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## Temporal partitioning of *Bullacris unicolor* (Orthoptera: Pneumoridae) calling activity to avoid predation

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### ABSTRACT

Ecological interactions, including competition, predation, and environmental conditions, may significantly impact acoustic signalling behaviour. Here we characterise nocturnal signalling patterns in the bladder grasshopper *Bullacris unicolor* and relate this to biotic and abiotic factors, thus providing insights into ecological drivers of acoustic signalling behaviour. Passive acoustic recorders monitored nocturnal calling activity of the focal species, competitors, and predatory bats across the distribution of *B. unicolor*. Results indicate that *B. unicolor* calls preferentially at certain times of the night, but that peak activity period varies across the geographic range. There was a strong relationship between *B. unicolor* activity and bat activity. *Bullacris unicolor* populations further north showed an overall avoidance of bat echolocation call period, whereas further south an overlapping of call periods between *B. unicolor* and bat echolocation was observed. Bats at northern sites showed a distinct activity period early in the night and *B. unicolor* may thus reduce predation risk by shifting signalling activity to later in the night. In contrast, bats were active throughout the night at southern sites and *B. unicolor* did not delay calling activity in this region of its distribution, although the species did shift signalling slightly to reduce peak overlap with co-existing pneumorid species.

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grasshopper; predator  
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## Introduction

Within a diel period, animals allocate time for performing their daily activities, such as foraging, mating, or avoiding predation (Winandy et al. 2016). This time management strategy is known as temporal partitioning (Halle et al. 2000; Presley et al. 2009; Pretorius et al. 2020). Environmental changes during diel cycles act as a clock for species (Kronfeld-Schor and Dayan 2003), and species may adapt to perform certain activities within a specific period due to the constraints created by environmental pressures. Both internal and external factors play a role in an organism's diel activity patterns (Pretorius et al. 2020). These factors may include predation, foraging, weather conditions, interspecific interactions, and physiology. For example, the calling activity of the cane toad *Rhinella marina* is influenced by temperature and varies with season (Brodie et al. 2020).

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Weather conditions may directly influence acoustic signalling, particularly in ectothermic insects (Gerhardt and Huber 2002; Cusano et al. 2016). For example, at lower relative humidity, certain sound frequencies may experience increased levels of attenuation (Harris 1966; Chaverri and Quiros 2017). Windy conditions will further add to the distortion and degradation of sound as it travels through the atmosphere (Snell-Rood 2012). Orthopteran insects produce calls when ideal body temperatures are reached (Crawford and Dadone 1979; Sanborn et al. 2002), which varies from species to species. The variation of peak body temperature, and thus acoustic signalling initiation, may lead to temporal partitioning of multiple species calling in the same spatial environment (Sanborn et al. 2002; Cusano et al. 2016; Chaverri and Quiros 2017).

Intraspecific competition may also influence acoustic signalling. Species which call in the same frequency bandwidth may devise avoidance strategies to prevent masking each other's calls (Endler 1992; Römer and Brumm 2013; Schmidt and Balakrishnan 2014). These strategies may include temporal or spatial partitioning of calls or adjusting call amplitude or call structure (Allen-Ankins and Schwarzkopf 2021). In this way organisms can maximise the likelihood of their call being heard by a potential mate (Sueur 2002; Endo and Osawa 2017). For example, *Conocephalus* sp. X and *Conocephalus melanus* are co-occurring crickets which reach their peak calling activity at different times (Tiwari and Diwakar 2018).

Although temporal partitioning is a mechanism often used by competing species to promote coexistence, it can also be used as an avoidance mechanism by prey to reduce predation (Winandy et al. 2016). Some predators exploit acoustic signalling by eavesdropping on senders' calls and using the sound to home in on prey (Peake and McGregor 2005; Li et al. 2014). Avoidance mechanisms, such as call inhibition, may present low energy solutions to prey to reduce their predation levels. Males of species which display extravagant mating rituals such as visual and acoustic advertisement signals, may stop signalling when predators are near (Greig and Greenfield 2004).

