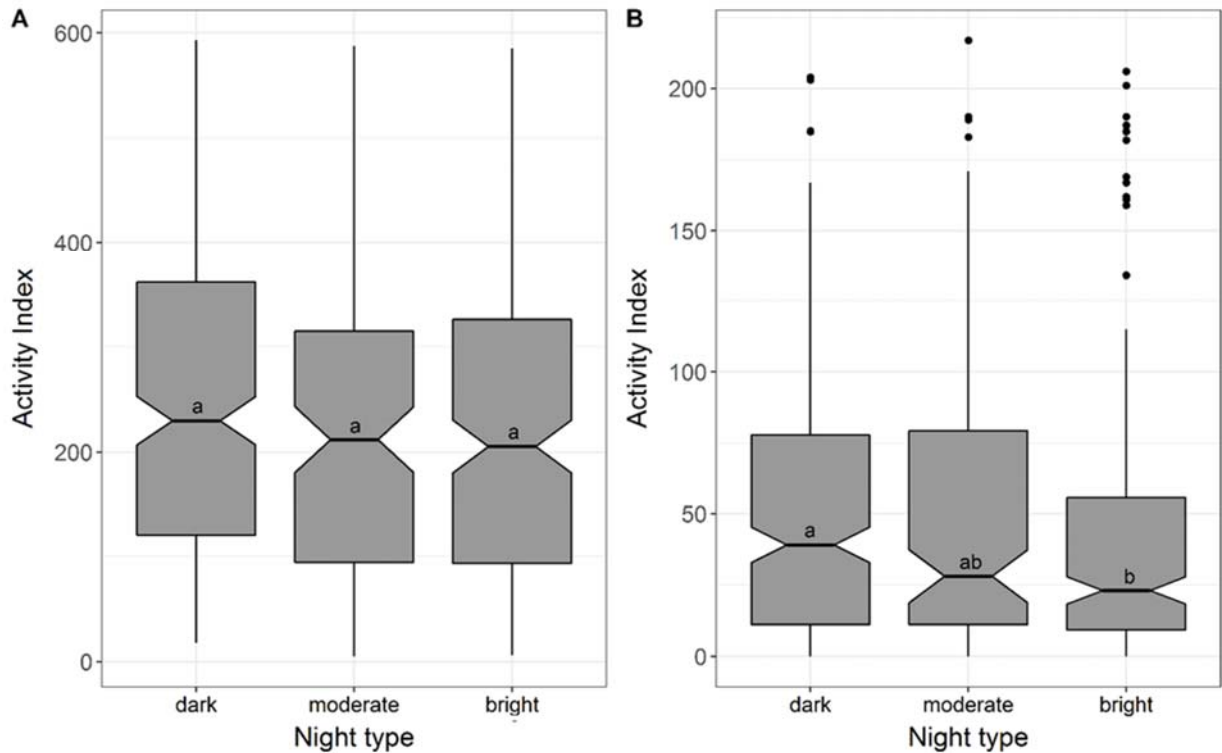


Figure 3 Medians and SE (whiskers) at 95% CI (notches) of the effect of night type (lunar illumination; dark: 0 - 39%, moderate: 40 - 69%, bright: 70 - 100%) on the Activity Index (number of one-minute time periods of detection per night) for *Miniopertus natalensis* during the maternity (A: 1 September – 28 February) and non-breeding (B: 1 March - 31 August) seasons recorded across four years from 2014-2018 at the Madimatle Cave, Limpopo Province, South Africa. Notches of boxes that do not overlap and different letters denote significant differences between groups according to Kruskal-Wallis pairwise posthoc tests. Note the different scales on the Y-axis of each season indicating variable activity levels

Emergence and return times

Overall, *M. natalensis* emerged 20 minutes after sunset and returned 41 minutes before sunrise. Emergence times differed significantly between the maternity and non-breeding seasons ($H_{(1)} = 251.71, p < 0.001$). During the maternity season, bats emerged sooner after sunset than during the non-breeding season. Return times were also significantly different between the maternity and non-breeding seasons ($H_{(1)} = 282.50, p < 0.001$). In relation to the sunrise, bats returned to the roost sooner during the non-breeding period than during the maternity season.

