Social communication and interactions among echolocating bats in urban ecosystems

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Declaration

This is to certify that the content of this thesis is my own work. This thesis has not been submitted for any other degree or purpose.

I certify that the intellectual content of this thesis is the product of my own work, and that all assistance received in preparing this thesis and all sources have been acknowledged.

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Title page photos

Top left: Illustration of landscape, drawn by M. Kao

Top right: *Chalinolobus gouldii* roosting in a tree hollow, photo by M. Kao

Bottom left: *Chalinolobus gouldii* roosting in a bat box, photo by M. Kao

Bottom right: Illustration of *Chalinolobus gouldii*, drawn by M. Kao

Author attributions

Chapter 2 of this thesis is "Kao, M.-T., Law, B., Hochuli, D. F., Welbergen, J. A., and Threlfall, C. G. (2025) Characterization and seasonal variation in the social vocal repertoire of *Chalinolobus gouldii*, Australia's most widespread bat."

All authors conceived the ideas and designed methodology. MTK collected and analysed the data and wrote the drafts of the manuscript. All authors contributed critically to the drafts and gave approval for the final version.

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Mei-Ting Kao, 30 September 2025

As supervisor for the candidature upon which this thesis is based, I can confirm that the authorship attribution statements above are correct.

Dieter Hochuli, 30 September 2025

Use of generative AI in this thesis

During the preparation of the thesis, I used ChatGPT for the purposes of statistical code debugging and text enhancement. The use of this generative AI tool includes correcting R code, grammar refinement, and paraphrasing.

I also confirm that where text was checked or modified by generative AI, the content was reviewed for possible errors, inaccuracies, and bias. The author takes full responsibility for the submitted thesis and ensures the work is their own and has used generative AI within the parameters of use.

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Abstract

Urbanisation affects wildlife communication in many ways. Animals alter their vocal signals in response to urban noise and habitat degradation resulting from urban expansion. The sophisticated audio-vocal systems of echolocating bats, who use echolocation calls for navigation and foraging and social calls for communication, may be particularly susceptible to this. However, understanding of the impacts of urbanisation on echolocating bat vocal communication and social interactions is still limited.

The aim of my study was to assess the role of social vocalisations in echolocating bats and investigate how social vocalisations change across different landscapes, particularly in urban and rural areas. Here, I focused on the Gould's wattled bat, *Chalinolobus gouldii*, social vocalisations at their key habitats, foraging and roosting sites. I undertook acoustic surveys and evaluated the repertoire of social vocalisations this species emits across seasons and sites. I also broadcast *C. gouldii* vocalisations in the field to investigate behavioural responses to different vocalisations by conspecific and heterospecific individuals. Finally, I assessed the effects of habitat attributes on social vocalisation rates in *C. gouldii*, and the effect of roost density on social networks and variation in social vocalisations.

After reviewing the literature in **Chapter 1** to address the current knowledge and gaps as a general introduction, I generated four data chapters in this thesis: **Chapter 2** demonstrated that *C. gouldii* have at least five social vocalisations in addition to making a broadband chatting sound. I hypothesised that *C. gouldii* social vocalisations varied over time, potentially associated with different functions at different stages of the life cycle. I found

that these social vocalisations did not show seasonal variation. In **Chapter 3**, I broadcast *C. gouldii* vocalisations, including three types of social vocalisations (Syllable 1, 2, and a broadband chatting sound), search-phase echolocation calls, echolocation calls with feeding buzzes, and ambient control sounds in the field. I hypothesised that *C. gouldii* responded to conspecific vocalisations differently depending on information the vocalisations conveyed. *Chalinolobus gouldii* responded to conspecific social vocalisations, particularly Syllable 2, potentially functioning as group cohesion calls. I also hypothesised that heterospecifics with overlapping ecological niches of *C. gouldii* may eavesdrop on *C. gouldii* social vocalisations to exploit information to improve resource discovery or acquisition. I found that a heterospecific *Miniopterus orianae oceanensis* potentially eavesdroped on *C. gouldii* vocalisations, approaching *C. gouldii* vocalisations when *M. orianae oceanensis* were already in the area. In **Chapter 4**, I examined the effects of habitat attributes, including canopy cover, waterbodies, and level of urbanisation (via housing density), on *C. gouldii* echolocation activity and social vocalisation rates. I hypothesised that *C. gouldii* would produce social vocalisations at different rates to potentially reflect differences in resource availability in urban versus rural areas. Alternatively, the social vocalisation rates did not change, instead the number of social vocalisations produced might reflect conspecific activity rather than habitat attributes. I found that there was an interactive effect of urbanisation and canopy cover on social vocalisation rate. The rates of social vocalisations in *C. gouldii* increased faster in urban areas with greater canopy cover, but not in rural areas. I also hypothesised that *C. gouldii* might adjust their social vocalisations to mitigate masking from increased impervious surfaces or noise in urban areas. In support of this hypothesis, I found that *C. gouldii* shifted their social vocalisations toward higher frequencies and shorter durations in urban areas, whereas echolocation calls did not show the same pattern. In

Chapter 5, I investigated the association between urban roost density and *C. gouldii* social networks and the effects of roost social network structure on the characteristics of their social vocalisations. I hypothesised that roost density might affect *C. gouldii* roosting social networks, which in turn might drive variation in their social vocalisation. Areas with low roost density resulted in higher network density and lower network modularity compared with areas with high roost density. *Chalinolobus gouldii* also exhibited greater distances from the overall centroid in social vocalisations in areas with lower roost density. In **Chapter 6**, I concluded that urbanisation negatively affects *C. gouldii* echolocation activity, social vocalisations, and roosting behaviours. However, by using social vocalisations, *C. gouldii* can persist in urban areas, potentially sharing information about prey and roosts. These findings extend the understanding of animal communication in the ultrasonic range beyond well-studied taxa such as birds and provide preliminary guidance for habitat management, including the retention and enhancement of canopy cover.

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Chapter. 1 General introduction

1.1 Using echolocating bats to study vocal communication in anthropogenic environments

Communication is a fundamental process by which individuals and groups exchange information, often to influence the behaviours of conspecifics and heterospecifics (Beecher 1989, Kastein et al. 2013, Carlson et al. 2020). Communication signals are transmitted through multiple modalities, including visual, chemical, tactile, and acoustic. The functions of these signals range from mate attraction and parental care to territorial defence and acting as alarms (Bradbury and Vehrencamp 2011). While different sensory modalities are used across the animal kingdom, acoustic communication is the most commonly observed in vertebrates, as sound is suited to long-distance, rapid, and directional transmission, and conveys complex information efficiently (Wiley and Richards 1978, Bradbury and Vehrencamp 2011). As a result, acoustic signals represent one of the most versatile and exploited sensory forms of communication (Chen and Wiens 2020).

While the mechanisms and functions vary widely, the use of sound for communication is clearly widespread across the animal kingdom. Within the human audible range, songbirds and amphibians are well-studied, with research focusing on their vocal repertoire, social interaction, and social learning (Janik and Slater 2000). For example, bird song has been extensively examined in the contexts of mate attraction, territorial defence, and cultural transmission (Candolin and Wong 2019), while frog calls are widely recognized for their roles in mate choice and species recognition (Higham et al. 2021, Zaffaroni-Caorsi et al. 2023). Because the signals made by vocalisations of these taxa are conspicuous, widespread, and audible to humans, they have received more attention in conservation and habitat management. In contrast, animals that communicate within the ultrasonic range (>20 kHz) are comparatively overlooked, such as some rodents, some insects, and most echolocating bats (Chaverri et al. 2018). Expanding research into ultrasonic communication would allow for a more comprehensive understanding of the diversity of acoustic communication in animals.

The order Chiroptera is the second most diverse mammalian group after rodents and comprises about 20% of all classified mammal species in the world. Of the 1,500 described bat species, 70% belong to the echolocating bats, hereafter called bats in this thesis, (Simmons and Cirranello 2025). Bats show great taxonomic diversity and a variety of functional traits, including echolocation behaviours (Schnitzler et al. 2003, Denzinger and Schnitzler 2013, Denzinger et al. 2018), roosting strategies (Lewis 1995), thermoregulation (Stawski et al. 2014, Nowack et al. 2017), and social organisation (Dorrestein et al. 2024). These characteristics enable bats to inhabit a wide range of environments across the globe, although they are limited by extreme climatic regions, such as high latitude or isolated oceanic islands (Parker et al. 1997, Procheş 2005). Bats can also be good bioindicators of anthropogenic disturbance because different species are sensitive to environmental changes, occupy diverse ecological niches, provide important ecosystem services, and can be monitored effectively through acoustic surveys across a wide range of habitats (Kunz and Lumsden 2003, Jones et al. 2009, Russo and Ancillotto 2015, Russo and Jones 2015).

In this introduction, I first discuss the range of vocalisations made by bats and outline how they relate to foraging and social interactions. I then consider how this communication can be affected by landscape modification, focusing on urbanisation. I conclude by identifying key research gaps and how my work addresses key aims relating to these topics.

1.2 Vocalisations in echolocating bats

Bats have well-developed auditory-vocal systems, predominantly producing sounds for navigation, foraging, and communication with species-specific characteristics. Conventionally, their vocal calls are separated into two categories: (1) echolocation calls: that function for orientation, detection, identification of environments, and localising prey (Fenton 2003, Denzinger and Schnitzler 2013), which has been extensively explored; and (2) social calls: differing from echolocation calls in that they intentionally convey information and facilitate social associations among individuals, with diverse call structures conveying contextual and individual information (Fenton and Bell 1981, Fenton 2003, Pfalzer and Kusch 2003).

1.2.1 Echolocation calls and feeding calls

Bats mainly use echolocation for navigation and foraging. Echolocation calls are comprised of sequences of pulses, including search-phase calls and feeding buzzes (Kalko and Schnitzler 1989, Schnitzler and Kalko 2001). Search-phase calls are used for detection and are characterised by regular pulse intervals, with subsequent changes in pulse structure as the bat approaches the target focusing on determining and tracking its location (Schnitzler and Kalko 2001, Schnitzler et al. 2003). When approaching prey, bats change the echolocation patterns, including increasing pulse rate and bandwidth, to improve detection resolution, by forming a rapid series of short, high-repetition calls, known as the feeding buzz. Feeding buzzes reflect the final stages of prey pursuit and capture (Griffin 1958, Griffin et al. 1960, Kalko and Schnitzler 1993). Both search calls and feeding buzzes are not only important for the producer but also function as public information, unintentionally conveying cues, such as foraging locations and prey availability, to nearby conspecifics and heterospecifics (Lewanzik et al. 2019). Thus, echolocation calls, including search calls and feeding buzzes, can have social and ecological dimensions that shape both within and between species interactions.

