Climatic correlates of migrant Natal long-fingered bat *Miniopterus natalensis* phenology in north-eastern South Africa

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Running page head: Migrant *Miniopterus* phenology

Abstract

Context. For migratory animals, particularly those with long generation times, changing weather patterns may cause a mismatch between periods of expected and actual resource availability, termed phenological mismatch. The cave-dwelling Natal long-fingered bat *Miniopterus natalensis* is a regional migrant within South Africa for which the phenology of migration may be affected by climate but are hitherto unknown.

Aims. To investigate the migration phenology of the Natal long-fingered bat in relation to climate at a maternity cave in South Africa.

Methods. We used five years (2014-2018) of echolocation data from a maternity cave site in Limpopo, South Africa. Separate stepwise General Linear Models (GLMs) were constructed for each season using photoperiod, minimum temperature, dew point, rainfall, barometric pressure, humidity and maximum wind speed. Arrival and departure dates between years were also compared.

Key results. Photoperiod had the greatest effect on the magnitude of Natal long-fingered bat phenological patterns in activity across all seasons. Whilst spring arrival at the maternity site was variable across years, summer departure dates did not differ, resulting in a shorter breeding period in the 2017-2018 sample year. During the 2016-2017 sample year, the magnitude of Natal long-fingered bat activity was significantly lower than other years, which coincided with El Niño-induced drought conditions and likely impacted resources and led to a reduction in activity and population size.

Conclusions. Photoperiod is a strong predictive cue of the phenology of migration of the Natal long-fingered bat and likely cues migration for this species. The narrow departure dates of these bats from the maternity site supports these results.

Implications. This study indicates that Natal long-fingered bats use photoperiod as a migration cue and do not appear to shift their spring-summer breeding season, likely making them vulnerable to phenological mismatch and population decline. Our research highlights the need for systematic population monitoring for the Natal long-fingered bat.

Additional keywords: bat, phenology, photoperiod, South Africa

Introduction

Migratory species return seasonally to areas that are familiar and offer increased foraging success and a higher likelihood of successful reproduction (Dingle 2014). The phenology of spring reproductive events is shifting and occurring earlier, resulting in a mismatch between the availability of resources during breeding periods (Parmesan and Matthews 2009) and, subsequently, may lead to a decrease in reproductive success and, in some cases, population decline (Møller et al. 2008). By tracking the timing of seasonal activities (phenology) of organisms, researchers can make inference on the impacts of climate change (Menzel 2002). Phenology can show large inter-annual variation, with some events occurring reliably at specific dates and others showing high inter-annual variation (Gwinner and Helm 2003). Rather than clear phenological patterns explained by extreme temperature fluctuations, phenological cycles in southern latitudes are less distinct (Chambers et al. 2013). In tropical and subtropical systems, the dry-wet cycle is pronounced, and species in these regions show a lessened response to temperature, with phenology more linked to rainfall (Morellato et al. 2000). Similarly, these two regions are governed by climatic anomalies imposed by El Niño Southern Oscillation (ENSO) climate cycles (Brown et al. 2010). These cycles of climatic anomalies cause drought and fires in tropical regions and floods in arid regions over the tropical and subtropical Pacific zones (Canale and Henry 2010; Benkenstein 2017) and southern Africa (Stige et al. 2006).

Organisms with a slow generation time and low reproductive output (k-selected species) are likely to be particularly susceptible to changes in spring breeding resource phenology (Canale and Henry 2010; MacMynowski and Root 2007), because phenological changes through microevolution may occur too slowly for any adaptive benefit in a rapidly changing climate (Visser 2008). This phenomenon is termed phenological mismatch (Renner and Zohner 2018). Phenological mismatch and the subsequent population declines have been widely documented, including in birds (Tøttrup et al. 2012), plant-pollinator relationships (Kudo and Ida 2013) and large herbivores (Post et al. 2008). Bats are one of the few small-bodied mammals that exhibit k-selected life-history strategies (Becker et al. 2013), with females of most species producing a single offspring per reproductive season (Sheffield et al. 1992; Racey and Entwistle 2000). As small endothermic mammals, insectivorous bats are especially sensitive to changing climatic conditions, since a large portion of metabolic energy is spent on maintaining constant body temperature (Fristoe et al. 2015). In the Pacific

Northwest, temperature and rainfall have been suggested as the best phenological predictors of bat activity, where low temperatures and rainfall suppresses bat activity (Erickson and West 2002). Alternatively, tropical and subtropical bat phenology may be regulated by geographic and temporal variability in food availability (Popa-Lisseanu and Voigt 2009). The migratory behaviour of bats is still largely understudied (Jonasson 2017) and the cues that bats use to initiate migration are not well known (Popa-Lisseanu and Voigt 2009), although factors that may affect migratory decisions may include temperature, rainfall, barometric pressure, wind speed and photoperiod (Pettit and O'Keefe 2017). Investigating which phenological factors affect migration is important in understanding the basic ecology of bats to better inform conservation strategies (Bowlin et al. 2010).