Animals are expected to conduct a risk assessment to detect any threats and may need to trade-off potential threats with vital activities (Lima 1998b, 1998a; Winandy et al. 2016). In this way, the individual can establish if executing an essential task is worth the risk of any perceived threat. It is hypothesised that prey partition their time to minimise predation risk (Lima and Bednekoff 1999; Winandy et al. 2016). Temporal activity will thus vary according to the current perceived level of threat (Ferrari and Chivers 2009; Winandy et al. 2016). Prey organisms may avoid peak predation periods and limit their activity to times when predators occur in their lowest numbers. Vocal plasticity allows species that signal acoustically to shift their signalling to more advantageous times (Lopez et al. 1988; Brumm and Zollinger 2017; Zhao et al. 2018; Allen-Ankins and Schwarzkopf 2021).

Geographic variation between populations is influenced by varying environmental pressures at each locality (Hernández-Herrera and Pérez-Mendoza 2020). Prey intimidation is one such pressure that has strong consequences in ecological communities (Catano et al. 2015). For example, the tungára frog, *Physalaemus pustulosus*, performs extravagant calls, which most females prefer; however, these calls also attract bat predators (Tuttle and Ryan 1981; Greig and Greenfield 2004). The counter-selection created by predation is a key evolutionary force in sexual selection, especially for acoustic signalling. Prey may adopt various mechanisms to avoid predators (Hermann and

Landis 2017). When prey species are unable defend themselves physically or chemically, they may be more likely to develop predator avoidance strategies (Pintar et al. 2021). For example, the moth *Achroia grisella* makes use of acoustic signalling to attract mates and has a very specific frequency range to which they respond (Greig and Greenfield 2004). Coincidentally, gleaning bats, a predator of *A. grisella*, use echolocation of a similar frequency range and amplitude to male *Achroia grisella*, but with a significantly slower pulse rate. When *Achroia grisella* hear signals with this slower rate, they inhibit all calling and movement. *Plutella xylostella* (L.) caterpillars show a similar response to predation, by reducing their feeding and deserting their host plants (Ingerslew et al. 2018).

The south-western region of South Africa is home to *Bullacris unicolor*, a species of grasshopper belonging to the Pneumoridae family. This species makes use of acoustic signals to attract mates. The males rub their hind legs against a file on their abdomen, creating a loud sound, which females respond to by emitting a softer signal. The geographic distribution of *B. unicolor* extends predominantly along coastal regions of the Northern Cape and Western Cape Provinces, along the west coast of South Africa (Sathyan et al. 2017). Couldridge and Gordon (2015) found that the calling times of *Bullacris unicolor* vary across geographical regions. Grasshoppers occurring in southern locations begin calling much earlier in the night than those occurring in the north. Despite these locations differing in vegetation type and climate, which may affect the transmission of their long-range signals, differences in sound transmission could not be linked to the observed differences in calling times. Couldridge and Gordon (2015) suggested that this variation could be due to predation. However, no studies have been conducted on the predation of *Bullacris unicolor* previously.

This study uses passive acoustic monitoring to investigate the factors, including weather conditions, interspecific acoustic competition, and bat predation, that may lead to variation in diel signalling activity in *B. unicolor* in geographically separated populations, in order to provide a better understanding of the selective pressures responsible for driving geographic variation in signalling behaviour.

## Materials and methods

### Study sites

Recording devices were placed at six locations within the geographic distribution of *Bullacris unicolor*. All six sites were relatively undisturbed, with natural vegetation.

Sites representing the northern distribution ( $N = 3$ ) included Springbok (29°42'59.76" S; 17°54'34.56" E), Nababeep (29°39'5.04" S; 17°48'34.919" E) and Garies (30°28'51.24" S; 17°56'36.959" E). These three sites fall within the succulent Karoo biome, occurring within the Namaqualand region of the Northern Cape Province of South Africa. This area contains a sparse mixture of Fynbos shrubbery and mostly low-lying vegetation (Couldridge and van Staaden 2004). The area experiences semi-arid conditions, with winter rainfall and an average annual temperature of 16.8°C (Powrie et al. 2006).

Sites representing the southern distribution of *B. unicolor* ( $N = 3$ ) included Tygerberg Nature Reserve (33°52'39" S; 18°36'14.759" E); Koeberg Nature Reserve (33°39'54" S; 18°26'16.799" E) and the Darling Renosterveld Reserve (33°23'21.48" S; 18°22'55.92" E). These sites occur within the Fynbos biome where shrub-like vegetation with a maximum