Echolocation calls passively convey social information, despite being primarily used for navigation and foraging (Jones 2008, Dechmann et al. 2009, Schuchmann and Siemers 2010, Voigt-Heucke et al. 2010, Gillam and Fenton 2016, Russo et al. 2017, Bohn and Gillam 2018, Barclay and Jacobs 2023). Bat echolocation activity in a given area often indicates foraging, swarming near roosts, or the mating season before hibernation in temperate areas (Furmankiewicz et al. 2013, van Schaik et al. 2015, Bergmann et al. 2022a, Bergmann et al. 2022b). Moreover, echolocation calls themselves can act as honest signals, providing information about species (Dorado-Correa et al. 2013), sex (Tan et al. 2022), age, group (Kazial et al. 2001), and even individual identity (Yovel et al. 2009, Voigt-Heucke et al. 2010, Tan et al. 2022). Such information encoded in echolocation calls can attract conspecifics (Gillam 2007). By eavesdropping on these cues, bats can facilitate behaviours such as conspecific roost finding (Ruczynski et al. 2007, 2009), cooperative foraging (Dechmann et al. 2009), and prey locating (Gillam 2007). Thus, echolocation calls can be a rich source of social information.

The terminal phase of echolocation before a bat attacks prey, known as a feeding buzz, provides a reliable cue for conspecifics and heterospecifics to eavesdrop on prey locations and potential prey abundance (Fenton 2003, Gillam 2007, Dorado-Correa et al. 2013, Lewanzik et al. 2019). Recently, studies demonstrated that bats integrate the cues of echolocation calls and feeding buzzes from bat individuals to optimise their foraging efficiency. By assessing the local levels of conspecific and heterospecific activity and density, bats adjust foraging movement (Lewanzik et al. 2019, Kohles et al. 2022, Krivoruchko et al. 2024), potentially to reduce niche overlap or avoid intraspecific and interspecific aggression (Voigt-Heucke et al. 2016, Marggraf et al. 2023). These studies have revealed considerable complexity in how these call types are used for decision making (Lewanzik et al. 2019, Barclay and Jacobs 2023).

1.2.2 Social calls – understudied intraspecific communications in bats

Social calls are used to communicate with conspecifics (Fenton 2003, Pfalzer and Kusch 2003). Studies on bat social calls have mostly emerged in the last few decades. Unlike echolocation calls used for navigation and foraging, with explicit structure and pattern within species, social calls in bats are sometimes synonymous with social vocalisations and communication sounds, covering a wide acoustic range and function. I define the terminology that relates to social calls, and the terms I use in my thesis, mostly based on the definition from Kanwal et al. (1994), Bohn et al. (2008), and Odom et al. (2021) (Figure 1.1).

- *Vocalisation*: any sound produced by the vocal apparatus.

- *Syllable*: the most fundamental acoustic unit (and vocalisation) identified in bat social communication. It is defined as one continuous emission surrounded by silence. Note: *element* is often used interchangeably with syllable.
- *Harmonics*: higher-frequency and whole-integer multiples of the fundamental frequency. In this study, the dominant harmonic containing the greatest energy of each syllable was analysed.
- *Call*: the simplest emission of a vocalisation. A call can be *monosyllabic* (one syllable) or *multisyllabic* (a group of syllables). In terms of '*social call*', it is the unit to be associated with a specific interaction or purpose. Note: the term *call* as used here refers to social vocalisations or social calls, and it differs from an echolocation *call*, which is equivalent to pulse.
- *Song*: a highly complex, multisyllabic vocal display, subject to sexual selection (e.g., territorial or courtship songs), as opposed to calls. Song is also synonymous with '*courtship vocalisation*', '*courtship song'*, and '*territorial song*'.

Other peripheral terminology of communication sounds in bats:

- *Phrase*: a sequence of syllables from at least two different classes of syllables.
- *Bout*: a group of calls or vocalisations, which is not used for sexual selection.

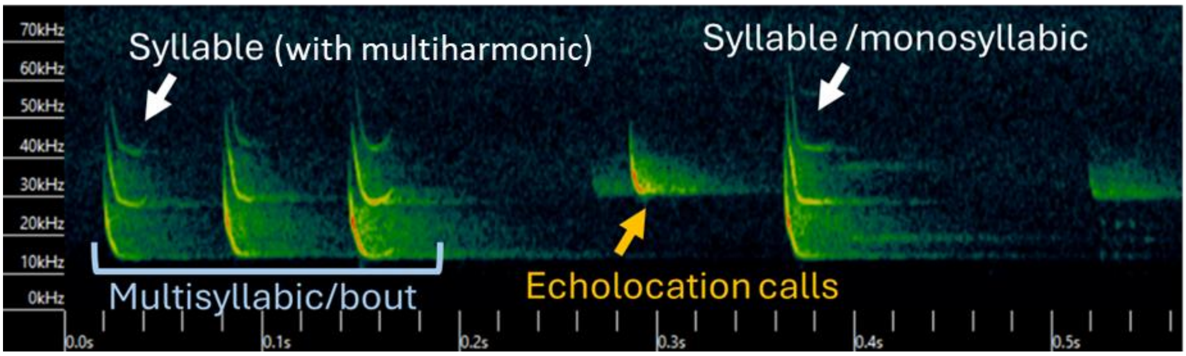


Figure 1.1. Example spectrogram of a *Chalinolobus gouldii* social vocalisations, showing a single syllable, harmonics, a multisyllabic bout, and accompanying echolocation calls.

In this thesis, I focus on the fundamental units of vocalisations in bats, *Syllables*, and discuss *multisyllabic vocalisations.* Also, to avoid confusion, I use '*social vocalisation*' to describe vocalisations with uncertain functions and '*social call*' to describe the vocalisations with known functions throughout the remaining chapters of this study.

Isolating social vocalisations is a challenge because bats produce vocalisations over a broad range of frequencies and durations. Gradation between social vocalisations also often occurs, making it difficult to define clear boundaries and separations. Most studies of social vocalisations have relied on qualitative approaches, visually inspecting spectrograms to group vocalisations based on spectro-temporal contours and shapes (Melendez et al. 2006, Knörnschild et al. 2010, Clement and Kanwal 2012, Gadziola et al. 2012, Lin et al. 2015, Nardone et al. 2017, Guo et al. 2019, Lattenkamp et al. 2019, Springall et al. 2019, Fernandez et al. 2021) (Table 1.1). Only a few studies have employed quantitative methods, such as agglomerative clustering without prior classification, to determine the optimal separation of social vocalisations based on call measurements (Andrews et al. 2006, Lin et al. 2016, Hanrahan 2020). These approaches have the advantage of efficiently obtaining an objective classification that is reproducible, impartial and minimises observer bias, with discriminant function analysis applied to validate the resulting categories. Such methodological approaches provide the foundation for investigating the complexity and diversity of bat social vocal repertoires.

Studying the social vocalisation repertoire of bats provides varied insights into the diversity of vocalisations and reflects the complexity of bat social interactions across different species and contexts (Knörnschild et al. 2020). Across different species, repertoire sizes range from a few to a dozen distinct types (Table 1.1). This variation is possibly driven by the difference in social organisation, ecological demands, and life history strategies (Bradbury 1977, Gillam and Fenton 2016, Chaverri et al. 2018). Species that require social coordination often have more diverse vocalisations to mediate relationships, such as in cooperative breeding, foraging and communal roosting (Wilkinson and Boughman 1998, Xiao et al. 2018, Lattenkamp et al. 2019, Springall et al. 2019, Hanrahan 2020). Repertoire size also varies with habitat contexts, with urban-dwelling species likely producing more social vocalisations to maintain communication in novel environments (Melendez et al. 2006, Guo et al. 2019, Springall et al. 2019). Physiological demands further contribute to variation, as vocal repertoires often expand during nursery and mating seasons (Andrews and Andrews 2003, Andrews et al. 2006). Understanding how repertoire size and composition are shaped by ecological, social, and physiological pressures offers a valuable framework for exploring the links between environmental challenges and social communication.

Table 1.1. Summary of studies on social vocal repertoires in echolocating bats, including repertoire size, identification methods, recording conditions, and statistical validation approaches.

Species	**Repertoire size (No. of syllables)**	**Identification method**	**Recording condition**	**Validation**	**Reference**
Ectophylla alba	10	Visual identification	Field sites at the roost	DFA: 88.8%	Fernandez et al. 2021
Eptesicus fuscus	18	1. Visual identification 2. Automated classification	Lab recording (summer)	NA	Gadziola et al. 2012
Eptesicus fuscus	7	Visual identification	Lab recording	DFA: 94.9%	Wright et al. 2013
Eptesicus fuscus *Nycticeius humeralis* *Tadarida brasiliensis*	EpFu: 6 NyHu: 5 TaBr: 4	Visual identification	Field sites – foraging (summer)	DFA: EpFu: 86.9% NyHu: 96.9% TaBr: NA	Springall et al. 2019
Glossophaga commissarisi	8	Visual identification	Lab setting	DFA: 95.8	Knörnschild et al. 2010
Glossophaga soricina	15	Visual identification	Lab setting	DFA: 98.7	Knörnschild et al. 2010
Hipposideros armiger	13 single syllables 5 multi-syllables	Visual identification	Lab setting	NA	Gu et al. 2023
Hipposideros armiger	18	k-means clustering algorithm	Field	DFA: 86.4%	Lin et al. 2016
Hypsugo savii	5	Visual identification	Field sites – foraging (summer)	DFA: 77.1%	Nardone et al. 2017
Macroderma gigas	12	Hierarchical agglomerative clustering	Field sites – roost (all seasons)	DFA: 94.4%	Hanrahan 2020
Murina ussuriensis	5	Visual identification	Field	NA	Fukui et al. 2012

Table 1.1. (continued) Summary of studies on social vocal repertoires in echolocating bats, including repertoire size, identification methods, recording conditions, and statistical validation approaches.

Species	**Repertoire size (No. of syllables)**	**Identification method**	**Recording condition**	**Validation**	**Reference**
Murina leucogaster	17	Visual identification	Lab recording (summer and autumn)	NA	Lin et al. 2015
Myotis acrodactylus	8	Visual identification	Field sites – foraging + near roost (summer)	DFA: 76.4%	Guo et al. 2019
Myotis macrodactylus	4	Visual identification	Field	NA	Xiao et al. 2018
Pteronotus parnellii	15	Visual identification	Lab recording	NA	Clement and Kanwal 2012
Rhinolophus ferrumequinum	12	Visual identification and Agglomerative clustering	Field Hibernaculum Nursery Roost	NA	Andrews and Andrews 2003, Andrews et al. 2006
Rhinolophus ferrumequinum	17	Visual identification	Lab recording	NA	Ma et al. 2006
Myotis lucifugus	5	Visual identification	Lab recording (autumn and spring)	CART: 89.71%	Melendez et al. 2006
Saccopteryx bilineata	7	Visual identification	Field	DFA: 49%	Behr and von Helversen 2004
Tadarida brasiliensis	16	Visual identification	Lab recording	NA	Bohn et al. 2008
Phyllostomus discolor	8	Visual identification	Lab recording (spring)	DFA: 87%	Lattenkamp et al. 2019

Note: NA: non-available

Understanding the functions of social vocalisations relies on behavioural observation and experimentation. Acoustic recordings combined with video footage allow researchers to document the real-time cause and consequences of behaviours associated with vocal production (e.g., Gadziola et al. 2012, Lattenkamp et al. 2019, Hanrahan et al. 2022). Experiments can be conducted both in the field and in the laboratory, each with its advantages: field studies capture natural behaviours and context-dependent interactions (e.g., Lin et al. 2015, Springall et al. 2019, Fernandez et al. 2021), whereas laboratory experiments provide greater control over variables (e.g., Gadziola et al. 2012, Wright et al. 2014). Playback experiments are another valuable approach, enabling the exploration of signaller and receiver interactions and the validation of the functions of recorded vocalisations (e.g., Barlow and Jones 1997, Prat et al. 2015). Moreover, the emotional state can be encoded in the vocalisation, known as motivation-structural rules (Morton 1977), allowing vocalisations to be assigned to potential function categories once sufficient acoustic and behavioural data are available across species (Lattemkamp et al. 2019, Gadziola et al. 2021). Pfalzer and Kusch (2003) also classified bat social vocalisations into four categories based on spectro-temporal contours and shapes: Type A calls are squawk-like, noisy signals associated with aggression and threat; Type B calls are repeated trill calls linked to distress, consisting of rapid frequency-modulated vocalisations; Type C calls are cheep-like and curved frequency-modulated calls used in mother-infant recognition and group cohesion; and Type D calls are complex, song-like vocalisations used in mate attraction or territorial defence, combining several distinct syllables. These methodological approaches are not mutually exclusive and can be combined depending on the research aims. Thus, the complexity and context-dependence of social calls make them difficult to classify, underscoring the need to consider both call structure and associated behaviours together (Jahelková et al. 2008, Wright et al. 2013, Springall et al. 2019).

