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Ghost bats exhibit informative daily and seasonal temporal patterns in the production of social vocalisations

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Abstract. The ghost bat (*Macroderma gigas*) is a colonial and highly vocal species that is impacted by human visitation of caves. The ability to document behaviours inside the roost by recording vocalisations could provide an important new tool for the management of this disturbance-prone species by removing the need for in-person confirmation of reproductive activity, and, in turn, identifying roosts of conservation importance. To assess whether vocalisations are indicators of daily and seasonal behavioural events, we aimed to determine whether total vocal activity significantly varied by time of day and time of year and, further, how the relative frequencies of occurrence of three common social vocalisations ('Chirp-trill', 'Squabble' and 'Ultrasonic Social') aligned with previously reported seasonal reproductive behaviour. We recorded sound inside the largest known maternity roost, extracted all vocal signals and classified them into types using semiautomated methods. Total vocal activity varied significantly by time of day and time of year, peaking around sunrise and sunset, and during the mating and nursing seasons. The relative frequencies of occurrence of vocalisation types varied significantly seasonally, with the Chirp-trill and Squabble produced most during the mating season and first flight periods, whereas the Ultrasonic Social peaked during parturition and weaning periods. This timing aligns with a previously suggested vocalisation function, providing further evidence that these signals are important in mating and maternity behaviours. Further, this suggests that peaks in the relative frequency of occurrence of distinct social vocalisations may act as indicators of in-roost reproductive and pup development behaviours and provides a low-disturbance, semiautomated method for using long-term acoustic recordings to study and monitor behaviour in this sensitive species.

Keywords: Chiroptera, *Macroderma gigas*, threatened species, social communication, in-roost behaviour, acoustic, reproduction, semiautomated classifier.

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Introduction

Acoustics have been at the forefront of chiropteran research for decades (Griffin *et al*. 1960; Neuweiler 1989) because the detection of species-specific echolocation calls is a convenient and standardised method for determining the composition of bat community assemblages (Yates and Muzika 2006; MacSwiney *et al*. 2008; Adams *et al*. 2012). At present the role of sound in bat social communication is receiving increased attention, with bats now known to produce a variety of function-specific calls and songs (e.g. territorial defence: Behr *et al*. 2006; Smarsh 2015; Knörnschild *et al*. 2017; mate attraction: Adams and Snode 2015; contact: Esser and Schmidt 1989; Knörnschild and von Helversen 2008; Arnold and Wilkinson 2011; Carter *et al*. 2012; Gillam and Chaverri 2012; Montero and Gillam 2015; aggression: Bastian and Schmidt 2008; Jiang *et al*. 2016; Prat *et al*. 2016; Walter and Schnitzler 2019; appeasement: Clement and Kanwal 2012; Gadziola *et al*. 2012; distress: Russ *et al*. 2004; Carter *et al*. 2015; Eckenweber and Knörnschild 2016; Huang *et al*. 2018; Wu *et al*. 2019). Many social vocalisations have strong functional links to specific behaviours or behavioural contexts (Bohn *et al*. 2008; Gadziola *et al*. 2012; Bohn *et al*. 2013; Prat *et al*. 2016, 2017), suggesting that such vocalisations can be useful for studying non-vocal behaviours in bats by acoustic proxy. Despite this potential, the use of acoustic signals has largely been limited to presence–absence studies and has rarely been used to investigate social behaviour in bats (but see Andrews *et al*. 2017).

The ghost bat (*Macroderma gigas*; Megadermatidae, 150 g) is a highly social and vocal species that forms large colonies in subterranean structures in northern Australia (Toop 1985; Churchill 2008). Population numbers are currently in decline, in part because the ghost bat is adversely affected by human visitation at its roosts (Armstrong and Anstee 2000). Thus, passive acoustic monitoring techniques could be an important tool for monitoring this disturbance-sensitive and cryptic species. The functions of several of the ghost bat's social vocalisations have been suggested but are based solely on short-term captive behavioural observational studies or anecdotal evidence. Little is known about temporal patterns in the production of these vocalisations, and correlations between vocalisation types and daily and seasonal events can provide further information on function, ultimately acting as acoustic indicators of these events. Our study focussed on a maternity roost located in the Top End of the Northern Territory. We based the timing of mating and parturition on the accounts specific to the Northern Territory provided in Churchill (2008). From this, we adapted the timing of crèching and first flight periods relative to parturition based on estimates in Toop (1985) from northern Queensland colonies. In the Northern Territory, the ghost bat mating season occurs from April to May (Churchill 2008), and is followed by parturition in July to August after 11–12 weeks of gestation (Churchill 2008). Pups are carried by the mothers until they are four weeks of age (August–September) when they are crèched in a roost nursery (Toop 1985). At seven weeks, the pups first become volant ('first flight') and join their mothers in foraging, beginning in late August, before they are weaned completely by March (Churchill 2008). Each of these life history events, from mating to weaning, can be expected to have its own specific patterns of vocal activity based on vocalisations that are associated with that behaviour (e.g. mating calls in epauletted fruit bats: Adams and Snode 2015; pup isolation calls in Mexican free-tailed bats: Balcombe 1990), and, as such, can potentially be identified acoustically.