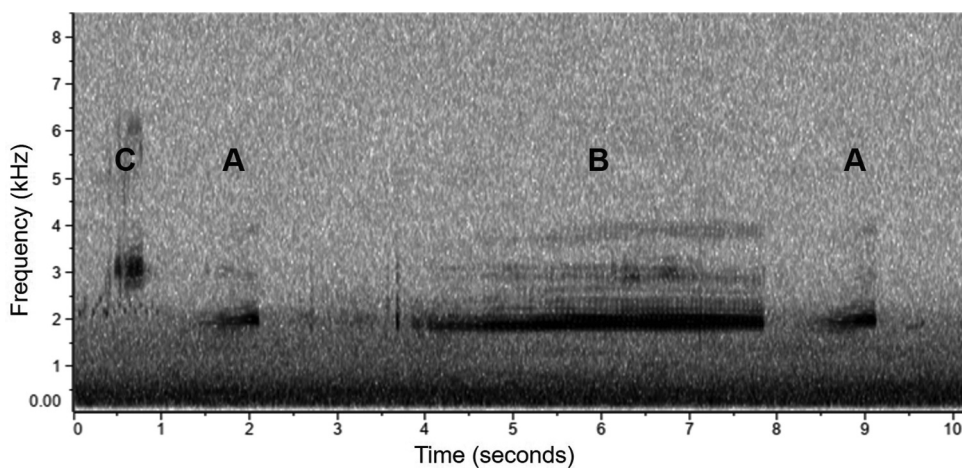
height of 2 m is dominant (Couldridge and van Staaden 2004). Average annual precipitation within the Fynbos region is 480 mm, and mean temperature of 16°C, varying according to each region (Rebelo et al. 2006).

### Acoustic monitoring

Acoustic monitoring was conducted from September to November during 2016 (two sites = Springbok and Tygerberg Nature Reserve) and 2021 (four sites = Nababeep, Garies, Koeberg Nature Reserve and Darling Renosterveld Reserve). This corresponds to the peak seasonal occurrence of *B. unicolor*. Two long-deployment acoustic recorders (SM3 and SM3BAT, Wildlife Acoustics Inc., Maynard, USA), for audible and ultrasonic frequencies, were mounted at each site. Acoustic monitoring was standardised to three nights per site, to ensure that sufficient calls were detected. The devices recorded continuously from sunset to sunrise each night, as *B. unicolor* is nocturnal (Couldridge and Gordon 2015). Environmental conditions (temperature, relative humidity, and wind speed) were simultaneously recorded at 10-minute intervals during the night using a Kestrel 4000 Weather Meter. The acoustic recording devices and the weather meter were mounted at a height of approximately 1.5 m from the ground, to reduce sound attenuation (Couldridge and van Staaden 2004).

### Sound analysis

Raven Pro 1.6 (Cornell Laboratory of Ornithology, USA) was used to analyse the sound recordings. The number of times *Bullacris unicolor*, co-existing pneumorid species and bat species called during each 30-minute interval, over three consecutive nights, was counted. This was done both audibly and visually in a spectrogram view, by observing frequencies between 1.5 kHz and 3 kHz for grasshopper species (see Figure 1 and supplementary material). *Bullacris unicolor* calls at frequencies between 2 kHz and



**Figure 1.** Spectrogram view of the advertisement calls of: (a) *Bullacris unicolor* (b) *Bullacris obliqua* and (c) *Physemacris variolosa*.

3 kHz, with each call having two short syllables followed by a longer one, and a total call length of approximately 3 seconds (Figure 1(a)) (Couldridge and Gordon 2015). Two co-existing species were detected at the southern sites, *B. obliqua* and *Physemacris variolosa*. The calls of *B. obliqua* can be distinguished from *B. unicolor* by having a lower peak frequency of around 2 kHz and a longer total call length of approximately 5 seconds (Figure 1(b)). *Physemacris variolosa* calls at a carrier frequency of approximately 3 kHz and has a very short call (Figure 1(c)). Although *Peringueyacris namaqua* is known to coexist with *B. unicolor* in Namaqualand, the species is believed to be rare and its call was not detected at any of the three northern sites. Bat echolocation calls were counted from the ultrasonic recordings and were distinguished from other animal sounds by their characteristic short sweeping structure. Bat species were identified from their calls using Kaleidoscope Pro software (Wildlife Acoustics, USA).

### Statistical analysis

Statistical analysis was performed using R software 4.1.0 (R Core Team 2021). Grasshopper and bat echolocation calls were inserted into a data frame along with the following weather conditions: average relative humidity (%), average wind speed ( $\text{m.s}^{-1}$ ) and average temperature ( $^{\circ}\text{C}$ ), for each 30-minute period.