Bat social calls serve a variety of functions that facilitate interaction both within and between species (Russ et al. 2004, Gillam and Fenton 2016, Chaverri et al. 2018, Huang et al. 2018). For example, social calls can facilitate group hunting at foraging sites, where social calls may attract more individuals to the area; conversely, social calls can repel intruders when used for territorial defence, thereby reducing the activity of competitors (Bohn et al. 2009, Chaverri et al. 2018, Gotze et al. 2020). Near roosts, social calls function to advertise roost locations and assist conspecifics to relocate roosts (Ruczynski et al. 2007, 2009, Chaverri and Gillam 2010, Chaverri et al. 2012, Chaverri et al. 2018). Also, nursing female bats can identify their own offspring through the specific social calls produced by pups (Thomson et al. 1985, Bohn et al. 2007, Chaverri et al. 2018). In addition, individuals eavesdrop on social calls of heterospecifics, most commonly congeneric species, to obtain social information, for example, by listening for alarm calls (Russ et al. 2004, Chaverri et al. 2018, Huang et al. 2018) or reducing activity to avoid competition after detecting territorial songs (Voigt-Heucke et al. 2016). Social calls can comprise sequences of complex syllables that form songs (Bohn et al. 2008, 2009, Collier and Parsons 2022) and are often associated with mating displays (Bohn and Gillam 2018). For example, male greater sac-winged bats *Saccopteryx bilineata* produce mating songs and display courtship behaviours, facilitating mate choice (Voigt and von Helversen 1999, Voigt et al 2008). The complex territorial/countship songs in Brazilian free-tailed bats *Tadarida brasiliensis* (Bohn et al. 2008, 2009), Seba's short-tailed fruit bats *Carollia perspicillata* (Knörnschild et al 2014), lesser short-tailed bats *Mystacina tuberculata* (Toth and Parsons 2018, Collier and Parson 2022), and greater mouse-eared bats *Myotis myotis* (Rrintz et al 2026) have also been recorded. These complex sequence songs can encode individuality in lesser short-tailed bats (Toth and Parsons 2018) and greater sac-winged bats (Behr and von Helversen 2004) and can be an honest signal to show body condition (Toth et al 2018). Taken together, social calls represent a context-dependent communication that not only mediates interactions within species but also affects heterospecific dynamics in bat communities.

1.3 Urbanisation as an environmental stressor that affects wildlife behaviour

The rapidly urbanising world has created major challenges for wildlife through significant habitat modification and the introduction of anthropogenic stressors, including deforestation, fragmentation, noise, and light pollution (Bunkley et al. 2015, Theodorou 2022, Moreno-García et al. 2025). These negative effects often lead to population declines and local extinctions (McDonnell and Hahs 2015, Piano et al. 2020, Moreno-García et al. 2025), particularly among habitat specialists with strict ecological requirements (Hahs et al. 2023). By contrast, some species can persist or even thrive in urban environments, owing to their broader environmental tolerance (Bonier et al. 2007) or behavioural flexibility (Lowry et al. 2013). For example, generalists can adapt successfully to urban areas by exploiting built structures, artificial light, or anthropogenic food sources, often by altering activity patterns, foraging strategies, movements, or social interactions (Lowry et al. 2013, Ives et al. 2016, Ritzel and Gallo 2020, Villarroya-Villalba et al. 2021). Thus, urbanisation acts as an ecological filter, disadvantaging specialist while favouring generalist and behaviourally flexible species (Jung and Threlfall 2018, Hahs et al. 2023).

For species living in urban areas, studies across diverse animal taxa, including mammals (Santini et al. 2019), birds (Møller 2009), and reptiles (French et al. 2018), reveal that animals adjust their behaviours in response to urbanisation. For example, limited resources can lead to increased aggression and competition, observed in birds (Scheun et al. 2015, Hardman and Dalesman 2018, Önsal et al. 2022), squirrels (Parker and Nilon 2012), and bats (Starik and Göttert 2022). Diurnal lizards have shifted to more nocturnal activity under increased artificial light at night (Taylor et al. 2022). Some animals decrease their home range in response to urbanisation, such as opossums *Didelphis virginiana* (Harveson et al. 2005) and white-tailed deer *Odocoileus virginianus* (Harveson et al. 2007). In contrast, groups living striped field mouses *Apodemus agrarius* in urban areas exhibit increased social tolerance to avoid conflicts with conspecifics (Łopucki et al. 2021). Examining the behavioural adjustments of urban-tolerant species is critical to improve understanding of the ways individuals interact and communicate under increasing urban pressures.

Noise pollution in urban areas can mask, distort, or even block acoustic signals, particularly those used in communication. Species relying on acoustic communication often alter their signal patterns in response to urbanisation. For example, birds adjust their calling behaviour under increased anthropogenic noise by shifting song rate, frequency, or amplitude to improve signal transmission (Halfwerk et al. 2012, Önsal et al. 2022, Munoz-Santos and Ríos-Chelén 2023, Hawkins et al. 2024). Amphibians such as frogs increase call pitch (producing higher-frequency calls) and calling rate in noisy environments (Higham et al. 2021, Zaffaroni-

Caorsi et al. 2023). These signal adjustments can further influence ecological processes such as mating success and social interactions (Cole 2013, Candolin and Wong 2019). Given that bats are highly vocal and taxonomically diverse, they are a good model taxon for studying the impacts of urbanisation on acoustic communication and social interactions. Yet, despite their reliance on both echolocation and social calls, how bats adjust their communication and social interactions in response to urbanisation remains largely unknown.

1.3.1 Species specific responses to urban habitat change

Numerous studies consistently reveal that bat species richness, abundance, and activity decline with increasing urbanisation, though these effects are mitigated by the presence of green spaces (Theodorou 2022, Moreno-García et al. 2025). Greater canopy cover and other vegetation, in addition to accessible sources of water, provide essential food resources and roosting opportunities (i.e., tree hollows), supporting higher bat diversity and activity (Luck et al. 2013, Ancillotto et al. 2016, Silva de Araújo and Bernard 2016, Callas et al. 2024). In contrast, impervious surfaces such as buildings and concrete infrastructure have a negative effect on bat activity (Dixon 2012, Luck et al. 2013). These consistent patterns suggest that green spaces within urban areas are critical for sustaining bat diversity and facilitating the persistence of bats in urban areas (Silva de Araújo and Bernard 2016, Callas et al. 2024, Parsons et al. 2025).

Key traits influence whether bats can persist in urban areas, with species differing according to their ecological and behavioural adaptations. Based on echolocation call structures (Aldridge and Rautenbach 1987, Denzinger and Schnitzler 2013), wing shapes (Norberg and

Rayner 1987), and foraging strategies (Denzigner and Schnitzler 2013), bats can be commonly grouped into three foraging guilds: open, edge, and narrow space foragers. For example, open-space foragers typically emit low-frequency echolocation calls that travel further and possess long, narrow wings that allow fast, high-altitude flight to capture aerial prey in open habitats. These characteristics allow them to travel long distances where they do not need fine details of the surrounding environment. In contrast, narrow-space foragers use high-frequency calls that provide better resolution of the environmental background and have short, broad wings, enabling manoeuvrable flight within dense vegetation to detect prey at close range. Edge-space foragers combine features of both strategies, exploiting patchy prey near vegetation and show flexible movement patterns that often allow them to utilise fragmented or moderately disturbed habitats (Aldridge and Rautenbach 1987, Denzinger and Schnitzler 2013). In urban areas, some edge-space foragers may be particularly successful because they can take advantage of swarming insects around streetlights in urban areas (Stone et al. 2015, Haddock et al. 2019a, b). Much research has examined bat assemblage and foraging guilds in response to urbanisation, yet few studies have explored how urban environments affects bat social communication and interactions.

1.3.2 Urbanisation affecting resource availability and bat social interactions

Social calls in bats play an important role in mediating interactions during foraging, particularly in resource limited areas. Bats can vary their social interactions in response to urbanisation. For example, an urban tolerant species, the common pipistrelle *Pipistrellus pipistrellus* in Berlin produces agonistic and advertisement calls more frequently in urban areas, potentially reflecting territorial defence at foraging sites, whereas co-occurring species, serotine bats *Eptesicus serotinus* and common noctules *Nyctalus noctula*, do not show similar increase in agonistic calls in urban areas (Starik and Göttert 2022). Other studies have also found no consistent increase in social calls in urban areas (Silva de Araújo and Bernard 2016). Thus, social interactions mediated by using social calls in urban areas have species- and context-specific responses.

Urbanisation can drive structural modifications in vocal signals, with animals adjusting parameters such as frequency and duration to cope with anthropogenic noise and altered habitats. Only a few studies have found that spectral and temporal parameters of echolocation and social calls change in urban areas. For echolocation calls, bats increase frequencies and decrease durations, possibly to overcome change in habitat structure and anthropogenic noise to improve detection resolution (Starik and Göttert 2022, Yantén et al. 2022). Starik and Göttert (2022) is the only study to reveal that bats in urban areas adjust their social calls to higher frequencies and shorter durations, similar to adjustments observed in echolocation calls. The pattern is likely a response to anthropogenic noise and changes in habitat structure (i.e., more spatial complexity in urban areas), mitigating temporary disturbance despite the fact that the acoustic frequency of social calls is generally higher than those of anthropogenic noise. These findings suggest that urban pressures may affect acoustic signals, although current evidence in bats is limited.

The decline in roost density is another major challenge for bats in urban areas, with direct consequences for bat social roosting patterns. Most bats form social congregations in roosts, and the strength of associations are shaped by intrinsic and extrinsic factors, including population density, sex, and relatedness, and habitat structure and roost density, respectively (Kerth 2008, Johnson et al. 2013, Wilkinson et al. 2019). Studies indicate that bats form non-random associations, with social structure influenced by kinship, familiarity, and reciprocal interactions (Wilkinson et al. 2019). Deforestation and urban expansion reduce the availability of mature trees with cavities and hollows for many bat species, which may promote increased congregation in the few remaining roosts (Chaverrii 2010). Social network analyses provide a valuable framework to quantify these dynamics, offering insights into how differences in roost density shape group association patterns and overall colony structure (Johnson et al. 2013, Silvis et al. 2016). For example, areas with low roost density may drive more aggregative roosting, resulting in more potential connection between individuals (Chaverri 2010). Understanding the relationship between roost density and bat social networks provides insights into the role of social interactions in roosting behaviours.