Migration is an important behavioural adaptation for various bat species occurring in variable environments (Fleming and Eby 2003), with temperate bats making long-distance, regional or altitudinal migrations (McGuire and Boyle 2013). Some species, such as Nathusius's pipistrelle *Pipistrellus nathusii,* undertake north-south directional long-distance migrations, although most bat species make regional migrations of a few hundred kilometres (Rodrigues and Palmeirim 2008). Temperate bats that undertake long-distance migrations with a north-south pattern are suggested do so in relation to extreme climatic fluctuations (Fleming and Eby 2003). However, the drivers behind regional migrations are less well understood (Rodrigues and Palmeirim 2008). This is certainly true for migratory bats in southern Africa, where few studies on bat migration have been conducted. The Natal long-fingered bat (Chiroptera: Miniopteridae)*, Miniopterus natalensis* (A. Smith 1833), is classified as a migratory insectivorous bat in South Africa (Mills and Hes 1997; Miller-Butterworth et al. 2005). This species roosts in large groups within caves (Van der Merwe 1973) and appear to be restricted to regions that offer suitable cave environments and are sensitive to disturbances (Monadjem et al. 2017). Whilst *M. natalensis* is a known seasonal migrant between winter hibernacula and summer maternity cave roosts within the north-eastern region of South Africa (Mills and Hes 1997; Miller-Butterworth et al. 2003; Van der Merwe 1975), the phenological effects of climate on these migratory movements were hitherto unknown. Given the value of large populations of bats as insect suppressors (Kunz et al. 2011) and the current lack of a recovery plan or a systematic monitoring scheme for *M. natalensis* (Monadjem et al. 2017), this study provides valuable insight into the life history and ecology of this species. Our goal was to investigate phenological patterns in the activity and migration of *M. natalensis* at a maternity site in northeastern South Africa. The study focuses on the association of the magnitude of *M. natalensis* activity, measured via echolocation monitoring, with several climatic variables across four seasons to identify potential migratory cues and addressed the following questions: (1) Which climatic factor/s have the greatest effect on *M. natalensis* migratory phenology? (2) Does the magnitude of *M. natalensis* activity change across years and seasons? (3) What are the arrival dates, departure dates and duration of stay at the maternity colony each year? We expected the magnitude of *M. natalensis* activity to be low during the autumn and winter periods and high during the spring and summer maternity period, reflecting their migratory nature. If *M. natalensis* migration phenology is driven by variations in temperature, rainfall, barometric pressure or/and wind speed, we expected arrival and departure dates to differ between the study years. As a migrant species in a subtropical context, we predicted that *M. natalensis* migratory activity would be more closely associated with rainfall than other climatic variables.

Materials and methods

Study site

The Limpopo province where the study cave is located is mostly dominated by Savanna grasslands, sweet Lowveld Bushveld and Mixed Lowveld Bushveld vegetation types and experiences summer rainfall, with a hot and humid climate throughout the summer months (October – February) (Newbould 2003; Mucina and Rutherford 2006). The Madimatle Cave (24°37′S 27°39′E, also referred to as Gatkop cave or Sandspruit Cave No. 1) is a three-chambered dolomitic cave with a high intrinsic temperature (Van der Merwe 1987). The cave is used annually by an estimated 300,000+ *M. natalensis* from October - March for maternity purposes (Van der Merwe 1975; Pretorius et al. 2018).

Assessment of the magnitude of bat activity

Although echolocation calls cannot provide a direct quantitative relationship between call numbers and bat population numbers, it provides an estimate of the magnitude of bat activity in the landscape and, over long periods, can reflect changes in the magnitude of bat activity (Miller 2001; Ford et al. 2011). Activity patterns may then be used to infer trends in the population and the use of certain sites (Adams and Fenton 2017), such as estimating migratory phenology. We used five years of echolocation data collected from an SM2-BAT detector (Wildlife Acoustics Inc., Concord, MA, USA) set to zero crossing deployed 600 meters from the Madimatle Cave. The bat detector recorded continuously through each night from March 2014 to March 2018. Activity data were grouped into four equal sample periods (2014-2015, 2015-2016, 2016-2017 and 2017-2018), ranging from 20 March to 19 March, with sample nights totalling 365 for each year sample. Call sequences were passed through a filter developed to identify *M. natalensis* calls (filter smoothness set to 50) in AnalookW software version 4.2n (Corben 2017). The Activity Index (AI) for *M. natalensis* was calculated by summing the number of one-minute passes per night within which *M. natalensis* was recorded (Miller 2001), thus providing an estimate of the magnitude of bat activity at that site for each sample night. Free-flying *M. natalensis* occurring in the Highveld (Limpopo and Gauteng provinces) consistently echolocate at a frequency range of 52-56 kHz, which is unique and distinguishable from sympatric bat species (AfricanBats NPC unpubl.

data 2019). All statistical analyses were conducted using R (R Development Core Team 2014) in RStudio Desktop Software Version 1.1.383, with all graphing conducted using the packages *ggplot2* (Wickham 2009), *ggpubr* (Kassambara 2018) and *sjPlot* (Lüdecke 2019).

To assess whether the magnitude of *M. natalensis* activity differed between sample years and among the four seasons (defined below) across the different sample years, we used Kruskal-Wallis H-tests (kruskal.test) with pair-wise posthoc tests (kruskalmc) in the *pgirmess* package (Giraudoux 2019). Boxplots with notches were also used to visually assess whether there were significant differences between the medians of different categories (Crawley 2012; Krzywinski and Altman 2014). Boxes with non-overlapping notches have significantly different medians, whilst boxes with overlapping notches indicate no significant difference in median values (Crawley 2012; Krzywinski and Altman 2014).

Secondly, to determine arrival and departure of migratory *M. natalensis* bats at the cave, the AI variable was converted to a proportion by dividing each nightly AI by the total number of calls for that sample year. This was done to establish the number of nights where the proportion of *M. natalensis* calls exceeded the median calls for each sample year, which would indicate that activity had increased significantly (Adams et al., 2015). The first night where the proportion of calls exceeded 40% of the total number of calls for that sample year was scored as “arrival”, and the first night when the proportion of calls were less than 40% was scored as “departure”. This period between arrival and departure (duration of stay) denotes the summer breeding period for *M. natalensis* (see Pretorius et al. 2018). We then tested whether the magnitude of *M. natalensis* activity differed during the summer breeding periods between each sample year using Kruskal-Wallis H-tests with pair-wise post-hoc tests. We also report the number of days between arrivals and departures between the subsequent sample years.

Climatic data

Hourly climatic data were obtained from a Davis Vantage Vue® 6250 (Davis Instruments Corporation) weather station deployed at the site from 2014. Data obtained were minimum temperature (°C), dew point (°C), rainfall (mm), barometric pressure (mbar), humidity (%) and maximum wind speed (m/s) and averaged over the period of activity monitoring (i.e., nightly averages for readings between 18:00 and 06:00) following Smith and McWilliams (2016). Additionally, the total cumulative rainfall for each sample year period and average temperature over 24 hours were included in our analysis for comparative purposes. Seasonal calendar dates used to classify climatic data were provided by the South African Weather Service (Weather SA 2018; Autumn: 1 March – 31 May, Winter: 1 June – 31 August, Spring: 1 September – 30 November, and Summer: 1 December – 28 February). As seasons are related to photoperiod (Hamner 1940), night length in hours was calculated using the R package *suncalc* (Agafonkin 2018) and offset by +2 hours to convert data to South African Standard Time (SAST). Summer is characterised by short nights and winter is characterised by long nights.