A generalised linear model (Poisson log link) was used to assess which biotic and abiotic variables predict calling activity in *B. unicolor*. The number of bat calls, number of heterospecific calls (where present), temperature, relative humidity and wind speed were used as independent variables in the model. Separate analyses were conducted for each of the six sites. Date and time were controlled for in the analysis. Generalised linear model graphs were constructed using *ggplot2* (Wickham 2016).

## Results

### Predation

A total of nine bat species were recorded throughout the study (Table 1), ranging from five to eight species per site. *Tadarida aegyptiaca* was the most commonly encountered bat species at two of the northern locations (Garies; Nababeep) and *Eptesicus hottentotus* at the third (Springbok), while *Neoromicia capensis* was the dominant bat species at all three southern locations.

There was a significant relationship observed between bat activity and *B. unicolor* calls at all six locations (Table 2). However, *B. unicolor* in the northern and southern locations showed a different response to bat presence. *Bullacris unicolor* calls at northern sites decreased with an increase in bat echolocation calls, indicating a negative relationship between bat activity and *B. unicolor* activity (Figure 2(a–c)). Bat activity at these three locations peaks in the evening between 19h30 and 00h00, whereas *B. unicolor* calling peaks from approximately 01h00 until 05h00 (Figure 3). When bat calling peaked, *B. unicolor* calls were absent or extremely low.

Sites in the south showed a positive response between the presence of bats and *B. unicolor* (Table 2), indicating that their activity patterns overlapped. At the southern locations it was found that bat calls occurred throughout the entire period sampled,

**Table 1.** List of bat species bats detected during the study at each of the six locations and the number of times each bat species was detected (average detections per night).

Bat species	Northern locations			Southern locations		
	Garies	Nababeep	Springbok	Darling	Koeberg	Tygerberg
<i>Chaerophon pumilus</i>	1	10	7	8	6	<1
<i>Eptesicus hottentotus</i>		9	9	1	2	<1
<i>Miniopterus natalensis</i>	1	2	8	5	0	<1
<i>Neoromicia capensis</i>	2	3	8	21	197	275
<i>Rhinolophus clivosus</i>		1	4			
<i>Rhinolophus hilderbrandtii</i>					1	<1
<i>Sauromys petrophilus</i>	1		<1	3	2	<1
<i>Scotophilus dinganii</i>		1	1	6	3	1
<i>Tadarida aegyptiaca</i>	168	22	6	5	51	3

between 19h30 and 05h00, and bats are thus active for a much longer period than further north (Figure 3). *Bullacris unicolor* is most active between 22h00 and 02h30 at these locations.