Changes in roosting patterns may also affect bat social communication, as roosting groups live with kin or familiar individuals. Acoustic signals are an efficient mechanism for maintaining social connections, facilitating roost-mate recognition, and assisting individuals to locate roosts and roosting mates (Gokcekus et al. 2021, Furmankiewicz and Jone 2022). Many bat species can discriminate roosting mates' social vocalisations (Arnold and Wilkinson 2011), and these vocalisations vary among colonies and individuals (Carter et al. 2012, Vrtilek et al. 2025). Given that roost density alters social networks by changing the frequency of interactions between individuals, the need to maintain group cohesion and recognition may drive adjustments in communication. Indirect evidence from common vampire bats *Desmodus rotundus* suggests that cohabitation can promote vocal similarity through social learning, even though individuals have unique vocal signatures (Vrtilek et al. 2025). Considering the roost density, a possible hypothesis for this is that in large colonies comprising lots of individuals, variation in social vocalisations may be driven by demands for individual recognition, whereas in colonies with subgroups comprising of fewer individuals, variation in social vocalisations may reflect not only individual signatures but also group-level signature shaped by social learning. Taken together, roost density may affect bat social networks (Chaverri 2010), which in turn potentially affect bat social communication. This idea has not yet been tested in bats, but it has important implications for urban habitat management. In particular, compensatory artificial roost installations may be necessary to support urban populations, as large colonies aggregated in a single roost may be more vulnerable to disturbance, such as habitat loss, than those distributed across multiple groups (Chaverri and Kunz 2011).

1.4 Research gaps and thesis structure

Very few studies have explored social vocalisations in Australian echolocating bats. To date, only ghost bats, *Macroderma gigas*, has been well-studied, including vocalisation analyses, playback experiments, and the application of social vocalisations in the field, such as acoustic lure for improving detection effectiveness (Guppy et al. 1985, Hanrahan et al. 2019, Hanrahan et al. 2022, Ruykys et al. 2023, Hanrahan et al. 2024). Except for ghost bats, no other echolocating bat in Australia has been systemically studied for its social communication.

The aim of my study is to categorise and interpret social vocalisations in echolocating bats and to investigate how these social vocalisations change in response to urbanisation. Bats inhabiting urban areas may encounter distinct environmental pressures, including impervious surfaces, limited roost resources, and vocal communication disruption. To address this aim, I used the Gould's wattled bat, *Chalinolobus gouldii*, as a model species. *Chalinolobus gouldii* is widely distributed across Australia, ranging from rural to urban areas (Scanlon and Petit 2008, Threlfall et al. 2011, Threlfall et al. 2012b, Godinho et al. 2019). It is an aerial-hawking, edge-space forager that forages primarily on Hymenoptera and Lepidoptera (Vestjens and Hall 1977, McKenzie and Rolfe 1986, O'Neill and Taylor 1898, Fullard et al. 1991). *Chalinolobous gouldii* shows relatively high activity in urban green spaces compared with other species (Scanlon and Petit 2008) and is tolerant to urban stressors (Threlfall et al. 2012a, Threlfall et al. 2012b), such as artificial light at night (Straka et al. 2016, Haddock et al 2019b). For male *C. gouldii* have been recorded foraging closer to their roosts than females (Evans and Lumsden 2011). They can roost in both tree hollows, some buildings, and bat boxes installed in urban areas (Griffiths et al. 2019, Griffiths et al. 2020, Lumsden et al. 2020, Velasco et al. 2023). During the breeding season, *C. gouldii* form maternity colonies with related females and having both preferred and avoided associations (Godinho et al. 2015, Eastick 2022), ranging from eight to 58 individuals (Godinho et al. 2015, Godinho et al. 2019). Compared to males, females show stronger pair association (Godinho et al. 2015).

Previous studies have found that *C. gouldii* is highly adapted to urban environments and predominantly use artificial bat boxes, yet little is known about the social interactions and vocal communication of this species. The central question of this thesis is: **Does *C. gouldii* adjust its vocal communication to cope with urban life?**

To answer this question, I first explored the social vocalisations of *C. gouldii* and then assessed how these social vocalisations varied across ecological contexts. Specifically:

Chapter 2: I described the repertoire of social vocalisations in *C. gouldii* at foraging and roost areas, over a one-year period. I hypothesised that *C. gouldii* social vocalisations varied over time, potentially associated with different functions at different stages of the life cycle, such as facilitating group cohesion during the nursing period and attracting mates in the mating period.

Chapter 3: I broadcast *C. gouldii* vocalisations in the field and observed conspecific and heterospecific responses using acoustic and video recordings. I hypothesised that *C. gouldii* respond to conspecific vocalisations differently depending on information the vocalisations conveyed. I also hypothesised that heterospecifics with overlapping ecological niches of *C. gouldii* may eavesdrop on *C. gouldii* social vocalisations to exploit information to improve resource discovery or acquisition.

Chapter 4: I assessed the effects of habitat attributes (canopy cover, water bodies, and urbanisation) on *C. gouldii* social vocalisation rates and evaluated vocal adjustments by the species in response to urbanisation. I hypothesised that *C. gouldii* would produce social vocalisations at different rates to potentially reflect the differences in resource availability, such as prey and roosts, in urban versus rural areas. Alternatively, the social vocalisation rates did not change, instead the number of social vocalisations produced might reflect conspecific activity rather than habitat attributes. I also hypothesised that *C. gouldii* might adjust their social vocalisations to mitigate masking from increased impervious surfaces or noise in urban areas.

Chapter 5: I did a preliminarily exploration of the association between roost density, social networks, and variation in *C. gouldii* social vocalisations in urban areas. I hypothesised that roost density might affect *C. gouldii* roosting social networks, which in turn might drive variation in their social vocalisation.

Chapter 6: I synthesised the findings from the above experiments and observations to explain how *C. gouldii* cope with urbanisation through vocal communication and highlighted key research gaps.

Chapter 2

Characterization and seasonal variation in the social vocal repertoire of *Chalinolobus gouldii*, Australia’s most widespread bat

Note: This chapter was submitted to the *Journal of Mammalogy* (July 2025); and is currently being revised for resubmission after review, using American English. Reviewer feedback has been incorporated into the version in this thesis.

Abstract

Communication plays crucial roles in survival and reproduction of animals in a changing world. Bats are known for their exceptional auditory and vocal abilities, and it is increasingly recognized that bats, like other social animals, have sophisticated acoustic communication systems. Studies of social vocalizations can provide valuable new insights into the behavioral ecology of bats and other cryptic animals. Gould’s wattled bats *Chalinolobus gouldii* are a widely distributed species using various habitats across Australia. However, nothing is known about the species’ social vocalizations. This study aimed to collect and categorize the social vocalizations of *C. gouldii* at foraging and roosting sites to examine seasonal patterns corresponding to the life-cycle periods in repertoire size and composition. I statistically identified at least five social vocalization syllables and an additional human-audible, broadband sound. Social vocalizations occurred occasionally at foraging sites but were relatively common at roosting sites. In general, social vocalization rates decreased during winter, although site-specific variation was observed. Whilst the composition of social vocalizations did not change across the life-cycle periods, multi-syllable sequences were observed during the pregnancy, nursing and mating periods. Among the identified social vocalization syllables, two types (Syllable 1 and 2) were used more frequently than the other three at both foraging and roosting sites across all seasons, suggesting a potential role in facilitating affiliative interactions. Further research should investigate the behavioral significance of *C. gouldii* social vocalizations and the effect of habitat characteristics on the use of specific social vocalizations.

Keywords

Chiroptera, Gould's wattled bats, Hierarchical Agglomerative Clustering (HAC), motivation-structural rules, social calls, social communication, syllables

Introduction

Acoustic communication is a widespread phenomenon across mammals. Communication via sound has the benefit of rapid, long-distance information transfer, and is effective in environments where visual signals are obstructed. Studies on the vocal repertoire of species increase our understanding of their behavioral ecology, especially for those animals with complex societies. In general, social complexity positively correlates to vocal complexity and vocal repertoire size in animals including birds (Leighton and Birmingham 2021), primates (Bezerra and Souto 2008), and lemurs (Batist et al. 2023). Whilst this has been studied extensively in the human-audible range, vocalizations also occur in the ultrasonic range. Knörnschild et al. (2020) suggest a positive relationship exists between social complexity and vocal complexity in bats. Approximately 1,500 described bat species worldwide heavily rely on vocalisations to communicate (Simmons and Cirranello 2025). Among these, echolocating bats (called bats hereafter) have an outstanding auditory-vocal system and can be a good model taxon to study acoustic social interactions (Salles et al. 2019). They emit not only high frequency echolocation calls for navigation but also produce diverse non-navigation sounds such as social vocalizations for communication. For bats, social vocalizations are crucial to efficiently convey social information due to their nocturnality and group-living behaviors. Hence, a greater research focus on the vocal repertoire of bats will assist in understanding behavioral dynamics within and between species.

Studies of bat social vocalizations have only emerged in the last few decades compared to studies on echolocation. The challenges of studying bat vocalizations result from their dual functions and purposes, meaning that bats produce sounds for both navigation and communication (Pfalzer and Kusch 2003, Jones 2008, Jahelková 2011), and their nocturnality, requiring specialist equipment. Studies on bat vocal repertoires use a variety of methodologies. A common method is to describe the nomenclature of calls by visual discrimination of temporal-spectral structure identified via a spectrogram, including the modulation of frequency over time and the shapes of calls (Springall et al. 2019). Some studies focus on the association between specific social vocalizations and their relevant behaviors, for example contact calls for group reunion and isolation calls for mother-offspring recognition (Knörnschild et al. 2013, Chaverri et al. 2018). Other studies link the description of temporal-spectral patterns on the spectrogram with behavioral responses to interpret the functions of vocalizations (Gadziola et al. 2012, Lattenkamp et al. 2019). However, these approaches of using visual discrimination may be subjective and difficult to replicate. A further challenge is the gradation between calls. For example, for big brown bats *Eptesicus fuscus*, vocal classifications differ between human observers due to differences in how observers manually identify the vocalizations (Gadziola et al. 2012, Springall et al. 2019), affecting the consistency of further analyses. Therefore, where possible, an objective classification method should be employed (Sainburg et al. 2020). Many studies of mammal vocal repertoire apply objective methods, such as Hierarchical Agglomerative Clustering (HAC) to effectively separate sound types. These have been successfully used in ghost bats *Macroderma gigas* (Hanrahan 2020), blue monkeys *Cercopithecus mitis stuhlmanni* (Fuller 2014), black and white ruffed lemurs *Varecia variegata* (Batist et al. 2023), humpback whales *Megaptera novaeangliae* (Fournet et al. 2015), and quolls *Dasyurus viverrine* (Dorph and McDonald 2017), showing promise in being widely applicable across taxonomic groups.