To examine the acoustic signature of key behavioural events, we passively recorded ghost bat vocalisations at the largest known colony. We optimised an algorithm to extract ghost bat vocalisations from recordings and constructed a second purpose-built algorithm to classify these vocalisations into type. Using these data, we aimed to determine whether total vocal activity varied across short-term (daily) and longer-term (seasonal) time scales. Further, we investigated whether specific structural types of vocalisations correlated with daily (e.g. sunrise and sunset) or seasonal (reproductive) events, and so provide insight into vocalisation function.

Materials and methods

Study subject and site

Our study was based in the Top End of the Northern Territory (Australia). This region has two distinct meteorological seasons: the wet season, beginning with the 'build-up' – a period of high humidity and thunderstorms from October to December and followed by monsoonal rains until April; and the dry season, characterised by low humidity and no rain, and taking place between May and September (Cook and Heerdegen 2001).

Ghost bats roost throughout several old mine workings in the vicinity of Pine Creek township (13.8°S, 131.8°E), one of which, Kohinoor adit, supports the largest known congregation of this species. This mine shaft is occupied year-round and is used for mating and parturition through to weaning of juveniles. Surveys conducted irregularly between 1981 and 2010 reported colony sizes from 300 to 1500, with the highest count recorded in July 1990 (Woinarski *et al*. 2014). Seasonal events greatly impact on colony size and demographic composition, such as the influx of males during the mating season, and the addition of pups produced by over half of females during the parturition period (Toop 1985).

Acoustic recording

Vocalisations were recorded inside the mine shaft in the centre of the main roosting area using an SM3Bat acoustic recorder (Wildlife Acoustics, MA, USA), set to record in full-spectrum format at a sampling rate of 256 kHz via an ultrasonic microphone (SMM-U1). The microphone was positioned at a 45° angle towards the roosting bats that were ~10 m away on the roost ceiling. To avoid causing disturbance, the recorder was installed and maintained at night after the colony had left the roost to forage.

The recorder was programmed to turn on for a period of 5 min during which it could be triggered to record a 15 s file if the amplitude of ambient sounds exceeded 12 dB. After 5 min, the recorder was programmed to sleep for 30 min before repeating this cycle. This schedule resulted in a moving recording window that allowed all times over the 24-h day to be sampled over a seven-day period.

Recordings were collected over a period of 2.5 years (22 March 2016 to 15 September 2018). Within this timeframe, acoustic data were successfully collected for the following periods: 22 March to 29 April 2016; 16 September to 16 October 2016; 13 to 29 November 2016; 9 December 2016 to 9 March 2017; 20 March to 7 April 2017; 1 March to 17 April 2018; 8 May to 13 June 2018; and 23 August to 15 September 2018. No data were collected in July in any year. Equipment failure was responsible for gaps in the data, including due to depleted battery power and memory card corruption.

Target vocalisations

In this study, we focussed on three common and structurally distinct ghost bat social vocalisations: the 'Chirp-trill', 'Squabble', and 'Ultrasonic Social' (defined in Hanrahan 2020) (Fig. 1). Briefly, the 'Chirp-trill' vocalisation is very common in the ghost bat's repertoire and consists of two previously described vocalisations: the Chirp (first described by Kulzer *et al*. 1984) and the Trill (briefly mentioned in Milne 2002). Subsequent semiautomated analysis of the ghost bat's repertoire grouped the Chirp and Trill into one vocalisation type (Hanrahan 2020) and therefore is referred to here as the Chirp-trill. The Chirp-trill has been suggested to function as a contact call while foraging (Tidemann *et al*. 1985) although a male-biased use of the Chirp-trill associated with resource

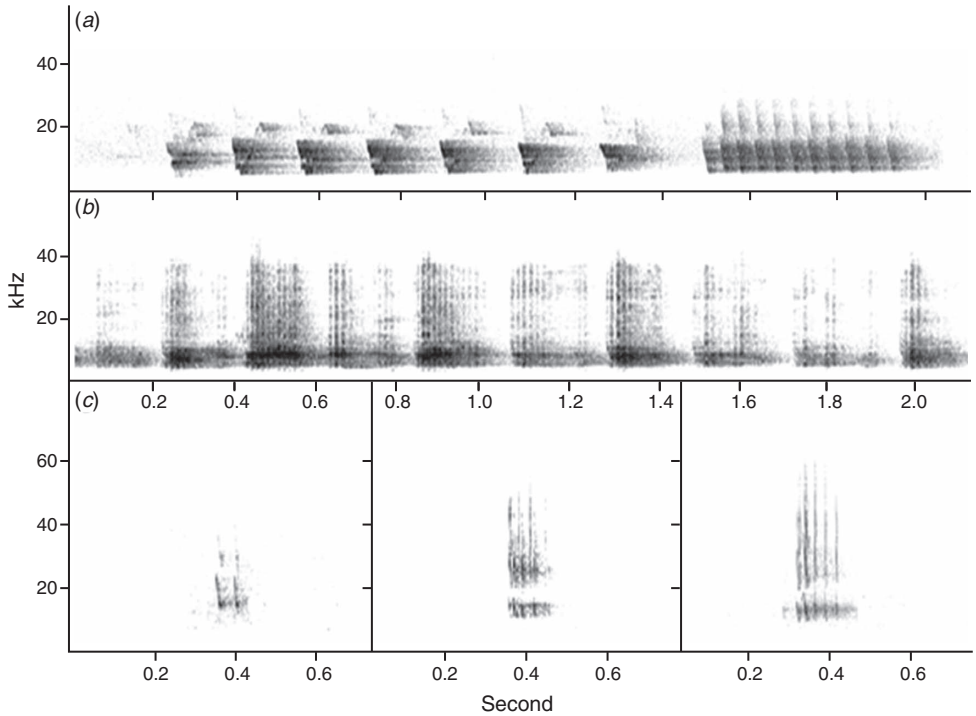

Fig. 1. Spectrograms of the three target vocalisations: (*a*) Chirp-trill, (*b*) Squabble, and (*c*) Ultrasonic Social vocalisation (three variants).