### Interspecific competition

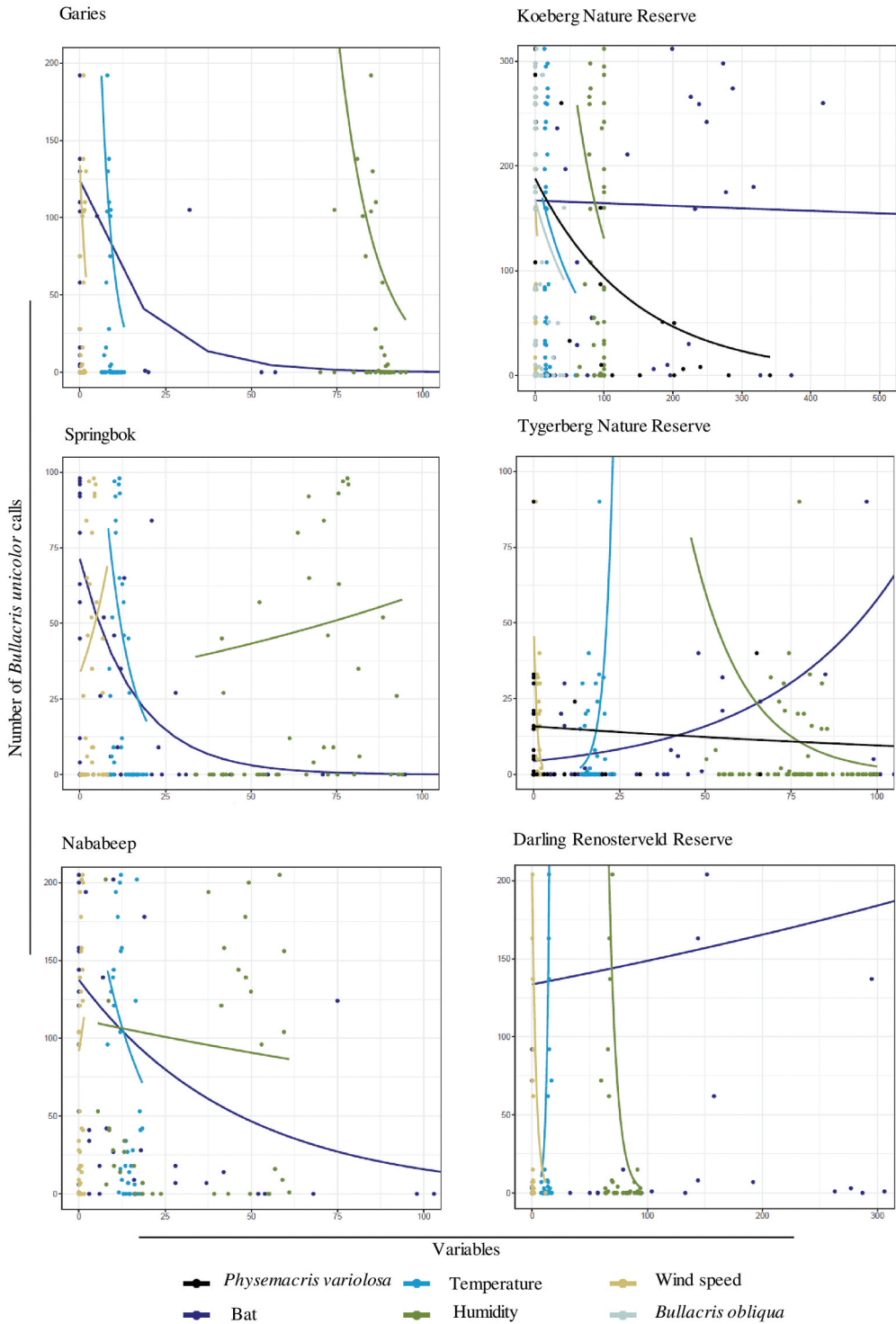
Heterospecific calls were only detected at southern locations. At both Tygerberg Nature Reserve and Koeberg Nature Reserve, the calls of two coexisting pneumorid species were detected – *Physemacris variolosa* and *Bullacris obliqua*.

*Physemacris variolosa* calls during the early hours of the evening, ending at approximately 22h30 (Figure 3). At both Tygerberg and Koeberg Nature Reserves, there was

**Table 2.** Results of generalised linear models of the predictors of acoustic signalling in *Bullacris unicolor* at six locations.