Understanding the characteristics and potential meaning of social vocalisations can inform our knowledge of species' communication, behaviors, and sociality (Chaverri et al. 2018). Many studies indicate that bat social vocalizations carry specific social information which is important for social interactions, particularly maintaining non-random associations and individual identity (Pfalzer and Kusch 2003, Chaverri et al. 2018). For example, common vampire bats *Desmodus rotundus* recognize individuals via calls (Carter et al. 2009), greater spear-nosed bats *Phyllostomus hastatus* produce the social vocalizations to coordinate foraging between social group members (Boughman 1997, Wilkinson and Boughman 1998), and Seba's short-tailed fruit bats *Carollia perspicillata* discriminate their offspring based on individual sounds (Knörnschild et al. 2013). Social vocalizations can also facilitate resource discovery. For example, Spix's disc-winged bats *Thyroptera tricolor* produce social vocalizations that benefit conspecifics by helping them find potential roosts (Sagot et al. 2018), and big brown bats *Eptesicus fuscus* indicate the ephemeral prey locations by emitting specific sounds (Wright et al. 2014). Bats produce aggressive calls in food limited areas to decrease the activity of other individuals (Starik and Göttert 2022). Moreover, social vocalizations may vary seasonally, comprising multiple syllables, in bats (Springall et al. 2019, Hanrahan 2020), such as autumn swarming courtship songs that potentially act to maintain territoriality or for mate attraction during the mating season (Russ et al. 2003, Middleton et al. 2014, Toth and Parsons 2018, Springall et al. 2019, Collier and Parson 2022). During the mating season, bats display courtship behaviors during vocalizing to facilitate mate choice (Voigt and von Helversen 1999, Voigt et al 2008, Collier and Parson 2022). These studies highlight the diversity of social vocalizations both between and within species; thus, exploring the range of vocalizations in species can aid in understanding of their habitat use and resource acquisition, knowledge which is increasingly important for conservation and habitat management.

Gould’s wattled bats *Chalinolobus gouldii* are an endemic but widely distributed species across the Australian continent, inhabiting both rural and urban areas, providing a good opportunity to study how their vocal behaviors differ in a variety of habitats. The life cycle of this bat in temperate regions follows an annual pattern, mainly being split into four periods: pregnancy in spring, from September to early November; nursing (birth and rearing) in summer, from early November to the February of the following year; mating in autumn, from March to May; and hibernation (low activity season) in winter, from June to August (Eastick et al. 2022). Two litters are sometimes produced by this species in a single season, which may slightly prolong the nursing period and delay the onset of mating (Eastick et al. 2022). This bat usually lives in familial groups at roosts during the nursing period (Godinho et al. 2015, Eastick 2022), which may confer cooperative breeding benefits or information transfer about roosts or foraging areas. It remains unknown whether *C. gouldii* individuals exchange social information through vocalisations while foraging and/or roosting in groups, as has been observed in other species in both during foraging and roosting (Kerth et al. 2001a, O'Donnell 2001).

The aim of this study is to describe the repertoire of social vocalizations in *C. gouldii* and examine how this repertoire varies at different times throughout its life cycle. I collected acoustic data across all seasons to address two specific questions: (1) How many types of social vocalizations does *C. gouldii* produce at foraging and roosting sites? (2) Does the composition of *C. gouldii* social vocalization change seasonally, corresponding to the key stages of the species’ life cycle, namely pregnancy, nursing, mating, and hibernation? I hypothesized that *C. gouldii* social vocalization behaviors vary over time, potentially associated with different functions at different stages of their life cycle, such as facilitating group cohesion during the nursing period and attracting mates in the mating period.

Materials and methods

Study site

The study was conducted across a range of landscapes in the Greater Sydney metropolitan area (New South Wales, Australia), located within the Cumberland Plain bioregion. This area is a sedimentary basin situated to the west of Sydney Harbor and extends across the Western and Southwestern Sydney, given rise to comparatively fertile clay soils (Tozer 2003). *Chalinolobus gouldii* is the most recorded echolocating bat species in these environments (Threlfall et al. 2011). I conducted at *C. gouldii* foraging (n = 11) and roosting sites (n = 4), 15 sites in total, from urban areas to farmlands (Figure 2.1, supplementary information S2.1). Eleven sites were selected from a larger pool of potential sites to include areas that have known high bat activity, increasing the likelihood of recording social interactions. Sites were centered on potential foraging areas or on known roost locations of the target species. I considered waterbodies to be likely foraging areas and were typically places where high activity of the target species has been previously recorded. As such, we established our 'foraging' sites adjacent to waterbodies, natural or human-made ponds, within bushland and parkland. In addition, we established our 'roosting' sites at four bat summer roosting sites, where *C. gouldii* have been observed to regularly occupy artificial bat boxes during the pregnancy and nursing periods. I selected one of the artificial bat boxes per site for sampling, where our selection was based on a box likely or previously used by the target species (Velasco et al. 2023). Detailed site information is provided in supplementary information S2.1. All recording locations of foraging and roosting sites were separated by at least 100 m. Bat activity across all foraging and roosting sites did not show spatial autocorrelation (supplementary information S2.2). Data collection was approved by Animal Research

Authority (2020/1825 and 2023/2386) of The University of Sydney.

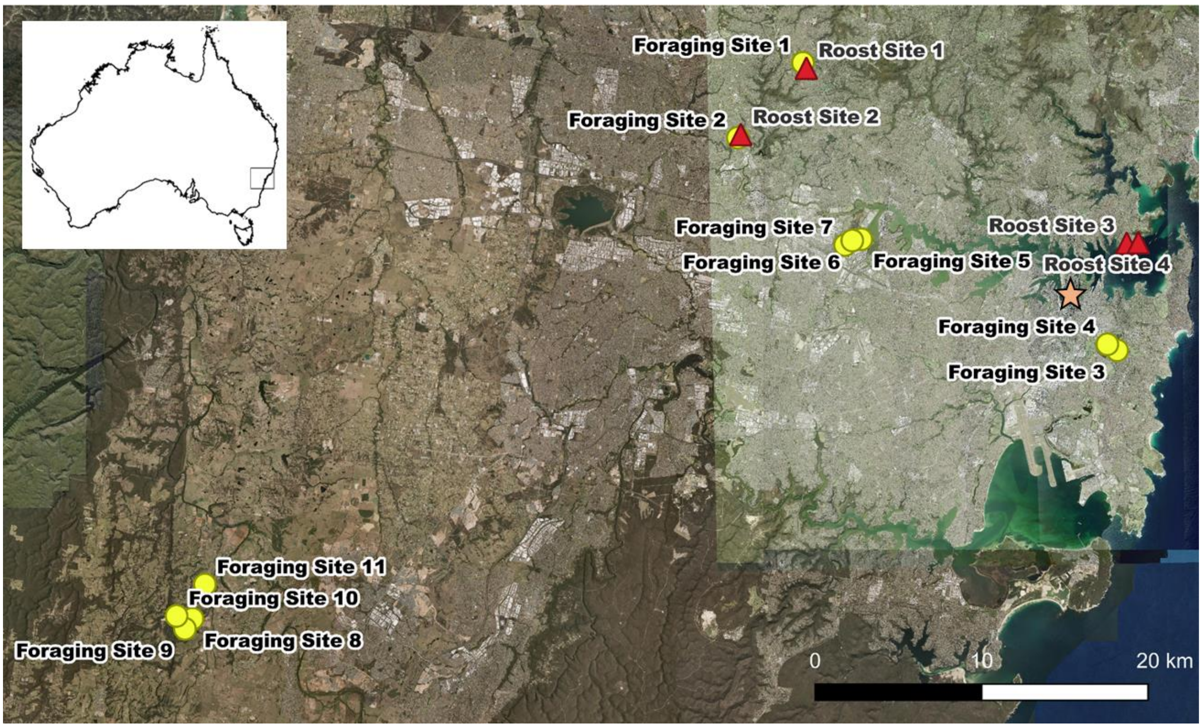


Figure 2.1. Map of the foraging (circles, n= 11) and roost (triangle, n= 4) sites in Sydney, NSW, Australia. Star symbol indicates Sydney city center.

Acoustic recording

Acoustic recordings were sampled from November 2022 to September 2023. Each of the four observation periods (pregnancy, nursing, mating, and hibernation) had at least three days of recording at foraging and roosting sites. Autonomous ultrasonic recording units were used to record vocalizations (for details, see supplementary information S2.1). To record vocalizations at foraging sites, an ultrasonic recorder was deployed and positioned 1.5 m away from the edge of waterbodies. The ultrasonic microphones were set at least 1.5 m high and horizontally faced the waterbodies to reduce recording high-altitude flying bats. To record vocalizations at roosting sites, an ultrasonic recorder was positioned 3.5 m away from the selected bat box and tilted at a 45-degree angle up toward the box.

All ultrasonic recorders recorded in full-spectrum format. Anabat Swift and Chorus (Titley Scientific, Australia) were set to record at a 256 kHz sampling rate, recording via omnidirectional ultrasonic microphones (Omni-directional Ultrasonic Microphone US-O V3 and Low-Profile Ultrasonic Microphone, Titley Scientific, Australia, respectively). The high pass filter was disabled on both Anabat Swift and Chorus. The sensitivity value setting of these recorders was 16, which is a level higher than the background noise. Recordings were triggered when the call frequency was higher than 10 kHz to reduce false triggers from lower frequency sounds and recorded sequences ranged from a minimum of two seconds to a maximum of 15 seconds per file. The new file started and was re-triggered after reaching the maximum file time. Notably, the minimal frequency of bat social vocalizations is typically above 10 kHz (Pfalzer and Kusch 2003). Some social vocalizations may fall below 10 kHz, but recordings were triggered because parts of the call occur above 10 kHz. AudioMoths were set to record at a 250 kHz sampling rate and with trigger settings of -34 dB and 10 kHz. Once the recordings were triggered, the recorded sequences ranged from a minimum of two seconds to a maximum of 55 seconds. Following a five-second pause, AudioMoth was ready to be re-triggered. AudioMoth files were split into 15-second sections for further analysis. All recordings were scheduled from 30 minutes before dusk to 30 minutes after dawn. The type of recording units did a minor effect on the results (supplementary information S2.3).

Terminology

The terms I used to describe vocalizations are commonly used for bat social vocalizations (e.g., Kanwal et al. 1994, Bohn et al. 2008) and vocalizations from other taxa, including birds (Odom et al. 2021). *Syllable* – a discrete sound surrounded by silences of at least 10 ms. For the sequences with more than one syllable, we defined *mono-syllabic sequences*: a sequence of repetition of the same syllables; and *multi-syllabic sequences*: a sequence of different syllables. *Repertoire* – a set of social vocalizations.

Social vocalization selection

All recording files (n = 75,232) were manually screened for *C. gouldii* vocalizations using Kaleidoscope Pro Analysis Software (Version 5.8.1, Wildlife Acoustic, Inc, USA). Here, echolocation calls are defined as rapid repetition of vocalization with relatively consistent pulses. Social vocalizations are defined as lower in frequency than the species echolocation calls and occur less frequently or are only used in specific situations (e.g., at roosting sites). If the vocalizations differed from the stereotypical echolocation call structure, i.e., the spectrogram of vocalizations presented a distinct shape from surrounding echolocation call sequences, those files with possible social vocalizations were extracted first. I only assessed social vocalizations that were surrounded by echolocation calls to avoid species misidentification. I then identified the species of those social vocalizations by using the program Anascheme software (Version 1.0, Titley Scientific, Australia) to identify the surrounding echolocation call sequences (Adams et al. 2010). Only *C. gouldii* social vocalizations were analyzed in this study.