defence and during mating attempts was observed in captivity (authors' unpubl. data). The Squabble is an agonistic vocalisation produced during altercations over resources such as food or roosting space (Guppy *et al*. 1985) and unwanted mating attempts (authors' unpubl. data). Several social vocalisations in the ghost bat's repertoire are in the ultrasonic range ('Ultrasonic Communication Signals': Guppy *et al*. 1985; 'Ultrasonic Social' vocalisations: Hanrahan 2020) (the latter term is used in this study) and are reminiscent of the ghost bat's echolocation call, although, like the 'Chirp-trill' and 'Squabble', it is used in a social rather than an orientation context (Guppy *et al*. 1985). For the purpose of this study we have grouped the variants of the Ultrasonic Social vocalisations into one class.

Classification of vocalisations

Passive acoustic monitoring often generates enormous quantities of data, which poses considerable challenges for postprocessing; however, processing can be expedited with specially designed species- or vocalisation-specific detectors and classifiers (Bittle and Duncan 2013; Binder and Hines 2014; Zhao *et al*. 2017; Kawakita and Ichikawa 2019). To detect ghost bat vocalisations within the recordings, a band limited energy detector (BLED) was designed in Raven Pro 1.5 (Bioacoustics Research Program 2014). The BLED was designed to detect calls measuring from 0.02 to 5 s in duration, falling between 2 and 80 kHz with a maximum intersyllable spacing of 0.1 s and a signal to noise ratio filter of above 10 dB. The window settings were Hann window with DFT of 1024 and a 50%-time grid overlap. The detector was run in batch mode, which allowed ~1500 files to be processed in a single run.

The following spectrographic measurements (Table 1) were collected for each detection: bandwidth (including 90% bandwidth, interquartile bandwidth), entropy (including minimum entropy, maximum entropy, aggregate entropy), frequency (including peak frequency, peak frequency contour (PFC) minimum frequency, PFC maximum frequency), duration and peak time (Charif *et al*. 2010). These variables were chosen from the multitude available in Raven because we identified them as the most informative for separating known distinct ghost bat vocalisation types, and they were not highly correlated ($r_s < 0.8$) with each other.

To determine when vocalisations of each type were present in our extensive dataset, a purpose-built algorithm ('*Macroderma gigas* classifier': 'MAGIC') was designed in R (R Core Team 2017). From the detections, 50 high-quality exemplars of each vocalisation type were manually selected that had low signal to noise ratios, were not clipped, and did not contain overlapping vocalisations. Using discriminant function analysis, a reference dataset from the exemplars was constructed, and an ellipse defining one standard deviation from the centroid of that vocalisation type was created. Unclassified detections were then plotted using the linear discriminants from the reference set. Detections that fell within the ellipse of a particular vocalisation type were identified as that vocalisation type and extracted for further analysis.

Statistical analysis

All statistical analyses were completed using the R platform (R Core Team 2017).

Table 1. Measurements used to differentiate vocalisation types
Adapted from Charif *et al*. (2010)

Measurement	Description
Aggregate entropy	The aggregate entropy measures the disorder in a sound by analysing the energy distribution within a detection. Higher entropy values correspond to greater disorder in the sound, whereas a pure tone with energy in only one frequency bin would have zero entropy.
Bandwidth 90%	The difference between the 5% (the frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in the selection) and 95% (the frequency that divides the selection into two frequency intervals containing 95% and 5% of the energy in the selection) frequencies.
Interquartile range (IQR) bandwidth	The difference between the 1st (the frequency that divides the selection into two frequency intervals containing 25% and 75% of the energy in the selection) and 3rd (the frequency that divides the selection into two frequency intervals containing 75% and 25% of the energy in the selection) quartile frequencies.
Length (proxy for Duration)	The number of frames contained in a selection. The number of frames equals the number of individual spectra in the selection in one channel.
Maximum entropy	The highest entropy value from across the sample. Entropy is recorded at each bin across the sample.
Minimum entropy	The lowest entropy value from across the sample.
Peak frequency	The frequency at which the signal is at its highest intensity.
Peak time	The first time in the selection that a signal reaches its peak amplitude (loudest point). Measured in seconds.
Peak frequency contour (PFC) maximum frequency	The PFC is the frequency at which the signal is at its highest intensity measured at multiple horizontal slices across the entire signal and joined to form the contour. The PFC maximum frequency is the highest frequency recorded along that contour within a signal.
PFC minimum frequency	The PFC minimum frequency is the lowest frequency recorded along the PFC within a signal.

Total vocal activity

To determine whether total vocal activity was significantly affected by daily and annual time periods we used linear regression ('lm' function from the 'stats' package: R Core Team 2017) with the global model consisting of total vocalisations per hour as the response variable, and hour, month and year as explanatory variables. Total vocalisations included all ghost bat signals detected inside the roost, including social vocalisations and echolocation calls. We chose to include social vocalisations as a measure of vocal activity for three reasons: (1) echolocation calls produced by species of the Megadermatidae are of low amplitude (Möhres and Kulzer 1957) and thus inconsistently detected, (2) ghost bats do not consistently use echolocation when in flight (Guppy *et al*. 1985), and (3) echolocation alone would not allow us to quantify all activity including when the bat is perched. All variants of the global model were modelled including interactions between the explanatory variables, hour and month, and month and year. The resultant models were ordered by AICc (Akaike Information Criterion corrected for small sample size) score and the model with the lowest score was chosen as the best (Barton 2018).