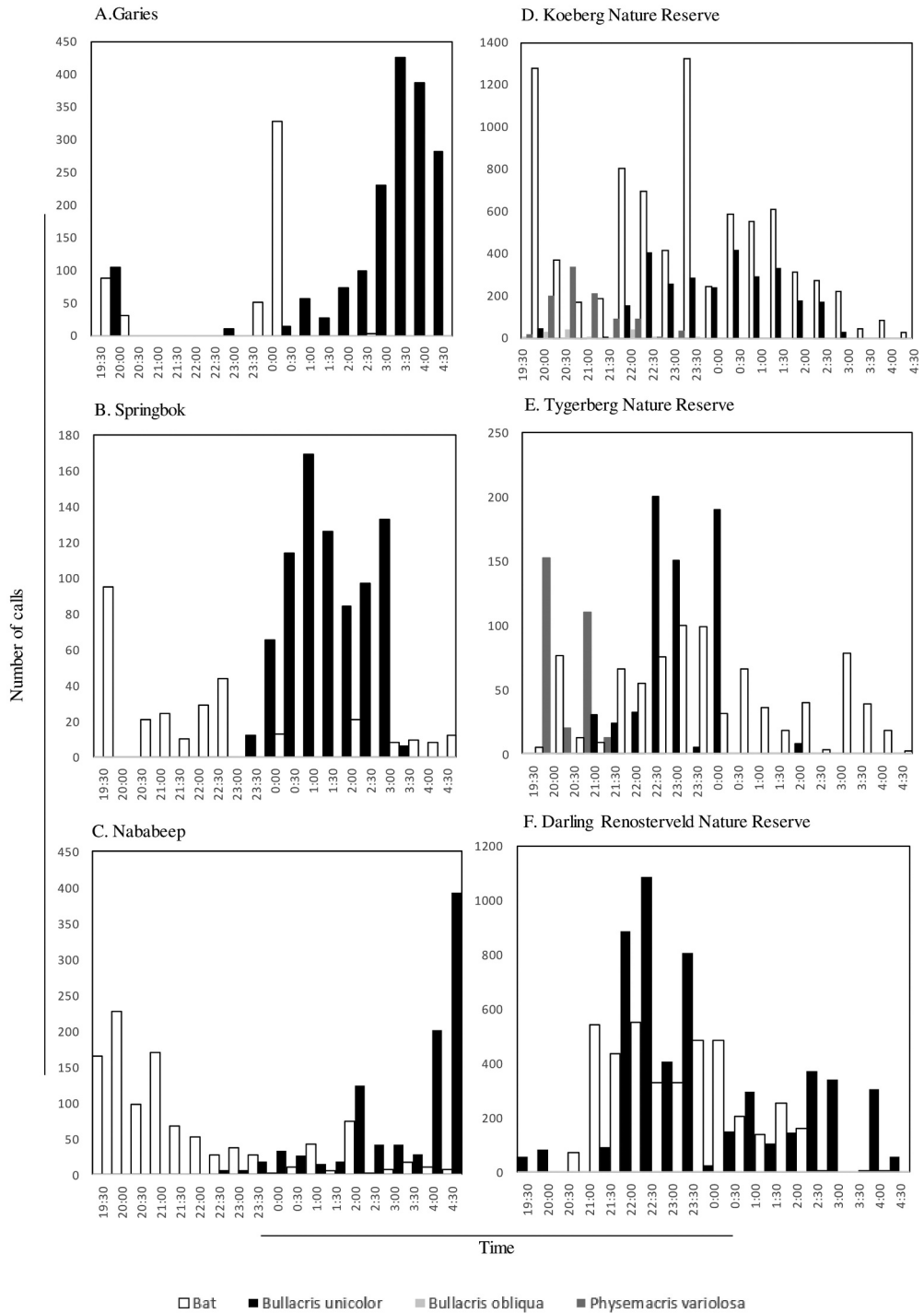
Location	Variable	Estimate (B)	Wald Chi-square	Sig.	
Northern	Garies	Bats	-0.050	315.784	<0.001*
		Relative humidity	-0.087	868.361	<0.001*
		Temperature	-0.471	591.226	<0.001*
		Wind speed	0.088	3.003	0.083
	Nababeep	Bats	-0.016	256.579	<0.001*
		Relative humidity	-0.019	128.062	<0.001*
		Temperature	-0.104	88.602	<0.001*
		Wind speed	0.073	2.288	0.130
	Springbok	Bats	-0.026	109.799	<0.001*
		Relative humidity	-0.022	74.378	<0.001*
		Temperature	-0.074	18.767	<0.001*
		Wind speed	-0.003	0.044	0.833
Southern	Darling	Bats	0.002	5.875	0.015*
		Relative humidity	-0.280	2663.415	<0.001*
		Temperature	0.489	1312.783	<0.001*
		Wind speed	-1.480	1432.432	<0.001*
	Koeberg	Bats	0.001	1060.508	<0.001*
		Relative humidity	-0.007	9.646	0.002*
		Temperature	0.134	152.573	<0.001*
		Wind speed	-0.102	19.994	<0.001*
		<i>B. obliqua</i>	-0.012	118.315	<0.001*
		<i>P. variolosa</i>	-0.013	1650.822	<0.001*
	Tygerberg	Bats	0.025	1154.772	<0.001*
		Relative humidity	-0.035	427.176	<0.001*
Temperature		0.266	28.275	<0.001*	
Wind speed		-0.546	286.444	<0.001*	
	<i>P. variolosa</i>	-0.016	86.279	<0.001*	

\* Significant ( $p < 0.05$ ).



**Figure 2.** Generalised linear models of *Bullacris unicolor* calls in response to heterospecific species (*Physemacris variolosa* and *Bullacris obliqua*); weather conditions (relative humidity, wind speed, and average temperature) and bat predation at each of the northern locations (left: A, B, C) and southern locations (right: D, E, F).





**Figure 3.** Bar graphs showing *Bullacris unicolor*, *Physemacris variolosa* and *Bullacris obliqua* advertisement calls and bat echolocation activity on the busiest night at each of the northern locations (left: A, B, C) and southern locations (right: D, E, F).