The influence of climatic variables on the magnitude of bat activity was investigated using general linear models (GLM's), with the AI as the dependent variable and night length, temperature, dew point, rainfall, barometric pressure, humidity and maximum wind speed as explanatory variables. To determine which of the climatic variables best predicted *M. natalensis* activity, we first performed variable selection using Variance Inflation Factors (VIF) using the R *car* package (Fox and Weisberg 2011). Variance Inflation Factors are used as an indication of the degree of collinearity between variables in regression models (O'Brien 2007). VIF's were calculated for each covariate. All VIF's were < 5, indicating low collinearity between covariates in the models (Sheather 2009).

Subsequently, all covariates were retained in the global models. Separate stepwise GLM models with Poisson error distributions were then constructed for each season to examine which climatic variables best predicted *M. natalensis* activity using the R *stats* package (R Development Core Team 2014). To select the best candidate GLM model for each season, we performed a multi-model selection using the Akaike Information Criterion (AIC) and delta Akaike (ΔAIC) with the *MuMIn* package (Bartoń 2019). Ten stepwise models were constructed per season, each using the same parameters to ensure that each had a fair chance for consideration in a refined confidence set of best models. We presented the top 3 models for each season with the lowest ΔAIC values. The information-theoretic approach using the AIC method compares a set of a priori models and favours the most parsimonious based on the data available; this process avoids overfitting (Burnham et al. 2011).

To describe the influence of climatic parameters on *M. natalensis* activity, estimates of the most parsimonious models for each season were visualised using *sjPlot* as graphed Incidence Rate Ratios (IRR; Lüdecke, 2019). The resulting graph is a forest-plot of exponentiated estimates that shows how much the expected *M. natalensis* call numbers changed per unit-change in each predictor, as well as the direction of the effect (Lüdecke, 2019). Interpretation of the IRR's is similar to that of Odds Ratios, where estimates falling to the left of the vertical intercept line that indicates no effect (x-axis position 1 for GLM's) show a negative effect of the explanatory variable on the response variable and estimates falling to the right of the line show a positive effect (Lüdecke, 2019). Estimates falling exactly on the vertical intercept line show a zero effect (Lüdecke, 2019). IRR estimate values indicate the magnitude of the effect. For example, if the IRR for night length during autumn is 0.66, for each hour of increase in night length, the magnitude of *M. natalensis* activity decreased by a factor of 0.66. To visualise the relationship of the predictor variable on the magnitude of *M. natalensis* activity from the best candidate models that returned the strongest effect, we created a scatterplot with a trend line (Burnham and Anderson 2002), in this case, a 3rd order polynomial regression line.

Results

Recordings from 1,404 nights of continuous echolocation call sampling from 20 March 2014 to 19 March 2018 yielded 205,100 identifiable *M. natalensis* echolocation call sequences. The largest proportion of *M. natalensis* call sequences (23%) were recorded in the 2014-2015 sample period, while periods 2013-2014 and 2016-2017 had the lowest (17% and 18%, respectively). Overall, there was a significant difference in the magnitude of nightly *M. natalensis* activity across sample years (Kruskal-Wallis H-tests; $H_{(3)} = 35.57$, $p < 0.001$). The magnitude of *M. natalensis* activity was lowest during 2016-2017 (median ± standard error, 46.00 ± 8.07). The highest magnitude of nightly bat activity was recorded during 2014-2015 (138.50 ± 7.49), with significantly lower activity during 2015-2016 (84.00 ± 8.66). There was no difference in the magnitude of *M. natalensis* activity between years 2015-2016 and 2017-2018 (90.00 ± 7.68). Except for summer throughout all years ($H_{(3)} = 2.01$, $p = 0.57$), magnitude of activity differed between each of the year sample periods within-season (Fig.1) for autumn ($H_{(3)} = 104.51$, $p < 0.001$), winter ($H_{(3)} = 30.41$, $p < 0.001$) and spring ($H_{(3)} = 28.28$, $p < 0.001$). The magnitude of *M. natalensis* activity was highest during 2014-2015 (110.71 ± 7.01) and lowest during 2015-2016 (42.94 ± 20.67) in autumn. Cumulative rainfall (summed over 24 hours) was highest for summer months, and the total cumulative rainfall was highest during 2016-2017 (Σ_{summer} 764.40 mm; S1 Table) and lowest during 2014-2015 (Σ_{summer} 380.00 mm). Additionally, the pooled mean temperature across all seasons (averaged over 24 hours) was higher during 2016-2017 (22.77°C) than either 2014-2015 (21.26°C) or 2016-2017 (21.56°C).

Miniopterus natalensis activity was characterised by a pulse of nightly activity during autumn (nights 1-70), a decrease in the magnitude of activity during winter (nights 71 - 162) and an increase in activity during spring and summer (nights 163 - 337; Fig. 2). The magnitude of activity then decreased again at the onset of autumn (nights 338 - 365). Time of arrival of *M. natalensis* at the study site was more variable than departure across sample years. Arrival at the site varied between mid-October to early November (31/08 – 05/11), and departure nights were during early February (03/02 – 08/02; Table 1). Duration of stay varied per sample year (92 -157days; Table 1) and the mean magnitude of *M. natalensis* activity differed significantly during the duration of stay over the summer breeding period ($H_{(3)} = 27.52$, $p < 0.001$) and was significantly lower during 2016-2017 ($\bar{x} = 157$) compared to 2017-2018 ($\bar{x} = 92$), even though duration of stay was longer during 2016-2017 than 2017-2018 (Table 1).