Relative frequencies of occurrence of distinct vocalisation types

To test for the effect of hour, month and year on the relative frequencies of distinct vocalisation types we used multinomial logistic regression using the 'nnet' package and 'multinom' function (Ripley *et al*. 2016). Our dataset consisted of all signal detections with all detections classified into one of four classes of vocalisation type. Three of the classes were represented by the target vocalisations (Chirp-trill, Squabble and Ultrasonic Social) and the fourth class contained all remaining unclassified detections of ghost bat signals, including echolocation calls ('Other'). Vocalisation type was used as the response variable with class Other used as the baseline factor level. The explanatory variables were hour of the 24-h day, month of the year, and year. The explanatory variables were modelled as additive effects in the same model, separately, and as interactions (hour and month, and month and year). These models were ordered based on AICc score and the best model was chosen based on the lowest value (Barton 2018). We used likelihood ratio tests to determine the significance of each variable using 'Anova' (Type III) from the 'car' package (Fox *et al*. 2012).

Results

Colony vocal activity patterns

In total, 854 906 ghost bat signals (social vocalisations and echolocation calls) were detected in our dataset. The vocal activity of the ghost bat colony varied with the time of day, with month and with year. Linear regression ($F_{268,6047} = 18.75$, $P < 0.001$) showed a significant effect of hour ($F_{23,6292} = 48.47$, $P < 0.001$), month ($F_{10,6305} = 77.47$, $P < 0.001$), and year ($F_{2,6313} = 308.20$, $P < 0.001$) on total detections of ghost bat vocalisations per hour. Over 24 h, total vocal activity peaked between 0500 and 0700 hours, before sunrise (Fig. 2*a*). Total vocal activity peaked for a second time between 1800 and 2000 hours, spanning the period before and after sunset. When the effect of month was examined, total vocal activity reached a maximum in October, coinciding with the estimated crèching and first flight periods (Fig. 2*b*). Despite a drop in November, total activity remained high through to January during the dependent juvenile period. Total activity then declined steadily through to March before rising again in April, at the start of the mating season. Total vocal activity