**Table 3.** The average (mean and standard deviation) weather conditions at each location.

		Temperature (°C)	Wind Speed (m/sec)	Relative Humidity (%)
		Mean ± SD	Mean ± SD	Mean ± SD
Northern locations	Springbok	12.8 ± 2.9	3.6 ± 2.2	62 ± 17.7
	Nababeep	13.9 ± 2.5	0.5 ± 0.4	30.4 ± 19.4
	Garies	9 ± 1.5	0.8 ± 0.5	85.4 ± 5.3
Southern locations	Tygerberg Nature Reserve	17.1 ± 2.4	1.3 ± 0.6	78.6 ± 14.5
	Koeberg Nature Reserve	16.6 ± 6	0.8 ± 0.6	91.7 ± 11
	Darling Renosterveld Reserve	13.4 ± 2.3	0.9 ± 1.5	74 ± 11.4

a negative relationship between the calling activity of *Physemacris variolosa* and *B. unicolor* (Table 2), *Bullacris obliqua* showed a similar calling activity to *P. variolosa*, although *B. obliqua* was present in much lower numbers. Although there were insufficient calls of *B. obliqua* for statistical analysis at Tygerberg Nature Reserve, there was a negative relationship with *B. unicolor* at Koeberg Nature Reserve (Table 2). No other coexisting pneumorid species were detected at any of the remaining four locations.

### Weather conditions

The relationship between *B. unicolor* calling activity and weather conditions (Table 3) varied between sites. Calling activity was negatively correlated with temperature at Garies, Nababeep and Springbok and positively correlated with temperature at Darling, Koeberg Nature Reserve and Tygerberg Nature Reserve (Table 2).

There was no significant relationship between *Bullacris unicolor* calling activity and wind speed at any of the three northern sites (Table 2). In contrast, all three southern locations showed a negative relationship between calling activity and wind speed (Figure 2(d–f)), with *B. unicolor* being less likely to call under windier conditions. Average wind speed varied across all sites, with Springbok having the highest average wind speed and Nababeep the lowest (Table 3). *Bullacris unicolor* activity showed a negative response to relative humidity at all six sites (Table 2).

### Discussion

The results indicate clear differences in the activity patterns of *Bullacris unicolor* from different locations, with the grasshoppers being active later in the night at northern locations compared to southern locations. This confirms a previous finding based on laboratory housed individuals (Couldridge and Gordon 2015) that there is geographic variation in diel signal timing in *Bullacris unicolor*. Considering that these population differences in signal timing remain apparent even under laboratory conditions, they are likely to be under at least partial genetic control. Genetic variation among geographically separated populations has previously been observed (Sathyan et al. 2017).

Bat activity also differed among locations, with bats being active earlier in the evening at northern locations, but active throughout the night at southern locations. *Bullacris unicolor* activity at northern sites shows very little overlap with bat peak activity periods (Figure 3), leading to a strong negative relationship between *B. unicolor* calls and bat echolocation calls at these locations (Figure 2(a–c)). This suggests that *B. unicolor* may be actively avoiding bat peak activity periods by shifting its calling activity to later in the night. Being active while predators are at their highest numbers may be costly to the prey,

and this cost may be significantly greater than prey shifting their activity to a time when predator numbers decline (Cunningham et al. 2019). This temporal separation would allow for *B. unicolor* to avoid predation from bat species that may be eavesdropping on them. Insectivorous bats have been shown to influence signalling behaviour in previous studies. For example, neotropical katydids reduce their calling and switch to vibrational communication to avoid bat predation (Belwood and Morris 1987; Römer et al. 2010), while the cricket *Teleogryllus oceanicus* prefers to call from the safety of burrows and alters the elements of its call to produce fewer trills when calling from exposed locations (Bailey and Haythornthwaite 1998).

Conversely, at the southern locations, bat echolocation and *B. unicolor* call periods overlapped, indicating that they are active at similar times. Due to greater urbanisation surrounding these locations, areas in the south experience more anthropogenic noise than sites in the north. Anthropogenic noise affects acoustically communicating species (Lampe et al. 2014). Bats increase their echolocation period under noisy conditions to maximise the likelihood of finding food. This foraging strategy is evident in *Miniopterus natalensis* behaviour during non-breeding seasons (Pretorius et al. 2020). Due to increased anthropogenic noises and bat predators being active for much of the night, *B. unicolor* would be exposed to different selective pressures than in the northern regions of its distribution. This could explain why at southern sites *B. unicolor* is active over a longer period. Sathyan and Couldridge (2021) conducted a study on anthropogenic noise and *B. unicolor* calling activity and found that *B. unicolor* may adjust its signalling to avoid overlap with increased levels of anthropogenic noise.