The seven different climatic variables used as predictors of *M. natalensis* activity showed differing levels of importance between the four seasons (Table 2). Cumulative rainfall was only an important predictor during spring, but was excluded from the most parsimonious models during autumn, winter and summer. Night length (photoperiod), minimum nightly temperature, mean dew point, maximum wind speed, mean barometric pressure and mean humidity were important predictors across all four seasons across the five years. Parameter estimates of the most parsimonious models were different in direction (+/-) and magnitude across the four seasons (Table 3). For all 5 years, and all four seasons, night length was the predictor variable that returned the strongest negative effect on the magnitude of *M. natalensis* activity (Fig. 3), with activity decreasing significantly as night length increased (Fig. 4). The rest of the climatic variables (minimum nightly temperature, dew point, maximum wind speed, barometric pressure, humidity and rainfall) had differing effects on the magnitude of *M. natalensis* activity depending on the season. During spring, summer and winter, the magnitude of activity increased by a factor of 1.01 (spring, summer) and 1.03

(winter) for each °C of temperature increase, but in autumn, the magnitude of activity decreased by a factor of 0.99 for each °C of temperature increase. In spring, the magnitude of *M. natalensis* activity decreased when mm of rainfall increased. As wind speed (m/s) increased, the magnitude of *M. natalensis* activity decreased during winter and spring but was not affected during autumn, whilst wind speed in summer positively affected the magnitude of *M. natalensis* activity. Table 4 shows the corresponding summary statistics for nightly (18:00 - 06:00) climatic variables across the four seasons.

Discussion

Understanding the environmental cues that bats may use for migration will aid in their conservation, particularly during crucial life history stages such as the summer maternity season. Contrary to our prediction, our data suggest that the magnitude of activity of the Natal long-fingered bat, *Miniopterus natalensis,* a migratory species of bat in South Africa, is more strongly affected by photoperiod than by climatic variables, including rainfall. The magnitude of *M. natalensis* activity increased exponentially as night length decreased, suggesting that photoperiod is a strong predictive cue in the seasonal activity and migration. Photoperiod is a reliable indicator of seasonal change, likely why various migratory animals use photoperiod as a cue to migrate (Bauer et al. 2011). Literature on how photoperiod affects bats is scarce, but Pettit and O'Keefe (2017) has shown that it likely also cues migration for the Indiana bat *Myotis sodalis*. Physiology and development are strongly coupled to photoperiod (Guenther and Trillmich 2012). Consistent arrival and departure dates of migratory bats (e.g. *Myo. sodalis*) at summer maternity sites indicates that physiology and development are reliable cues for migration (Pettit and O'Keefe 2017). For example, changes in the seasons cues preparation for migration, including fattening in the European migratory common noctule bat *Nyctalus noctula* (Voight et al. 2019) and reproduction in the fringed fruit-eating bat *Artibeus fimbriatus* (Lima and Fabián 2016). The narrow departure dates of *M. natalensis* at the Madimatle cave supports the results that photoperiod is the strongest predictor of activity for this species, but arrival, which was variable between years, is likely modulated by unpredictable climatic events before and during migration from the hibernation site, such as cold snaps, heavy rainfall or high winds (Pettit and O'Keefe 2017).

The climatic drivers of bat migration are not well understood, but temperature, precipitation, barometric pressure, wind speed, photoperiod and lunar illumination, as presented in the current study, may all be additional interdependent factors that affect the decision to migrate, likely through effects on local insect prey availability (Fleming and Eby 2003; Popa-Lisseanu and Voigt 2009). After photoperiod, increases in barometric pressure (except in spring) and minimum temperature (except in autumn) positively affected the magnitude of *M. natalensis* activity. This corresponds to the positive effects of increasing barometric pressure on bat activity (Milne et al. 2005; Berková and Zukal 2010; Bender and Hartman 2015), which has been linked to the positive effects of increasing barometric pressure on insect flight activity (Paige 1995; Fournier et al. 2005). Similarly, warmer temperatures are also associated with increased aerial insect activity (Yela and Holyoak 1997; Meyer et al. 2016) and translate to increased foraging success for bats (Meyer et al. 2004). However, colder temperatures suppress arthropod activity and impose additional thermoregulatory costs on foraging bats (Racey and Speakman 1987). Wind speed negatively affected the magnitude of bat activity in all seasons except for summer, with mean maximum wind speed recorded as 4.89 m/s, which was higher than either winter or autumn mean maximum wind speeds in the present study. This indicates that colder minimum temperatures coupled with faster wind speeds (> 4 m/s) make unsuitable flying and foraging conditions for bats (Linton 2009; Linton and Macdonald 2018). The Limpopo Province experiences mainly summer rainfall, with thunderstorms generally occurring late afternoon (Newbould 2003), supporting why rainfall was not included as an important predictor from the most parsimonious autumn and winter season models. During spring, rainfall during the evenings negatively affected the magnitude of *M. natalensis* activity. The majority of *M. natalensis* migrating to the Madimatle Cave maternity site during springtime consists of pregnant females (Van der Merwe 1975). Wet fur induces increased energetic costs to flying bats (Voigt et al. 2011) and may be particularly costly to reproductive females already under high energetic stress due to lactation (Koehler and Barclay 2000), prompting bats to remain in the cave rather than foraging in the rain.

Results here confirm that this species exhibits predictable and cyclical fidelity to the maternity site in north-eastern South Africa. Van der Merwe (1975) showed that an influx of females occurred during spring (October), and female occupancy lasted until the end of summer (February). Males may remain at the site throughout autumn and winter (Van der Merwe 1975), which our results here generally supports. The spike in the magnitude of activity observed during autumn is likely related to *M. natalensis* male individuals increasing feeding to prepare for hibernation and mating competition (Racey & Entwistle 2000; Dechmann et al. 2014). The lowest magnitude of *M. natalensis* activity was observed during the 2016-2017 period, particularly, the 2016-2017 spring period, compared to either during 2014-2015 or 2015-2017. Similarly, the mean activity over the 157 days of the duration of stay was lower than during the subsequent year. A lower proportion of lactating *M. natalensis* females was captured at this site during 2016, with a significantly higher proportion of the population consisting of sexually immature females compared to either December 2015 or December 2017 periods (Pretorius et al. 2018). This indicates that a lower proportion of females were breeding at the maternity site during 2016-2017, resulting in the lower magnitude of activity levels observed. Interestingly, the magnitude of *M. natalensis* activity was significantly higher during the 2017-2018 period, even though the duration of stay was observably shorter than in previous years. The highest proportion of breeding females was recorded in 2017, with a ~40% increase in breeders from the 2015 or 2016 periods (Pretorius et al. 2018).