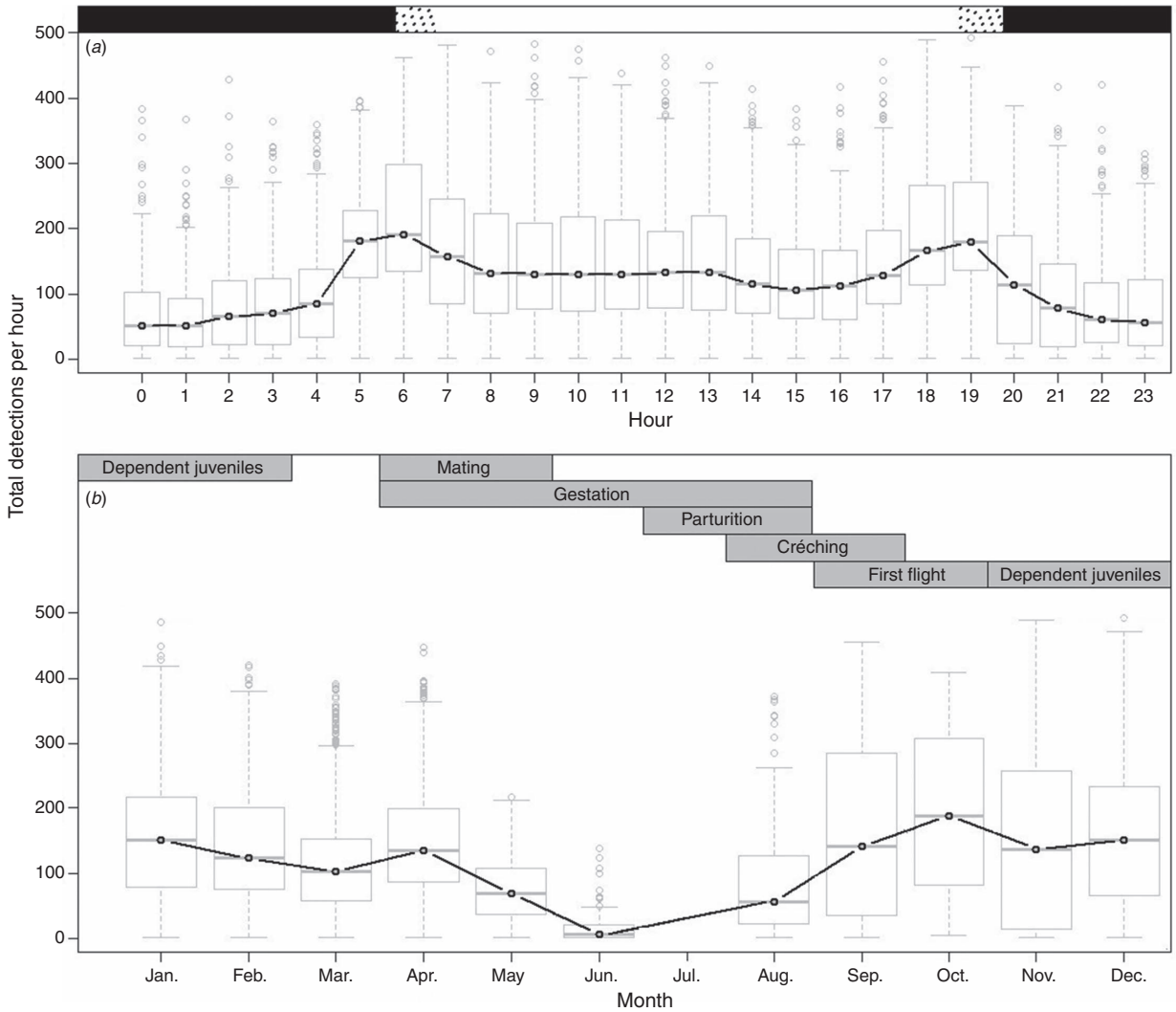

Fig. 2. (*a*) Total detections per hour, over the study period (March 2016 to September 2018). Total detections include all ghost bat signals detected, i.e. echolocation calls, the target social vocalisations and social vocalisations not targeted in this study. The black band above the graph indicates the dark photoperiod while the white band indicates the light photoperiod. Stippling indicates the range of minimum and maximum morning and evening astronomical twilight over the period of a year, obtained from Geoscience Australia (http://www.ga.gov.au/). (*b*) Total detections per hour by month. Data have been combined for months that have data from multiple years. The thick grey lines represent the median, grey boxes show the interquartile range, and the whiskers show the upper and lower extremes of the data. Open grey circles represent outlier data. The black line and circles show the median hourly (Panel *a*) and monthly (Panel *b*) trend in total detections per hour. Biological seasons are indicated at the top of Panel *b*.

then steeply fell, reaching a minimum in June, during the gestation period, before rising quickly over the parturition period (July–August).

The daily pattern of vocal activity also differed significantly with time of year (interaction term hour × month: $F_{263,6052}$ = 14.938, $P < 0.001$). Distinct peaks in vocal activity were observed at sunrise and sunset in January, February, March, April, May and August but these peaks were masked by high diurnal vocal activity in other months (September–December), coinciding with crèching, first flight and dependent juvenile periods. In June, overall vocal activity was low with no sunrise or sunset peaks observed. Vocal activity within each month also differed by year (interaction term month × year: $F_{263,6052}$ = 14.938, $P < 0.001$), with vocal activity in March and April in 2016 significantly higher than the same months in 2018, two of the three months for which data were available in more than one year (Supplementary Fig. S1).

Patterns by vocalisation type

Vocalisation detections were broken down into 126 438 detections of the Chirp-trill, 30 808 of the Squabble, 59 863 of the Ultrasonic Social and 637 797 Other vocalisations. Different vocalisation types dominated colony vocal activity at different times of day and season. A multinomial regression model fitted to explain relative frequency of occurrence of the

three structural types of social vocalisations ($\chi^2_{792} = 33909.03$, $P < 0.001$) included the effect of hour ($\chi^2_{69} = 5147.81$, $P < 0.001$), month ($\chi^2_{30} = 21308.21$, $P < 0.001$) and year ($\chi^2_{3} = 3600.59$, $P < 0.001$) (Figs 3, 4).

The relative frequency of occurrence of the Squabble peaked in the early morning at 0200 hours, before declining steadily until sunrise, when the production of the Squabble began to increase again and remained high throughout the day (Fig. 3*a*). The relative frequency of occurrence of the Squabble then decreased briefly after sunset before rising again until 0200 hours. The relative frequency of occurrence of the Chirp-trill followed a similar pattern but lacked the early morning peak. In addition, a midday decrease in the relative frequency of occurrence of the Chirp-trill was observed (Fig. 3*b*). The Ultrasonic Social vocalisation pattern was distinctly different, with the highest relative frequency of occurrence recorded during the night and the lowest before sunset (Fig. 3*c*).

The Squabble and Chirp-trill showed similar monthly patterns, with the first peak beginning in April, the start of the mating season and continuing through to the end of the mating season in May, nearly doubling the frequency of occurrence recorded in March (Fig. 4*a*). The second peak occurred in October during the first flight period (Fig. 4*b*) after a steady increase beginning in June for the Squabble (an increase of 56%) and August in the Chirp-trill (an increase of 25%). The relative frequency of occurrence of the Ultrasonic Social vocalisation began to increase in May (when females were likely to be pregnant) and doubled by August (the final month