Extracted social vocalization files were viewed in Raven Pro 1.6 (Version 1.6.5, Cornell Lab of Ornithology, US) to select the target social vocalization and obtain call measurements under full spectrum with Hann function, window size 1024 samples, 75% overlap, 256 hop size, 1024 discrete Fourier transform size. A Band Limited Energy Detector was conducted to detect potential *C. gouldii* vocalizations. The signal detect parameters were minimum frequency 10 kHz, maximum frequency 70 kHz, minimum duration 10.4 ms, maximum duration 100 ms, and minimum separation 10.4 ms. Signal-to-Noise Ratio (SNR) parameters were 50% minimum occupancy, 10 dB SNR threshold. Noise Power Estimation parameters were 1000 ms block size, 150.4 ms Hop size, and percentile at 40. Due to the slightly overlapping parameters between social vocalizations and echolocation calls, I manually removed echolocation calls and poor-quality social vocalizations such as call clipping, overlapping and echoing. The call selection boxes of social vocalizations were adjusted to fit the fundamental component because social vocalizations in echolocating bats usually have multi harmonics, and high frequency components may attenuate due to either sound amplitude or recording distance. After this process, only call selection boxes with a signal-to-noise ratio above 25% were retained. *Chalinolobus gouldii* also emitted wide bandwidth and noise-like sounds at roosts, which showed high variation. These sounds were not included in the analysis and shown in the spectrogram only.

Thirty temporal-frequency measurements of each selected vocalization were taken from Raven Pro 1.6 either directly from the default measurements or calculated from the program's measurements (e.g., slope is defined as the difference between the maximum and minimum syllable frequency divided by the syllable duration), seeing in supplementary information S.2.4. Correlation among these 30 measurements was examined, and if the correlation coefficient of measurement pairs exceeded 0.8, only the most important measurement was retained (Supplementary information Figure S2.4.1). This included the most biologically meaningful and straightforward measurement from each pair (supplementary information S2.4). This resulted in ten measurements being selected for further analyses. These were peak frequency, bandwidth, minimal frequency, aggregate entropy, duration, the proportion of time reached peak and center frequency, slope, and peak frequency contour min slope (Pfalzer and Kusch 2003). Although peak frequency and center frequency were highly correlated (0.95), I kept the two measurements due to potential importance in bat vocalizations.

Social vocal repertoire

To identify the number of different social vocalization types produced by *C. gouldii*, Hierarchical Agglomerative Clustering (HAC) was applied. I used the *NbClust* function from the NbClust package, which provided 30 indices to enable comparison of various combinations of cluster counts and distance between clusters to determine the optimal number of clusters (Cardiff et al. 2009). To build a hierarchy of clusters without having a fixed number of clusters, the ten identified measurements were applied by using *complete* linkage method in NbClust which maximized the distance between individual data points in different clusters (supplementary information S2.5).

To assess the accuracy of the vocalization clusters from HAC, a permuted discriminant functional analysis (pDFA) was performed using the *lda* function from the *MASS* package to account for potential non-independence within the dataset. A total of 1000 permutations was conducted for the analysis. In this analysis, peak frequency and centre frequency were distinguished to derive a new measurement (i.e., peak frequency minus centre frequency), and centre frequency was excluded from subsequent analyses because the two measurements were highly correlated.

To examine difference in measurements among social vocalization types, a non-parametric multivariate analysis of variance test (np-MANOVA) based on Euclidean distance with 999 permutations was applied, with device type included as a covariate. Where np-MANOVAs revealed significant effects, generalised linear mixed models (GLMMs) were applied to conduct pairwise comparisons for each call measurement. Individual measurements were set as response variables, social vocalisation types as predictor variables, and devices were included as a random effect. To compare measurements among types while accounting for the mixed-effects structure of the model, estimated marginal means (EMMs) were applied.

Social vocalization seasonal change

To determine seasonal changes in the composition of *C. gouldii* social vocalizations, I first calculated *C. gouldii* total vocal activity by counting the number of 15-second files that contained or did not contain (present or absent) *C. gouldii* echolocation calls or social vocalizations. I then counted the number of social vocalizations per night. If more than one syllable was produced within a 15-second file, the actual number of syllables produced was used as the count, summed over the night. A Spearman's rank correlation test was conducted to assess the association between the total vocal activity (e.g., echolocation calls and social vocalizations) and the actual number of *C. gouldii* social vocalizations per night. Secondly, I calculated the social vocalization rate, defined as the proportion of social vocalizations relative to the total vocal activity per night (e.g., social vocalization syllables produced over the night divided by the number of 15-second files containing vocalizations).

To test the changes in the proportion of syllables, multinomial logistic regression (using the *multinom* function from the *nnet* package) was applied (Ripley and Venables 2023). Social vocalizations recorded at foraging and roosting sites were tested separately. The types of social vocalizations rate from the result of HAC were used as the response variables. Fixed variables included either the life-cycle periods only or the interaction between the life-cycle periods and sites. The most common social vocalization was set as the baseline category, and the hibernation season was set as the seasonal variable baseline. The multinomial logistic regression model at foraging sites, Foraging Site 3, was set as the baseline due to the absence of social vocalization. The multinomial logistic regression model at roosting sites, Roost Site 2 was set as the baseline because its social vocalization rate was lower and differed slightly from other sites. For four of the 11 foraging sites (Foraging Site 8-11), no recording data were obtained during the hibernation period, and the social vocalization rate during the hibernation period varied across roosting sites. Therefore, an additional multinomial logistic regression model excluding all hibernation recording data was conducted.

All statistical analyses were conducted in R Project (Version 4.5.1, R Core Team) under RStudio surface (Version 2025.05.1, Posit Software, PBC) with a significance level alpha of 0.05.

Results

C. gouldii social vocal repertoire

I recorded a total of 4,286 *C. gouldii* social vocalization syllables across four seasons. This included 240 syllables within 68,111 total vocal activity files at foraging sites, equating to 0.4% of total vocal activity. At roost sites, 4,046 syllables within 7,121 total vocal activity files, equating to 56.8% of total vocal activity. Recordings contained *C. gouldii* social vocalizations at seven of the 11 foraging sites and four of the four roosting sites.

The result of HAC determined five optimal types of *C. gouldii* social vocalizations, along with visual validation (supplementary information S2.5). The percentage of correct classification (97.4%) was higher than chance (89.1%; binomial test, p <0.001) obtained from the permuted dataset. The rates and counts of each social vocalization type were shown in (Table 2.1). Syllable 1 and 2 were dominant vocalization types (Figure 2.2).

Table 2.1 The social vocalization rates (the number of syllables/the total vocal activity) and the counts (the number of syllables per night) of each syllable at foraging and roosting sites.

The average of social vocalization rate and count	Syllable 1	Syllable 2	Syllable 3	Syllable 4	Syllable 5
At foraging site					
Rate	0.006	0.003	<0.001	<0.001	<0.001
(SD)	(0.045)	(0.010)	(0.002)	(0.002)	(0.005)
Count	0.5	0.5	0.1	0.1	0.1
At roosting sites					
Rate	5.977	1.213	0.185	0.035	0.1146
(SD)	(12.950)	(3.117)	(0.433)	(0.067)	(0.402)
Count	66.8	13.3	2.0	0.4	1.6

In addition, broadband sounds, referred to as ‘chatting sounds’ were recorded at roosts (Figure 2.2). This sound type was excluded from the HAC analysis because of its high level of disorder and lack of structure. Sequences of *C. gouldii* multi-syllables were recorded as well, where the same syllable was repeatedly emitted multiple times, and sometimes, the sequences were composed of different syllable types (Figure 2.2).

C. gouldii social vocalization syllables

The five social vocalization syllables were distinguished by at least one of the ten measurements, although device type did significantly contribute to this variation (np-MAOVA: device: *df* = 2, sum of square = 13745, R^2 = 0.007, *F* = 17.861, *p* = 0.010; types: *df* = 4, sum of square = 278548, R^2 = 0.138, *F* = 180.983, *p* = 0.010) (Figure 2.3 and supplementary information S2.6). Syllable 1 and 2 were distinct from each other and from the other three syllables, as evidenced by differences in peak frequency, bandwidth, aggregate entropy, slope (bandwidth/duration), minimal frequency, duration, peak frequency contour slope. The other three syllables differed from one another in slope. The five social vocalization syllables had some gradations, as could be determined by visual inspection.

Syllable 1 – Quasi-constant frequency with variation in duration.

Syllable 1 was a relatively long, various duration, and shallow narrowband vocalization, mostly resembling a nearly constant frequency (Figure 2.2 and 2.3). Syllable 1 had the lowest minimal frequency, lowest peak frequency and narrowest bandwidth compared to other social vocalizations (supplementary information S2.6). Syllable 1 was dominant at both foraging and roosting sites (Table 2.1).

Syllable 2 – Curved frequency-modulation descending with variation in duration.

Syllable 2 was a relatively short duration and broadband vocalization, resembling a cheep-like curved frequency-modulation structure with multiple harmonics (Figure 2.2 and 2.3). Syllable 2 had lower minimal frequency, lower peak frequency, and wider bandwidth compared to Syllable 1 (supplementary information S2.6). Syllable 2 was also dominant at both foraging and roosting sites (Table 2.1).

Syllable 3 – Steep narrowband frequency modulation with short duration.

Syllable 3 was a short duration and steep broadband vocalization, having a steep frequency-modulation with a curved structure at the end (Figure 2.2 and 2.3). Syllable 3 had higher minimal frequency, higher peak frequency and wider bandwidth compared to Syllable 1 and 2 (supplementary information S2.6). Syllable 3 was recorded at both foraging and roosting sites, but infrequently.

Syllable 4 –Steep broadband frequency modulation with extremely short duration.

Syllable 4 was an extremely short duration and steep broadband vocalization, having a steep frequency-modulation with multiple harmonics and a subtle curved structure in the end (Figure 2.2 and 2.3). Syllable 4 had the highest minimal frequency, highest peak frequency and widest bandwidth compared to the other four syllables (supplementary information S2.6).

Syllable 5 – Steep broadband frequency modulation intergrading between Syllable 3 and 4.

Syllable 5 was a relatively short duration and steep broadband vocalization, having a steep frequency-modulation and similar to Syllable 3 and 4 (Figure 2.2 and 2.3). Syllable 5 had higher minimal frequency, higher peak frequency and wider bandwidth compared to the other four syllables (supplementary information S2.6).

Broadband ‘chatting sounds’

The chatting sounds were human-audible, low minimal frequency, broadband, disorder, and lack of structure. The sounds often occasionally had frequency modulation components at the initial and end of sounds. In general, the minimal frequency of the sounds was over 10 kHz. The sounds were recorded and produced consecutively near roosts.