Subtropical areas such as South Africa are affected by unpredictable El Niño-Southern Oscillation weather systems (ENSO; Chambers et al. 2013; Brown et al. 2010). From 1977, South Africa has experienced five major El Niño events and of these, the 2014-2016 El Niño episode was the strongest ever recorded (Zhai et al. 2016; Benkenstein 2017; Yin et al. 2018). The 2015-2016 summer rainfall period was characterised by delayed rainfall producing less than 75% of the annual rainfall average and above-average temperatures, signifying severe drought (Benkenstein 2017; Cook et al. 2004). Results from this study reflect this, as the 2015-2016 period had the lowest cumulative rainfall and highest mean temperature recorded. Unpredictable adverse weather conditions affect insect availability (Roberts 1978; Swain 2016), therefore affecting food availability for bats (Cumming and Bernard 1997). This ultimately affects breeding success, reflected by the decrease in *M. natalensis* activity and the proportion of breeding females during the 2015-2016 period (Pretorius et al. 2018). The work presented here further suggests that changes in the magnitude of bat activity may be a proxy for population trends and can be used in population monitoring schemes to an extent (O'Shea and Bogan 2003; Adams 2013). Global climate change is predicted to increase the frequency and duration of adverse weather events such as ENSO (Thornton et al. 2014). Whilst the *M. natalensis* population presented an increased reproductive output during the 2017-2018 period and appeared to reach pre-drought activity levels, the large impact of adverse climate on the population coupled with the apparent limited flexibility of their migratory system, particularly related to departure dates, may make this species vulnerable to changes associated with climate change, and phenological mismatch (Canale and Henry 2010; MacMynowski and Root 2007; Taylor et al. 2016). Our results indicate that longer termmonitoring on more *M. natalensis* sub-populations throughout southern Africa is necessary to evaluate our generalisations.

Conclusion

Animals that use seasonal-specific changes such as photoperiod as migratory cues are at risk in a changing climate (Rosenzweig et al. 2008), as the increasing occurrence of extreme weather events disrupt the timing of seasonal cues and the life history events reliant on these cues (Marra et al. 2011). Monitoring of species' phenology provides insight into their adaptive plasticity to changing environments (Gienapp et al. 2007). Using acoustic monitoring to understand bat activity is an important tool used to understand the ecology of bat populations (Adams 2013; Brigham et al. 2004). Here, acoustic data allowed us to investigate some aspects of the phenology of a southern African migratory bat species, *Miniopterus natalensis* in relation to climatic variables over five years. Results indicated that photoperiod was the greatest predictor of *M. natalensis* activity, more so than other climatic variables, including rainfall or temperature. Whilst arrival dates at the site appeared to be variable, departure dates were similar across the four years, indicating that photoperiod is a cue for this species to migrate away from the site. Decreases in the magnitude of activity during the 2016-2017 sample year reflect a decreased population size and was likely related to drought conditions in the previous 2015-2016 sample year due to El Niño effects. Although the population appeared to recover after the drought period, their reliance on photoperiod as a migratory cue, their predictable departure dates from the site and the negative effects of adverse climate on their breeding success may make *M. natalensis* vulnerable to phenological mismatch and population decline in a changing climate. The need for continued systematic population monitoring for this species is thus highlighted. This research provides crucial life history information as an important step toward the conservation of cave-dwelling bats in South Africa.

Conflicts of interest

The authors declare no conflicts of interest.

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Tables

Table 1. Arrival date, departure date, days between arrivals and departures and duration of stay of *Miniopterus natalensis* bats across four sample years at the Madimatle Cave, Limpopo, South Africa

Mean activity ± Standard Error in last column followed by the same letters in bold (a, b and ab) are not significantly different ($p < 0.05$) according to Kruskal-Wallis pairwise post-hoc test.

Year sample	**Arrival date**	**Days between arrivals**	**Departure date**	**Days between departures**	**Duration of stay (days)**	**Mean activity ± SE over duration of stay**
2014-2015	29/09/2014	345	04/02/2015	369	129	310.90 ± 10.45 **ab**
2015-2016	18/09/2015	348	08/02/2016	361	137	308.33 ± 12.17 **ab**
2016-2017	31/08/2016	431	03/02/2017	366	157	250.84 ± 13.22 **b**
2017-2018	05/11/2017	/	04/02/2018	/	92	358.05 ± 11.55 **a**

Table 2. Ranked Akaike Information Criterion (AIC) general linear regression models of climatic factor effects on the nightly activity of *Miniopterus natalensis*

Climatic variables are night length, minimum nightly temperature (MinTemp), nightly dew point (DewP), nightly maximum wind speed (MaxWind), nightly barometric pressure (Bar), nightly humidity (Humid) and cumulative rainfall per night (Rain). The most parsimonious models are indicated in bold.