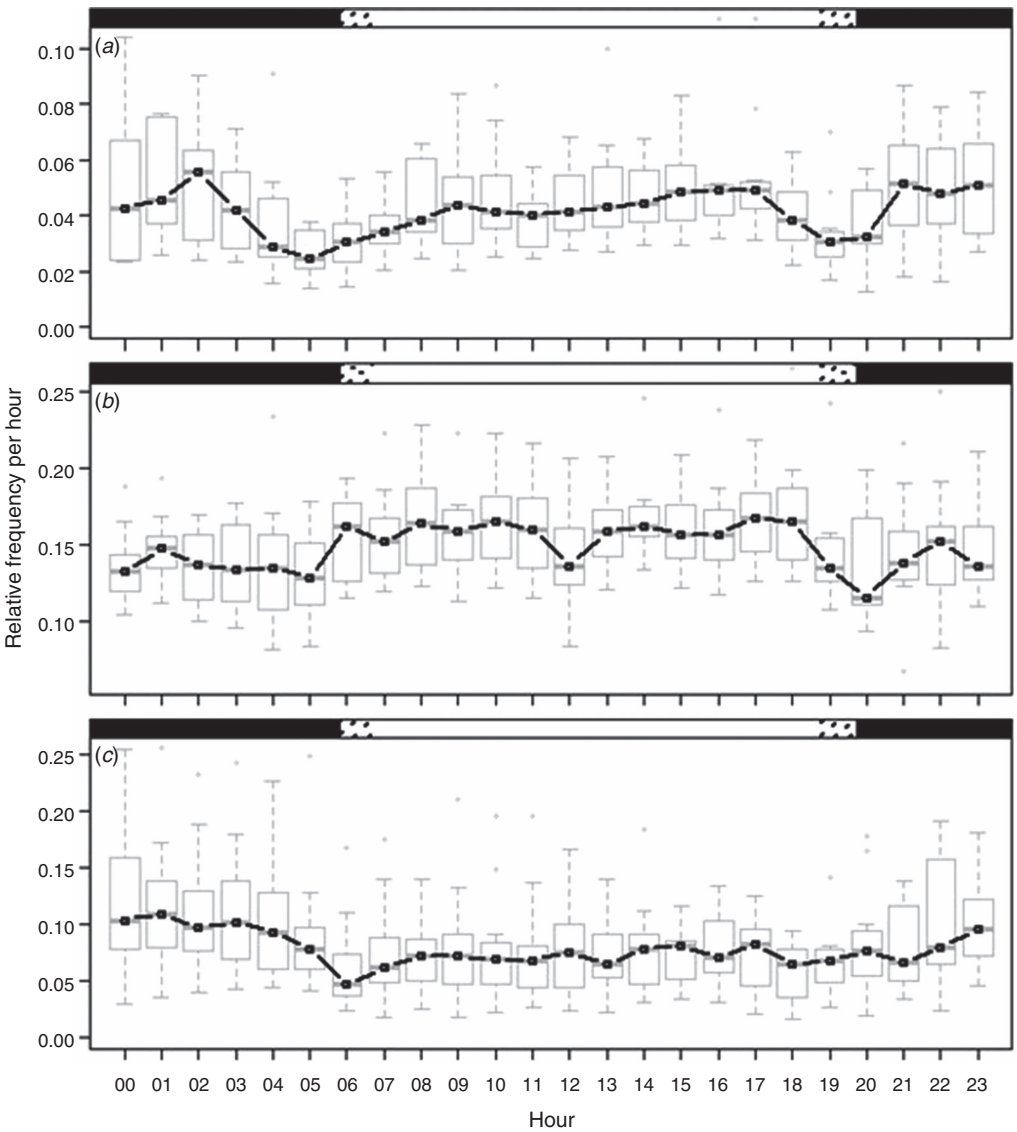

Fig. 3. Relative hourly frequency of occurrence of the (*a*) Squabble, (*b*) Chirp-trill and (*c*) Ultrasonic Social vocalisations over a 24-h period. The bar plot shows the median values (horizontal thick line), interquartile range (grey box) and the 1st and 4th quartiles (whiskers). The black line denotes the median value trend. The black band outlines the dark photoperiod and the white illustrates the light photoperiod; stippling indicates the range of minimum and maximum morning and evening astronomical twilight over the period of a year.