There was limited evidence of temporal partitioning between the activity of *B. unicolor* and competing bladder grasshopper species. *Peringueyacris namaqua* is the only species with which *B. unicolor* coexists at the three northern sites. However, this species was not identified on any of the recordings, and due to its rarity, it is unlikely to significantly impact the calling behaviour of *B. unicolor*. However, at southern locations, *B. unicolor* was found to coexist with both *B. obliqua* and *P. variolosa*. Although both co-existing species are documented to occur at all three sites, they were not equally common at all sites (Figure 3(d–f)). *Bullacris obliqua* was detected in large numbers only at Koeberg Nature Reserve (Figure 3(d)) and *P. variolosa* at Koeberg Nature Reserve (Figure 3(d)) and Tygerberg Nature Reserve (Figure 3(e)). *Physemacris variolosa* calls showed relatively little overlap with *Bullacris unicolor* calls. It was observed that *P. variolosa* generally starts calling earlier in the night than *B. unicolor* and tapers off as *B. unicolor* begins calling (Figure 3(d,e)). This could suggest an avoidance strategy so as not to mask each other's mating calls. *Bullacris obliqua* shows low activity compared to that of *B. unicolor* and *P. variolosa*, indicating that the species is less common. However, at the only location where it called in large enough numbers for analyses to be conducted, it called significantly earlier in the evening than *B. unicolor*. These avoidance patterns observed between *Bullacris unicolor* and coexisting species are not unexpected. Shifting of signal timing has often been cited as a mechanism to avoid the potential masking effects of acoustic competitors (Barker and Mennill 2009; Schmidt and Balakrishnan 2014; Stanley et al. 2016), as well as a mechanism to avoid inbreeding in closely related species (Sueur 2002). On the other hand, some studies conducted on crickets and katydids have found that species do not partition their calls in time to avoid overlap (Diwakar and Balakrishnan 2007; Schmidt et al. 2013). Interestingly, although *B. unicolor* calls later in the night than

heterospecifics at southern locations, it still calls earlier than it does at northern locations where there are no competing species.

Weather conditions had an additional influence on the calling activity of *Bullacris unicolor* in this study. This is unsurprising as invertebrate physiological factors are known to be affected by weather conditions such as temperature (Rebelo et al. 2010; Pretorius et al. 2020) and abiotic factors often correlate with acoustic signalling in insects (Franklin et al. 2009). Temperature had a positive influence on calling rate at southern locations and a negative influence at northern locations. These relationships with temperature, as well as the discrepancy between sites, may be because temperature drops as the night progresses and so by calling later at the northern locations, *B. unicolor* is thus calling at lower temperatures, even though overall activity levels may be higher on warmer nights. However, a previous study found temperature to correlate with characteristics of the acoustic signals of *Bullacris unicolor* (Sathyan and Couldridge 2021). Relative humidity and wind speed both had a largely negative influence on calling activity in *B. unicolor*, with males more likely to call when humidity was lower and conditions were less windy. However, these correlations with wind speed were only significant at southern sites.

Although not considered here, ambient nocturnal light levels may additionally influence activity patterns in both insects and their bat predators alike, and thus may have contributed to the observed variation in activity between sites. This includes the lunar phase, and corresponding moonlight intensity (Lang et al. 2006; Perks and Goodenough 2020), as well as artificial light sources (Owens and Lewis 2018; Mena et al. 2022).

This is one of only a few studies to examine intraspecific geographic variation in diel signalling patterns. The results show that variation in predator activity has likely led to inter-population divergence in diel signalling. As previous research has suggested that signal timing has become fixed, rather than a plastic response (Couldridge and Gordon 2015), and that genetic differentiation exists between the northern and southern populations (Sathyan et al. 2017), this divergence may have implications for species integrity. Weather conditions showed a limited effect on signal timing, but inter-specific competition may play an additional role in temporal partitioning between *Bullacris unicolor* and coexisting species. However, competition cannot account for the observed delayed shift in calling at northern sites.

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## Disclosure statement

No potential conflict of interest was reported by the author(s).

## Ethical statement

Due to the non-invasive nature of this study no ethical clearance was required.

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