Season	**Model**	***df***	**AIC**	**ΔAIC**	**Weight**
Autumn	NightL + MinTemp + DewP + Maxwind + Bar + Humid	**7**	**10888.30**	**0.00**	**0.53**
	NightL + MinTemp + DewP + Maxwind + Bar + Humid + Rain	8	10888.50	0.21	0.47
	MinTemp + Maxwind + Bar + Humid	5	11172.20	283.95	0.00
Winter	NightL + MinTemp + DewP + Maxwind + Bar + Humid	**7**	**6094.3**	**0.00**	**0.68**
	NightL + MinTemp + DewP + Maxwind + Bar + Humid + Rain	8	6095.80	1.47	0.32
	MinTemp + Maxwind + Bar + Humid	5	8261.80	2167.52	0.00
Spring	NightL + MinTemp + DewP + Maxwind + Bar + Humid + Rain	**8**	**15933.50**	**0.00**	**0.97**
	NightL + MinTemp + DewP + Maxwind + Bar + Humid	7	15940.50	6.96	0.03
	NightL + DewP + Maxwind + Bar + Humid + Rain	7	15962.40	28.81	0.00
Summer	NightL + MinTemp + DewP + Maxwind + Bar + Humid	**7**	**15369.90**	**0.00**	**0.67**
	NightL + MinTemp + DewP + Maxwind + Bar + Humid + Rain	8	15371.30	1.39	0.33
	NightL	2	16092.50	722.59	0.00

Table 3. Parameter estimates, standard error and associated z-values for variables in the best candidate models with several climatic variables for explaining the activity of *M. natalensis* bats across four seasons (autumn, winter, spring and summer) at the Madimatle Cave, Limpopo, South Africa

Variable	**Autumn**			**Winter**			**Spring**			**Summer**		
	Estimate	SE	Z-value	Estimate	SE	Z-value	Estimate	SE	Z-value	Estimate	SE	Z-value
Intercept	-6.06e+01	2.14e+00	- 28.34	12.08	2.78	4.32	15.31	0.85	17.96	1.46e+01	9.99e-01	14.64
Night length	-4.14e-01	2.44e-02	-16.91	-2.29	0.04	-47.06	-0.88	0.01	-83.77	-1.97	1.52e-02	-129.30
Minimum temperature (°C)	-1.44e-02	3.24e-03	-4.46	0.03	3.17e-03	9.99	7.02e-03	1.26e-03	5.55	7.75e-03	1.67e-03	4.63
Dew point (°C)	-5.26e-03	2.47e-03	-2.12	2.89e-03	2.23e-03	1.24	9.94e-03	7.86e-04	12.64	1.98e-02	8.84e-04	22.44
Maximum wind speed (m/s)	-2.53e-04	4.11e-03	-0.06	-0.04	5.40e-03	-7.70	-0.02	1.56e-03	-12.94	3.05e-03	1.41e-03	2.16
Barometric pressure (mbar)	6.75e-02	2.19e-03	30.82	0.02	2.69e-03	7.74	3.98e-04	8.90e-04	-0.44	1.12e-02	9.46e-04	11.89
Humidity (%)	2.34e-02	6.08e-04	38.52	-8.36e-03	9.46e-04	-8.83	6.03e-03	2.39e-04	25.27	-6.18e-06	2.40e-04	-0.02
Cumulative rainfall (mm)	-	-	-	-	-	-	-5.53e-03	1.85e-03	-2.98	-	-	-

Table 4. Summary statistics of mean nightly climatic variables (calculated between 18:00 – 06:00) and the associated 95% confidence intervals (CI) across autumn, winter, spring and summer (*N* in parentheses) at the Madimatle Cave, Limpopo, South Africa

Variable	**Autumn (330)**		**Winter (356)**		**Spring (364)**		**Summer (354)**	
	Mean	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**
Night length (hours)	12.36	0.05	13.10	0.03	11.37	0.06	10.64	0.03
Minimum temperature (°C)	14.18	0.44	7.79	0.43	17.43	0.37	19.96	0.23
Dew point (°C)	13.86	0.40	3.73	0.47	5.39	0.60	14.64	0.42
Maximum wind speed (m/s)	2.88	0.21	3.14	0.25	6.23	0.26	4.89	0.24
Barometric pressure (mbar)	1013.75	0.48	1022.95	0.40	1015.36	0.56	1009.47	0.36
Humidity (%)	70.72	1.36	51.56	1.48	46.38	1.81	67.00	1.73
Cumulative rainfall (mm)	0.68	0.34	0.09	0.06	0.34	0.18	1.59	0.57

Figures

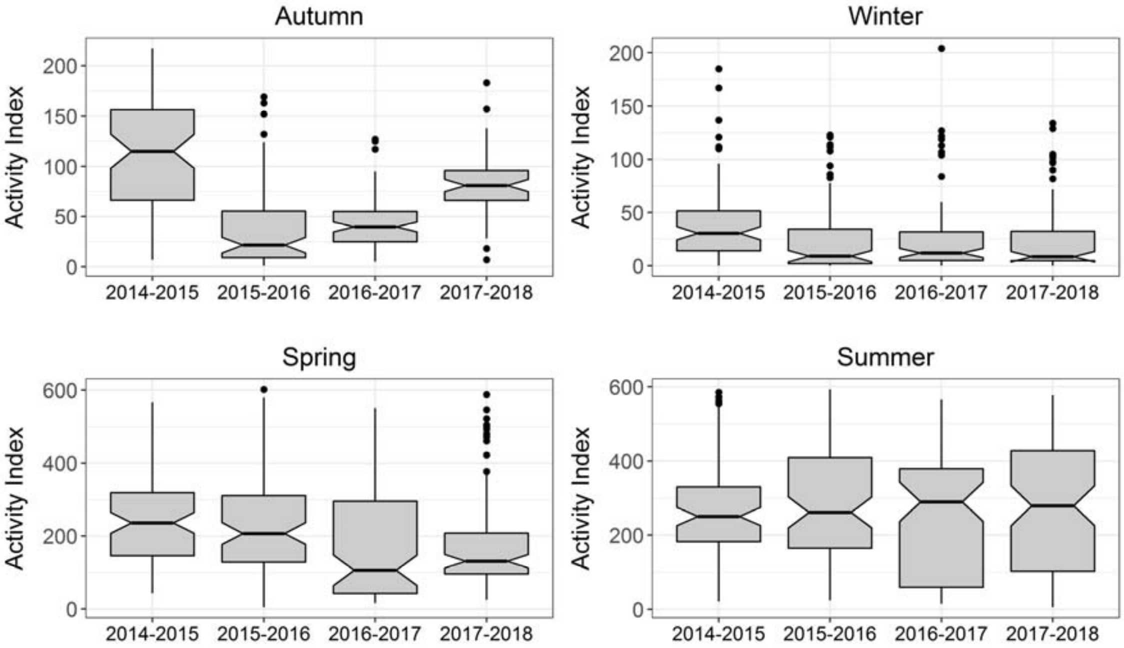

Fig. 1. Boxplot showing medians and interquartile ranges (IQR; Tukey-style whiskers extend to 1.5 _ IQR) at 95% confidence intervals (notches) of *Miniopterus natalensis* activity index (number of 1-min periods of detection per night) per season for 4-year sample periods collected at the Madimatle Cave, Limpopo, South Africa. Year sample periods range from 20 March to 19 March the next year and consist of *M. natalensis* echolocation call data from 2014–15, 2015–16, 2016–17 and 2017–18. Notches of boxes that do not overlap indicate significant differences in the magnitude of *M. natalensis* activity among samples. Outliers are indicated by black dots. Note the different scales on the *y*-axis of each season indicating variable activity levels.