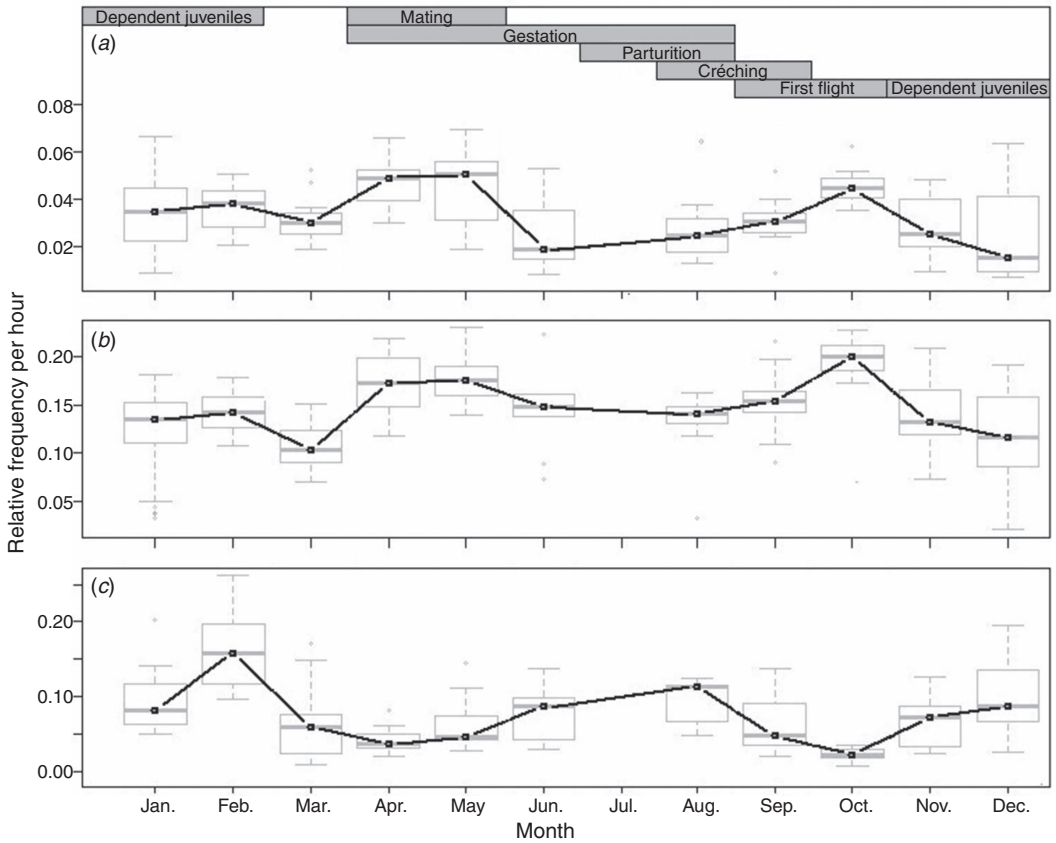

Fig. 4. Relative hourly frequency of occurrence per month of the (*a*) Squabble, (*b*) Chirp-trill and (*c*) Ultrasonic Social (no data for July). The bar plot shows the median values (horizontal thick line), interquartile range (grey box) and the 1st and 4th quartiles (whiskers). The black line denotes the median value trend. Data have been combined for months that have data from multiple years. Biological seasons are indicated at the top of Panel *a*.

of parturition). A striking peak in relative frequency of occurrence was also observed in February when juveniles are volant and in the process of being weaned.

The daily patterns in the relative frequencies of occurrence of vocalisations also differed significantly with time of year (interaction term hour × month: $\chi^2_{690} = 5017.90$, $P < 0.001$). Compared with other months, the Chirp-trill was more likely to be produced around sunset in October, during the first flight period, and less likely in the early morning hours in November and December, during the dependent juvenile period. The Ultrasonic Social vocalisation was more likely to be produced in the early morning in the dependent juvenile period, specifically in February, November and December compared with other months. In comparison, relative frequency of occurrence per hour of the Squabble remained relatively stable across months. In all vocalisation types, high variability in the relative frequency of occurrence per hour was observed in June and August (no data for July), coinciding with the putative gestation and parturition periods.

Discussion

Differences in vocal activity matched the timing of previously reported key daily and seasonal events in the ghost bat roost (Tidemann *et al*. 1985; Toop 1985; Churchill 2008). Overall, vocal activity peaked predictably before sunrise and at sunset but when examined individually, the Chirp-trill and Squabble were both produced most often outside of these periods. In contrast, the Ultrasonic Social showed less fluctuation and was most commonly produced during the night. Peak periods of Chirp-trill and Squabble production were correlated with the mating and the maternity seasons, whereas the Ultrasonic Social vocalisation peaked during the parturition period and in February when juveniles are becoming independent from their mothers. This suggests that the function of these vocalisations is linked to, and therefore can serve as, indicators of key reproductive and developmental events. Only one other study has demonstrated how acoustic surveillance of bat roosts could be used to infer the timing of events such as mating, parturition and first flight (Andrews *et al*. 2017). Our study therefore provides important evidence in support of using social vocalisations as acoustic proxies for non-vocal social behaviour.

Ghost bat vocal activity (social and echolocation calls combined) peaked before sunset and sunrise, consistent with the timing of emergence and returns. The consistency of emergence timing in relation to sunset across bat species is thought to represent a compromise between avoiding diurnal

predators and finding food (Erkert 1978; Hayes 1997; Petrželková *et al*. 2006; Welbergen 2006, 2008; Griffiths and Griffiths 2007; Kaňuch 2007; Holland *et al*. 2011). We presume, therefore, that these peaks in vocal activity inside ghost bat roosts are caused by increased physical activity. Little activity was recorded during the night inside the roost, suggesting that most bats in the colony did not return until just before dawn. This is consistent with flyout and return observations by Douglas (1967) at multiple roost sites in Western Australia. It has been suggested that ghost bats tend to forage in two nightly bouts, just after dusk on leaving the roost and again just before first light, separated by a period of rest (Tidemann *et al*. 1985). Ghost bats have been found to use separate 'night roosts' such as shallow mine shafts in the vicinity of Kohinoor adit, and these roosts are likely where these periods of rest occur (Tidemann *et al*. 1985; Schulz and Menkhorst 1986). Coupled with our acoustic results, this suggests that this behaviour is more common than previously appreciated and highlights the importance for such night roosts to be considered in conservation management plans. Compared with other times of the year, high diurnal vocal activity was recorded during key pup developmental stages (crèching, first flight and dependent juvenile), suggesting that young are particularly vocally active during the day (see Knörnschild *et al*. 2006).

More generally, our study found that high diurnal vocal activity inside the roost was common with few periods of relative inactivity during the day. Little is known about the activity patterns of bats during the day (Park *et al*. 1999; Muñoz-Romo 2006), and nothing has been published previously on in-roost diurnal behaviour of ghost bats. The study of in-roost acoustic activity patterns has largely focussed on bat thermoregulatory physiology (e.g. torpor use) (Turbill *et al*. 2003; Hope and Jones 2013), and recently to describe hibernation patterns in the context of predicting the impacts of white-nose syndrome (Reynolds *et al*. 2017). Conspicuous species have also been the target of studies of diurnal activity and include species that demonstrate atypical diurnal foraging (Russo *et al*. 2011*a*, 2011*b*; Chua and Aziz 2019), or flying-foxes (*Pteropus* spp.) that roost as large, dense colonies (Thomson *et al*. 1998; Markus and Blackshaw 2002; Klose *et al*. 2009; Hengjan *et al*. 2017). Our results indicate that diurnal social interaction is common within ghost bat colonies and that in-roost acoustic recording provides an opportunity to collect a range of social and behavioural information while the bats are congregated in one location.