Discussion

Miniopterus natalensis at the Madimatle cave showed inter-seasonal differences in their nightly temporal activity. Supporting our first prediction, the magnitude of activity was higher during the maternity season than the non-breeding season, when a greater number of females roost in the cave. Activity showed bimodal peaks during the maternity season and a single peak early evening during the non-breeding season. Bats also emerged sooner and returned later during the maternity season compared to the non-breeding season. Supporting our second prediction, temperature was the strongest positive predictor of activity across both the maternity and non-breeding seasons and relative humidity also positively influenced activity across both seasons, but to a lesser degree. The time of moonrise had no effect on the magnitude of nightly activity of *M. natalensis* in either the maternity or the non-breeding period. Lunar illumination (dark, moderate or bright nights) did not affect the activity of *M. natalensis* during the maternity season, somewhat supporting our third prediction. However, in the non-breeding season, activity was lower during nights with bright lunar illumination compared to dark nights. Therefore, results suggest that *M. natalensis* activity is driven more by temperature than humidity, but that the effect of moonlight may be season-specific.

Activity patterns

In the maternity season, the activity of *M. natalensis* exhibited two distinct peaks of activity; early evening after sunset and early morning before sunrise, with a decrease in activity towards midnight. These results conform to the expected bimodal pattern of bat activity following the dusk and dawn peaks in insect activity (Rydell et al. 1996; Ruczyński et al. 2020). These activity patterns are observed in Lepidopterans (Bowden and Church 1973; Gang and Chun-Sen 2012) and Dipterans (Kan et al. 2004; Gebresilassie et al. 2015), prey groups often

consumed by *M. natalensis* (Aldridge and Rautenbach 1987; Schoeman and Jacobs 2003). Because *M. natalensis* give birth and raise their young during the period from October to December at the Madimatle cave (Van der Merwe 1975), the decrease in activity observed between 100 and 400 minutes after sunset probably also signifies the return of lactating females to the roost to nurse young, before resuming foraging again a few hours later (Van der Merwe 1978). Similar patterns of activity are observed in females of several other bat species (Henry et al. 2002; Funakoshi and Maeda 2003; Murray and Kurta 2004). Patterns of observed activity are comparable between acoustic recordings and radio-tracking methods (Murray and Kurta 2004), testifying that echolocation data provide a reliable representation of the temporal activity level of bat colonies.

In the non-breeding season, the highest peak in activity occurred early evening after sunset and decreased throughout the night. Although the majority of *M. natalensis* is believed to hibernate in different cave systems in the Cradle of Humankind, Gauteng Province, some males remain at the Madimatle cave throughout the winter period (Van der Merwe 1973) and stay active throughout winter (Pretorius et al. 2020). Temperatures in this region are likely sufficiently warm to allow for insect flight throughout the early parts of the evening (Taylor 1963). Both insect and bat activity then decreases throughout the evening as temperatures drop (Rydell et al. 1996).

Effects of weather conditions

As predicted, temperature and relative humidity had positive effects on bat activity. Temperature was the strongest positive predictor of *M. natalensis* activity across both the maternity and the non-breeding season, supporting several other studies that have shown that air temperature explains the variation in bat activity (O'Donnell 2000; Russ et al. 2003; Meyer

et al. 2004; Barros et al. 2014; Wolbert et al. 2014; Dias-Silva et al. 2018; Appel et al. 2019). This observed pattern is strongly related to the increased flight activity of insects in warmer temperatures (Taylor 1963; Rydell 1992; Jaworski and Hilszczański 2013) and the thermoregulatory advantages of flying in warmer air (Klüg-Baerwald et al. 2016). Also similar to results presented here, increased relative humidity positively influences bat flight activity, likely related to lower evaporative water loss in these conditions (Lacki 1984; Wolcott and Vulinec 2012), but is likely less important than temperature in regulating activity.

Lunar phobia

Lunar illumination did not affect activity during the maternity season, supporting our prediction that, as a fast-flying, clutter-edge foraging insectivore, *M. natalensis* would not show lunar phobia. However, our results did not support the prediction during the non-breeding season. Activity during the non-breeding season was diminished on brightly illuminated nights. Some bat species decrease activity during high moonlight conditions, perhaps as a predator-avoidance strategy (Hecker and Brigham 1999; Saldaña-Vázquez and Munguía-Rosas 2013), whilst predators like owls experience increased hunting success during brightly moonlit nights (Clarke 1983; San-Jose et al. 2019). Barn owl *Tyto alba* are avid opportunistic depredators of *M. natalensis* (Van der Merwe 1980). Two *T. alba* individuals have been observed at the Madimatle cave throughout the year and analyses of owl pellets from the area showed that these owls increased their consumption of *M. natalensis* during the winter period when other food becomes scarce (Swartz et al. in press).