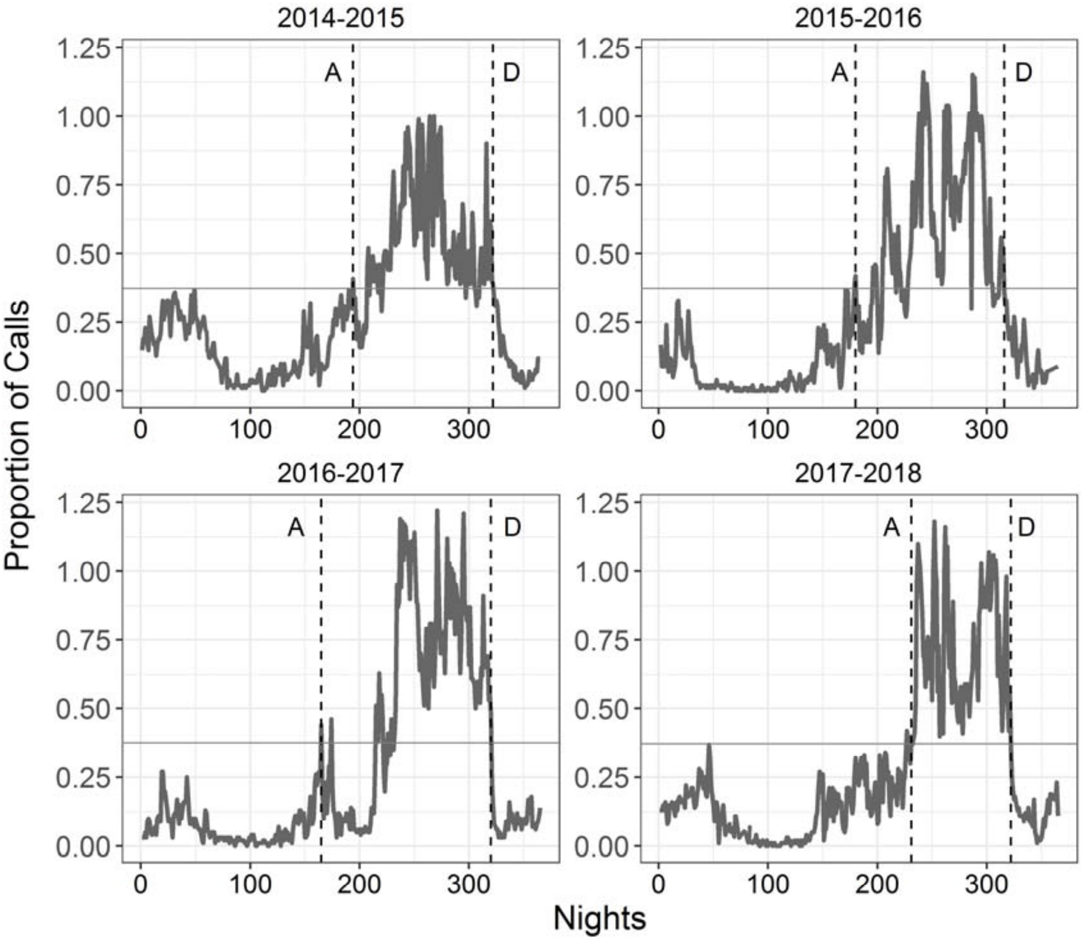

Fig. 2. Proportion of *Miniopterus natalensis* calls for 365 nights across 4-year sample periods: 2014–15; 2015–16; 2016–17; and 2017–18. Proportions of calls per night were calculated for each sample period using total activity index (the sum of detected 1-min bat passes per night) from echolocation calls recorded throughout each night from March 2014 to March 2018. Vertical dashed lines marked 'A' denote arrival and dashed lines marked 'D' denote departure of migratory bats at the Madimatle Cave, Limpopo, South Africa. The sections between the two lines are denoted as the summer breeding period. The darkened horizontal line at 0.40 indicates the threshold used to score arrival and departure.