Syllable sequence

The syllable sequences were composed of more than two syllables, formed by either the same syllable types or a combination of different types. The syllable sequence occurred between echolocation call sequences at some foraging sites (Foraging Site 1, 2, 5, 6, 8, 9, and 11) (supplementary information S2.7). These sequences of complex vocalizations predominantly occurred during the pregnancy, nursing and mating periods, with the syllable sequences over five syllables found specifically during the pregnancy and mating periods (Figure 2.4). However, the occurrence of syllable sequences showed slight site-specific variation (supplementary information S2.7). Bats at the roosts produced social vocalizations (non-chatting sounds) consecutively, without pauses and intervening echolocation calls. These were difficult to distinguish discrete multi-syllable sequences, and thus I could not estimate the quantity at roosting sites.

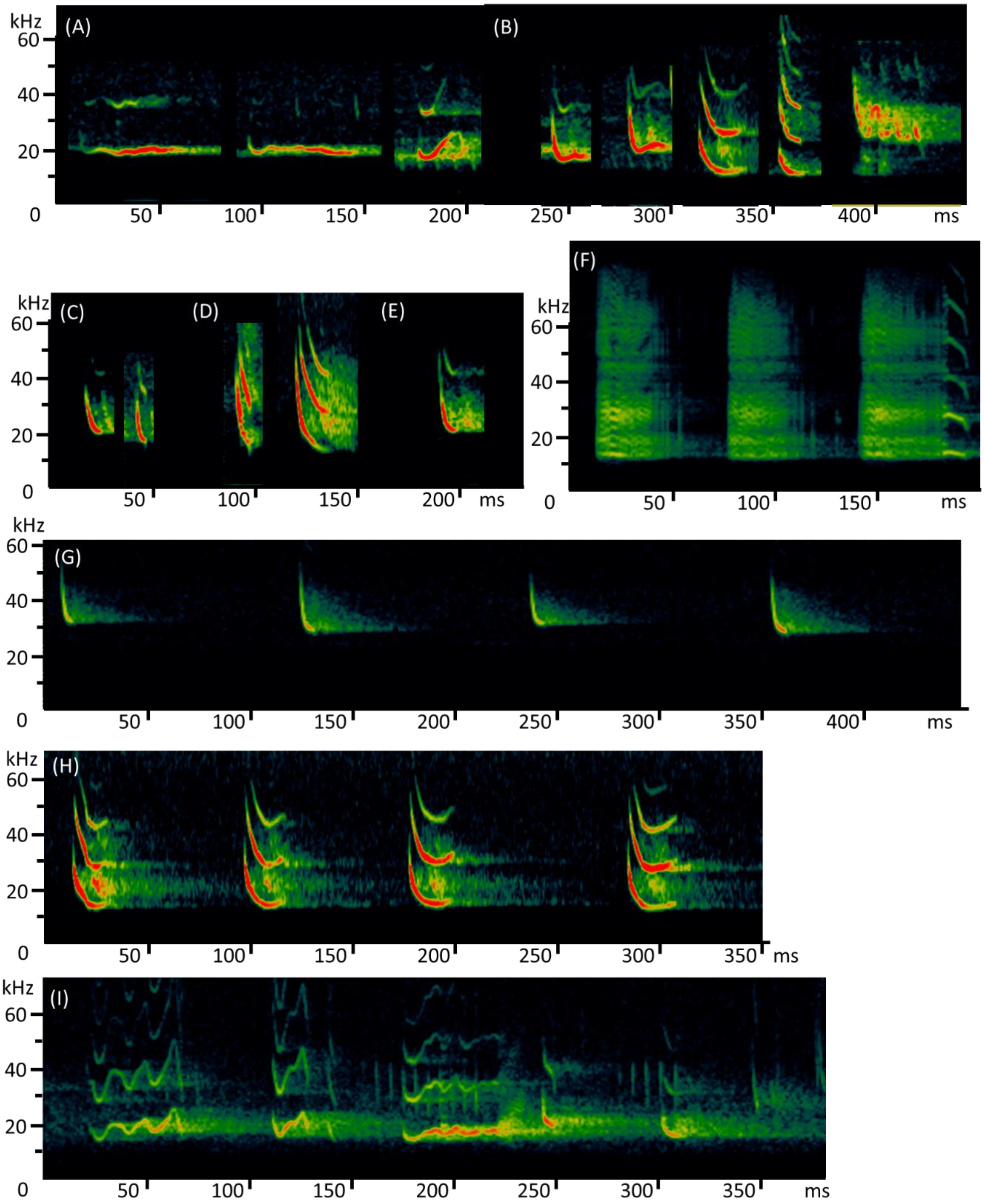


Figure 2.2. The spectrogram of *C. gouldii* vocalizations was displayed using Kaleidoscope. (A) Syllable 1; (B) Syllable 2; (C) Syllable 3; (D) Syllable 4; (E) Syllable 5; (F) broadband disorder chatting sounds; (G) echolocation calls; (H) repeated Syllable 2 mono-syllablic sequence; and (I) complex multi-syllabloc sequence, mainly composed of Syllable 1 and 2.

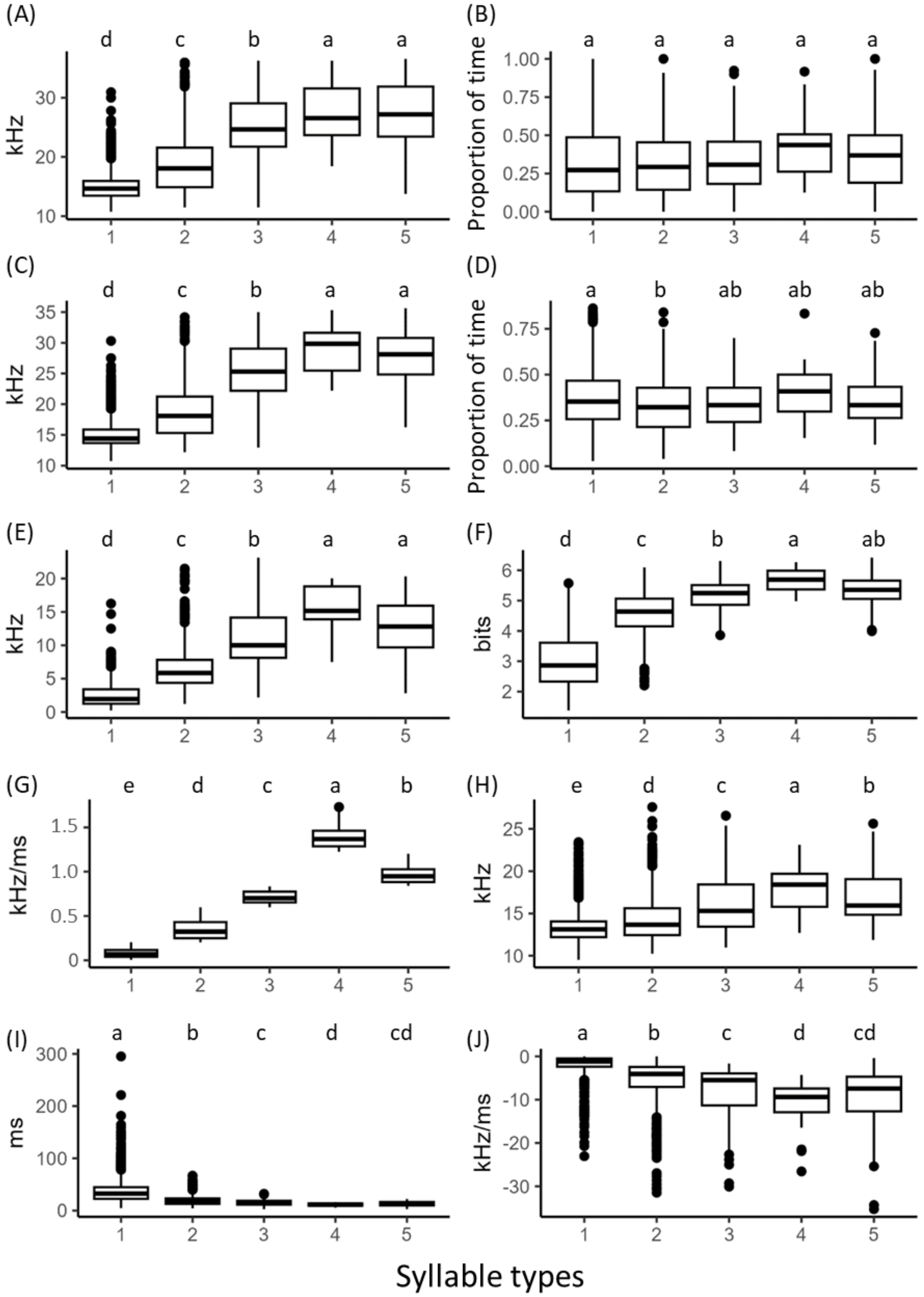


Figure 2.3. Boxplot of call measurement difference among the five social vocalizations (syllable type). (A) Peak frequency; (B) the proportion of time reaching peak frequency; (C) Centre frequency; (D) the proportion of time reaching 50% of the total energy; (E) bandwidth; (F) aggregate entropy; (G) slope (bandwidth/duration); (H) minimal frequency; (I) duration; and (J) peak frequency contour slope. Letters on top of graphs indicate where there are significant differences among the measurements.

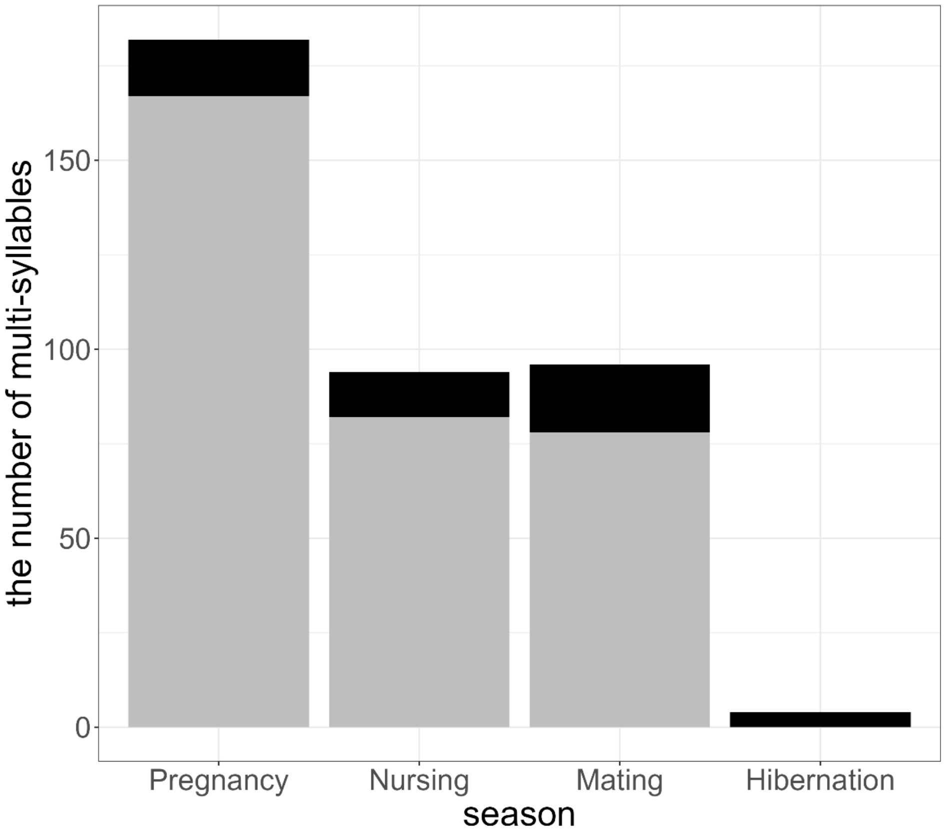


Figure 2.4. The histogram of number of multi-syllables. Grey represents syllable counts ranging from two to five; black represents syllable counts exceeding five.