Throughout the spring-summer maternity period, a large population of *M. natalensis* inhabit the Madimatle Cave (Van der Merwe 1978), mainly comprising reproductive females (Pretorius et al. 2019). As animals that must substitute reproductive costs with daily feeding

(income breeders), reproductive female *M. natalensis* bats experience a continuous and growing energy demand (Reynolds and Kunz 2000), requiring increased foraging effort and greater net daily intake compared to non-reproductive conspecifics (Koehler and Barclay 2000; Pretorius et al. 2019). Female income breeders, like bats, face a trade-off between obtaining resources to provision young and higher predation risk from increased foraging effort (Verdolin 2006). Lactating females are then forced to feed even if under high predation risk to maximise resource intake (Hamel and Côté 2008; Srinivasan et al. 2018), which likely explains why lunar phobia was not observed in *M. natalensis* during this time. For gregarious animal. In group-living animals, predation risk decreases as group size increases (dilution effect), with individuals having an increased ability to identify threats and a lower probability of being predated (attack-abatement) (Turner and Pitcher 1986; Roberts 1996; Childress and Lung 2003; Sorato et al. 2012). Likewise, the large *M. natalensis* population size during spring and summer may facilitate non-lunar phobic behaviour in relation to predation risk through the dilution effect. Therefore, bats wintering at the maternity cave may face increased predation pressure from predators like *T. alba*, necessitating predator-avoidance behaviours like decreasing activity during bright moonlight conditions and employ behaviour that maximises their long-term fitness prospects (Brown and Kotler 2004).

Our results showed earlier evening emergence and later morning return times by *M. natalensis* during summer than during other seasons. This indicates that during the breeding season, female *M. natalensis* likely optimised foraging time to maximise food intake when resources are most abundant and nutrient requirements are high (Van der Merwe 1978; Lee and McCracken 2001; Encarnação and Dietz 2006; Pretorius et al. 2019). This behaviour is common in insectivorous bats and relates to the dusk and dawn peaks in insect activity, particularly during the summer season when insects are most abundant (Thies et al. 2006;

Holland et al. 2011; Ruczyński et al. 2020). During evening emergence, bats likely also face a trade-off between resource needs, resource availability and predation risk (Thies et al. 2006). Delayed emergence behaviour is widely accepted as a predator avoidance strategy in various bat species (Kalcounis and Brigham 1994; Thies et al. 2006; Reichard et al. 2009; Thomas and Jacobs 2013). In summer, *M. natalensis* at the Madimatle Cave can comprise as much as 46.8% of *T. alba* diet (Swartz et al. in press). The early emergence of *M. natalensis* in the summer maternity period, despite the predation risk by predators like *T. alba*, suggests that the need to feed outweighs the risk of foraging in bright moonlight conditions.

Conclusion

Animals exhibit flexibility in their temporal activity with seasonality, habitat structure, resource availability and age and sex differences. Temporal activity of subtropical bat species is still relatively understudied and several studies suggest that some bat species alter their temporal activity in relation to lunar phases (Morrison 1978; Börk 2006; Saldaña-Vázquez and Munguía-Rosas 2013). In this study, the nightly temporal activity of the Natal long-fingered bat *Miniopterus natalensis* was described according to different seasons, temperature, relative humidity and moonlight conditions. Results showed that *M. natalensis* exhibits seasonal-specific peaks of nightly activity. Notably, activity in the maternity period showed bimodal peaks in early evening and early morning, most likely related to peaks in prey activity. As observed in many other bat species, temperature had the strongest positive influence on *M. natalensis* activity. *Miniopterus natalensis* activity was not affected by moonlight during the maternity season, but activity was diminished on nights with bright moonlight during the non-breeding season. Additionally, emergence times during the maternity season was earlier in relation to sunset than the non-breeding season and bats also returned to the roost closer to

sunrise compared to the non-breeding season. *Miniopterus natalensis* may maximise resource acquisition during the reproductive summer period, a priority which outweighs the risk of predation by predators such as the barn owl *T. alba* in higher moonlight conditions. Subsequently, *M. natalensis* exhibits nightly temporal activity behaviours that balance risk factors with intrinsic needs during different seasons.

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