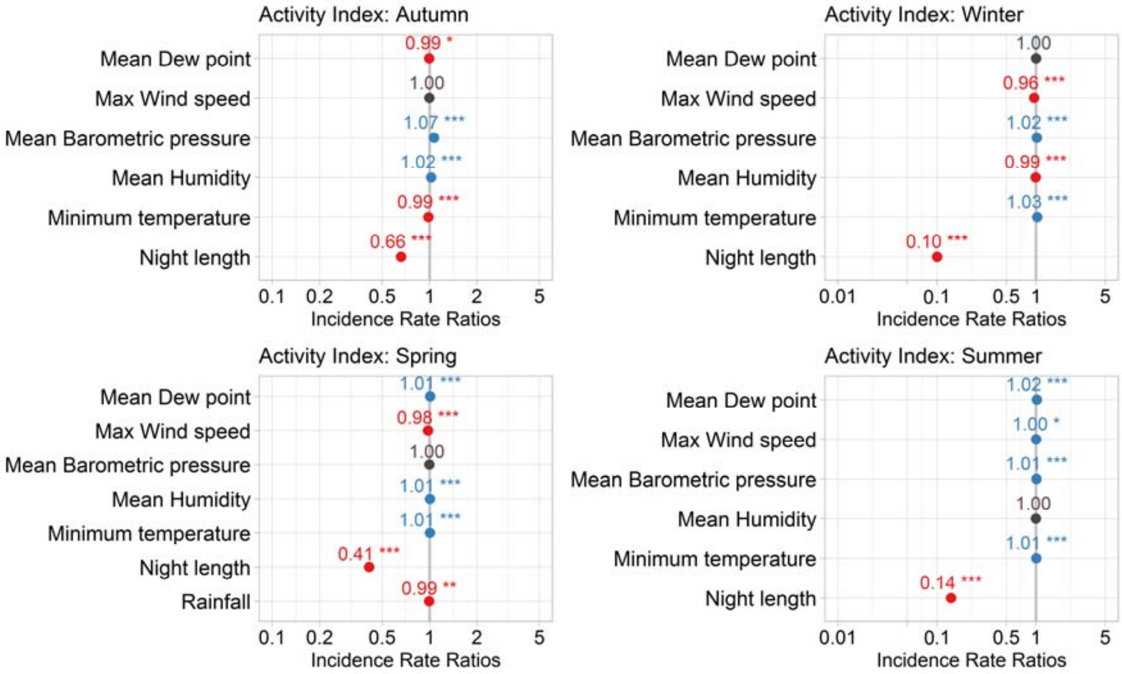

Fig. 3. Plotted incidence rate ratios (IRRs) of exponentiated estimates for climatic variables predictors (night length, nightly minimum temperature, nightly dew point, nightly maximum wind speed, nightly barometric pressure, nightly humidity and average cumulative rainfall per night) from the candidate general linear regression models assessing their effect on the activity index (the sum of detected 1-min bat passes per night) of *Miniopterus natalensis* across four seasons at the Madimatle Cave, Limpopo, South Africa. Estimates falling on IRR ¼ 1 indicate no effect (dark grey dots without '*'), IRR , 1 indicates a negative effect (black dots) and IRR . 1 indicates a positive effect (light grey dots). Dots are labelled with their corresponding exponentiated estimate values. Asterisks indicate significance levels of P-values (*P , 0.05, **P , 0.01, ***P , 0.001).

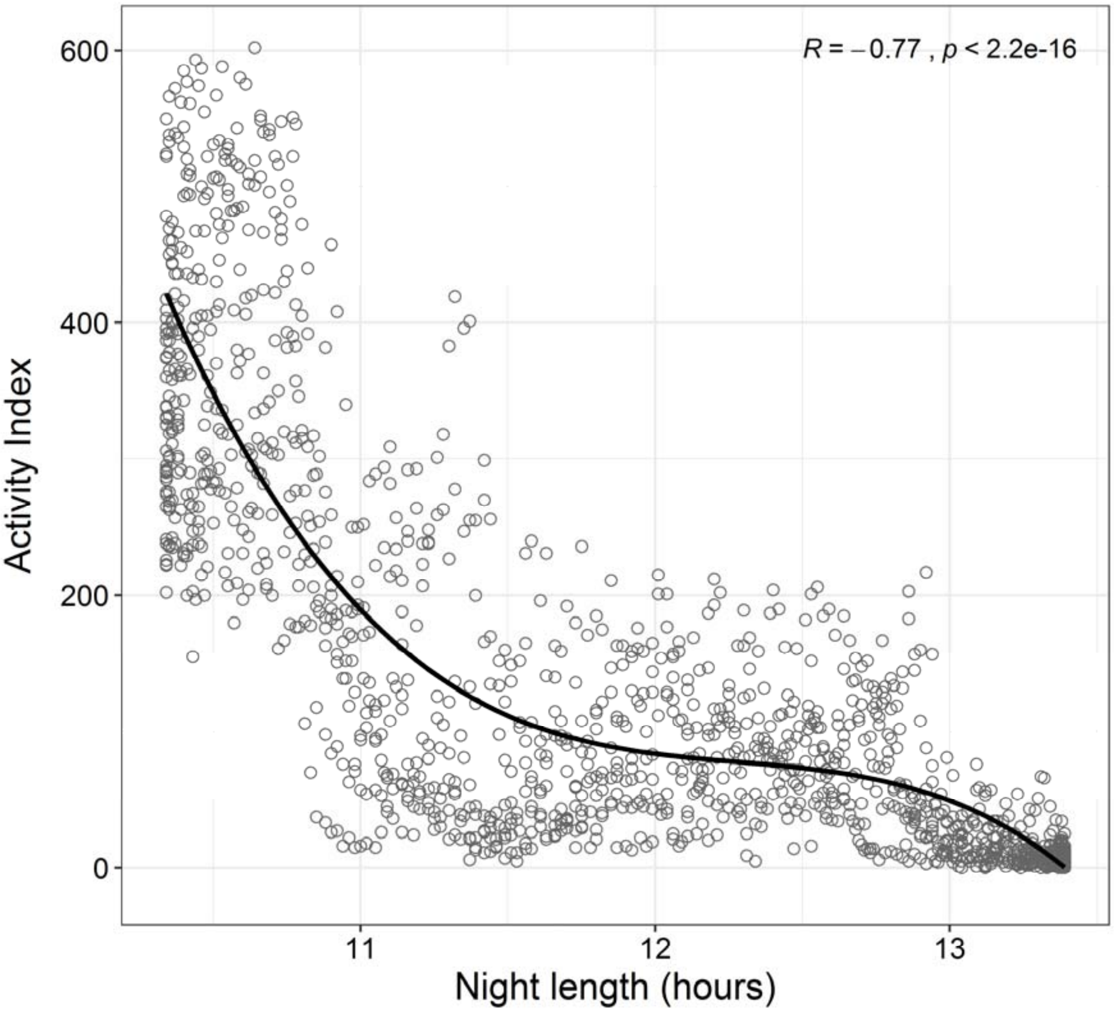

Fig. 4. The relationship between the nightly activity index (the sum of detected 1-min bat passes per night) of *Miniopterus natalensis* and night length (photoperiod) over four equal 365-day sample periods (2014–15, 2015–16, 2016–17 and 2017–18) at the Madimatle Cave, Limpopo, South Africa.