Our findings align with the timing of previously reported ghost bat social behaviours, providing further evidence towards functions in reproductive behaviours. Although we found that vocal activity varied between years, distinct vocalisation production was still strongly dependent on the time of year. For example, our data showed that the Squabble and Chirp-trill vocalisations were produced relatively more often during the mating season than at other times of the year (except during the period of first flights). In Queensland, Toop (1985) observed an influx of males from the surrounding region during the mating season, resulting in the colony doubling in size. The Squabble is produced during physical altercations between two (or more) ghost bats (Guppy *et al*. 1985; authors' unpubl. data) and in captivity most altercations are related to competition over space and food stealing (Guppy *et al*. 1985). The Squabble vocalisation is also produced in response to unwanted mating advances (authors' unpubl. data) and likely male–male aggression (Churchill 2008). This suggests that the rise in the absolute number of males in the roost and the increase in mating behaviour could be responsible for the increase in the Squabble vocalisation during this period. A captive study found that the Chirp-trill vocalisation was predominantly produced (95% of the time) by the males of the colony (authors' unpubl. data). It appears to function as a song used for the purpose of resource defence (roosting spot) in the roost and is also produced during mating attempts (authors' unpubl. data). Hence, peaks in the production of both the Squabble and Chirp-trill vocalisation types are likely important indicators of male presence and mating behaviour.

The production of the Squabble and Chirp-trill vocalisations peaked for a second time in October, corresponding to the period when juvenile ghost bats are thought to become volant, approximately seven weeks after parturition (Toop 1985). Chirp-trill production by a captive male (authors' unpubl. data) was significantly predicted by the flight behaviour of conspecifics, and thus the increased flight behaviour in the roost by juveniles might trigger males that remain in the roost to defend their roosting territory. We suggest that the peak in the production of the Squabble vocalisation is the result of increased physical interaction between juveniles and adults during the first flight period. In pipistrelles (*Pipistrellus pipistrellus*), prevolant juveniles regularly extend and flutter their wings while perched and first flights are short with multiple landings as juveniles have not yet mastered turning in flight (Hughes *et al*. 1995). This behaviour is likely to be common among bats and would result in increased physical interaction among colony individuals, potentially leading to more Squabble vocalisations being produced (by adults of both sexes and possibly juveniles). Thus, despite being elicited in differing contexts, the increase in the production of the Chirp-trill and Squabble vocalisations during the maternity season likely indicates the timing of juveniles becoming volant. Further observational studies of juvenile in-roost behaviour are required to confirm the link between the Chirp-trill and early flight behaviour.

The Ultrasonic Social vocalisation was most commonly recorded during the parturition period and also occurred relatively more often in February, coinciding with the period when juveniles are becoming independent from their mothers (Churchill 2008). Mother–pup vocal communication has been reported in several bat species (Bohn *et al*. 2007; Engler *et al*. 2017; Fernandez and Knörnschild 2017), including, anecdotally, in the ghost bat (Douglas 1967). The peak production in the parturition period suggests that the Ultrasonic Social vocalisation is related to the arrival of pups and may represent a pup isolation call. In some species, isolation calls are retained into adulthood and develop into adult vocalisations, such as contact/directive calls in another megadermatid, *Megaderma lyra* (Goymann *et al*. 1999), or appeasement calls in greater sac-winged bats (*Saccopteryx bilineata*) (Knörnschild *et al*. 2012), providing an explanation

for isolation-like calls being detected outside of the parturition period.

The distinct seasonal patterns in the relative frequencies of occurrence of social vocalisation types suggests that social vocalisations can be used as convenient acoustic proxies for non-vocal behaviour within the roost. We suggest that significant increases in the Squabble and Chirp-trill vocalisations during the mating season between April and May, identified by comparison to site specific acoustic baselines, is an indicator of the arrival of males and the presence of mating behaviour. Similarly, a relative peak in the Ultrasonic Social vocalisation in July to August indicates that the roost is being used as a maternity colony. Relative increases in the Squabble and Chirp-trill vocalisations in the September to October period suggests that volant juveniles are present. As our data collection was limited to one colony, studies at additional roost sites are needed to confirm that the patterns we observed are a reliable indicator of such behaviours. With ongoing improvements in methods of recording and storing full-spectrum acoustic files, long-term data collection is becoming increasingly more viable and affordable. We predict that studies using social vocalisations as a proxy for non-vocal behaviours will increase rapidly in the coming years, and their utility will increasingly improve as the functions of social vocalisations are categorised. The potential use of social vocalisations as a means for investigating bat behaviour by acoustic proxy is an exciting development, particularly for the ghost bat, as suitable methods for population monitoring are currently lacking for this species (Woinarski *et al*. 2014). This method has the potential to largely remove the impact of researcher visitation to roosts, allowing increased studies that can be used for guiding conservation actions to reverse the decline of this iconic species towards extinction.

Conflicts of interest

Justin A. Welbergen is a guest Associate Editor. Despite this relationship, he did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor of this journal. The authors have no further conflicts of interest to declare.

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