The effects of seasonality and habitats on C. gouldii social vocalization rate and proportion

At foraging sites, the number of *C. gouldii* social vocalizations was infrequent and varied among sites (mean = 1.3 per night, standard deviation = 4.6, range 0 – 42). The number of social vocalizations was positively correlated with the *C. gouldii* total vocal activity (including echolocation calls and social vocalizations) (Spearman's correlation: ρ= 0.468, p <0.001, Figure 2.5 (a)). In general, a relatively high social vocalization rate occurred during the pregnancy, nursing, and mating periods than during the hibernation period at most sites (Figure 2.6).

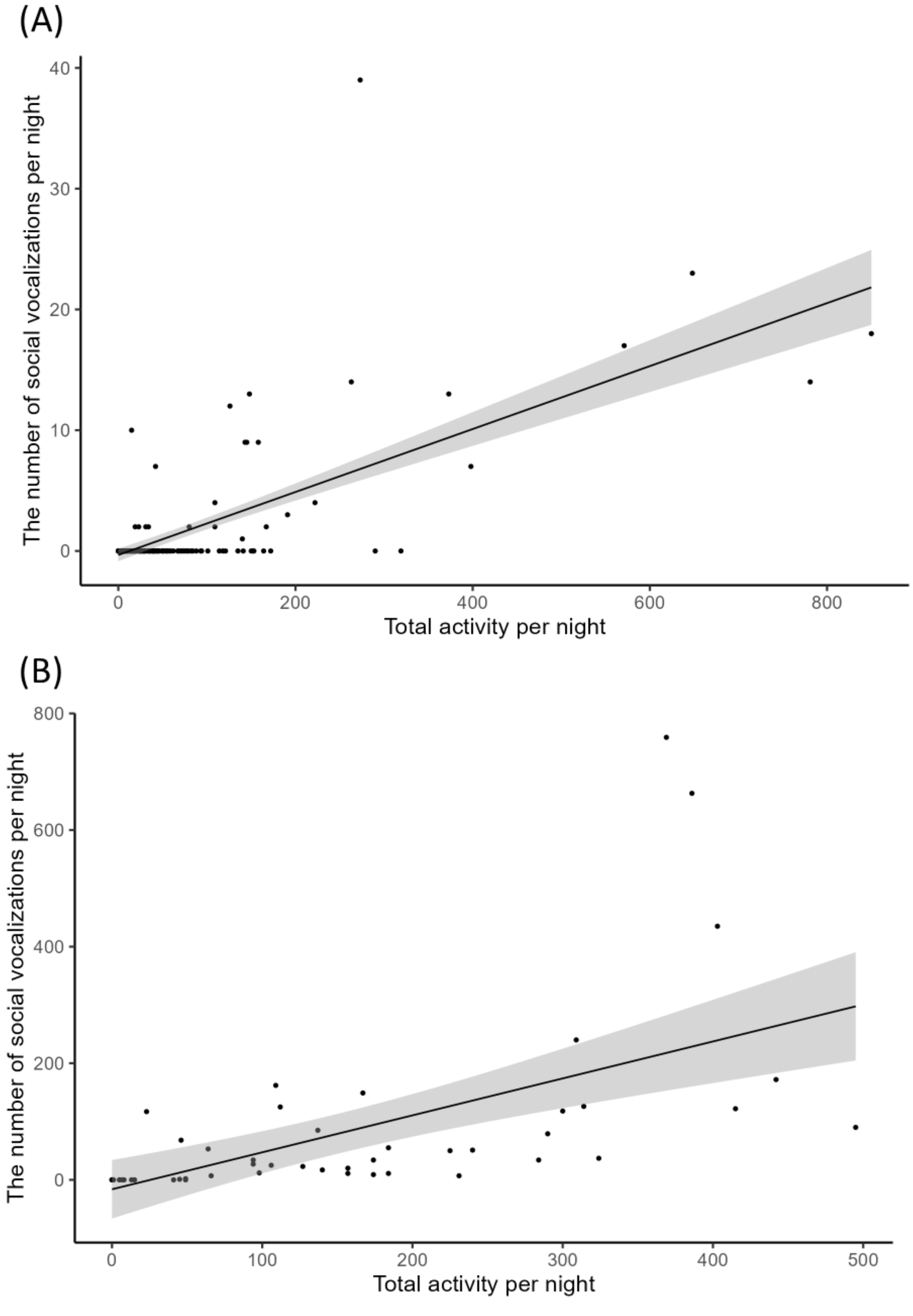


Figure 2.5. The positive correlation between *C. gouldii* activity and number of social vocalizations per night at (A) foraging sites and (B) roosting sites.

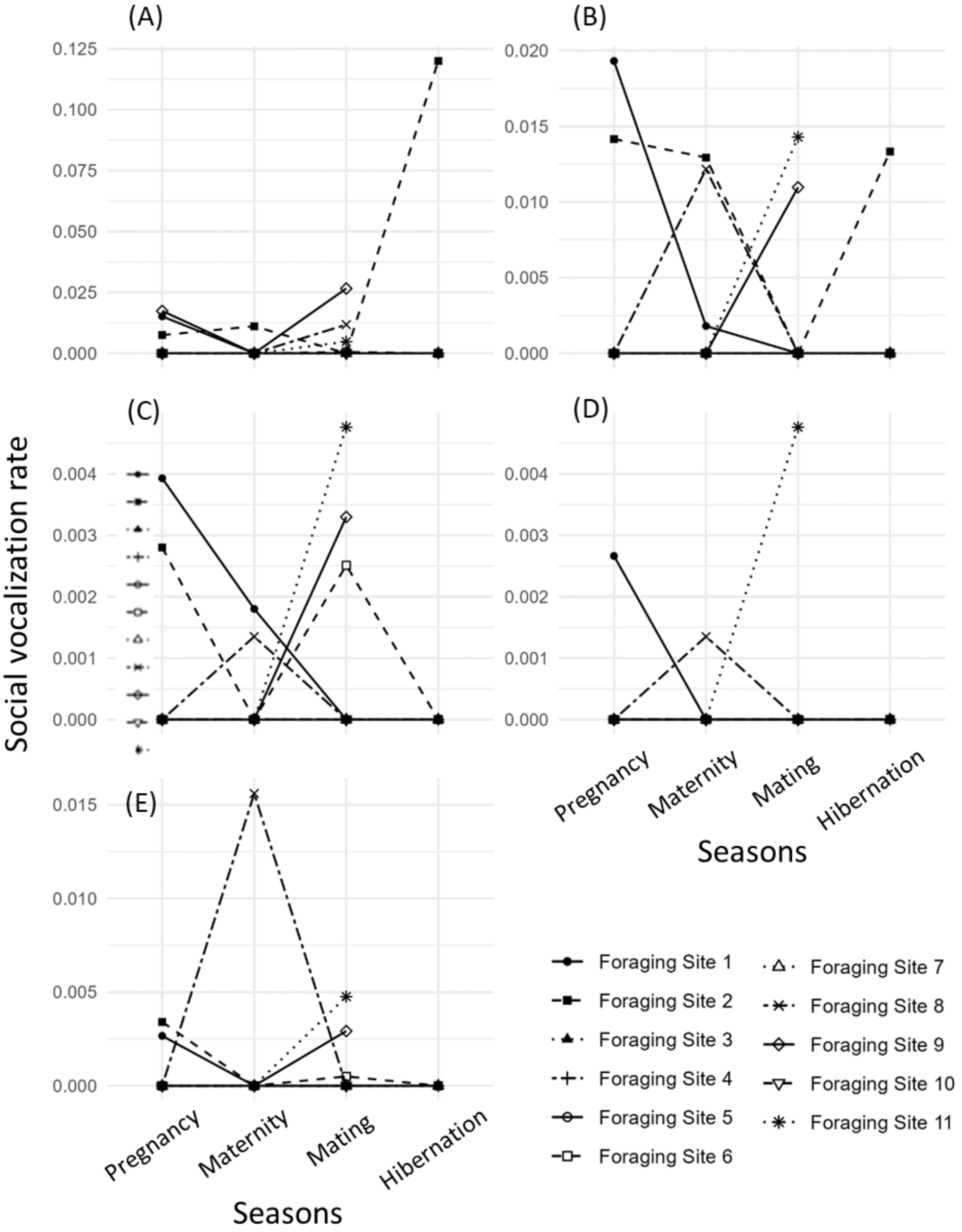


Figure 2.6. The five types of social vocalization rate (the number of social vocalization syllables/the total vocal activity) changes across the four life-cycle periods at 11 foraging sites. (A) Syllable 1; (B) Syllable 2; (C) Syllable 3; (D) Syllable 4; and (E) Syllable 5. Note: The y-axis levels vary in each chart to visualize the difference in the range of data values.

The proportional composition of the five social vocalizations did not change across the life-cycle periods, neither including (multinomial logistic regression: $\chi^2_{12} = 0.692$, $df = 12$, $p > 0.05$) nor excluding (multinomial logistic regression: $\chi^2_8 = 0.135$, $df = 8$, $p > 0.05$) the hibernation period. The proportional composition of the five social vocalizations did not change when the interactions between the life-cycle periods and sites were considered, neither including (multinomial logistic regression: $\chi^2_{176} = 1.388$, $df = 176$, $p > 0.05$) nor excluding (multinomial logistic regression: $\chi^2_{132} = 0.822$, $df = 132$, $p > 0.05$) the hibernation period.

Most *C. gouldii* social vocalizations often occurred at roosting sites (mean = 83.9 social vocalizations per night across all sites, standard deviation = 153.00, range 0 – 759). The number of social vocalizations was positively correlated with the *C. gouldii* total vocal activity (Spearman's correlation: $\rho = 0.762$, $p < 0.001$, Figure 2.5 (b)). *Chalinolobus gouldii* social vocalizations had site-specific variation across the life-cycle periods. The social vocalization rates at Roost Site 2 and 3 were similar, where the social vocalization rates were increased during the pregnancy and nursing periods, then decreased from the mating to the hibernation period. The social vocalization rate at Roost Site 4 varied considerably throughout the recording period but was increased in the nursing and hibernation periods. The social vocalization rate at Roost Site 1, unlike other sites, was the lowest in the nursing periods, while it gradually increased in the hibernation period (Figure 2.6).

The proportional composition of the five social vocalizations at roost sites did not change across the life-cycle periods, neither including (multinomial logistic regression: $\chi^2_{12} = 1.902$, $df = 12$, $p > 0.05$) nor excluding (multinomial logistic regression: $\chi^2_8 = 0.229$, $df = 8$, $p > 0.05$)

the hibernation period. When including the interaction between the life-cycle periods and sites, the proportional composition of the five social vocalizations did not change, neither including (multinomial logistic regression: χ^2_{64} =6.995, *df* = 64, *p* >0.05) nor excluding (multinomial logistic regression: χ^2_{48} = 5.311, *df* = 48, *p* >0.05) the hibernation period.

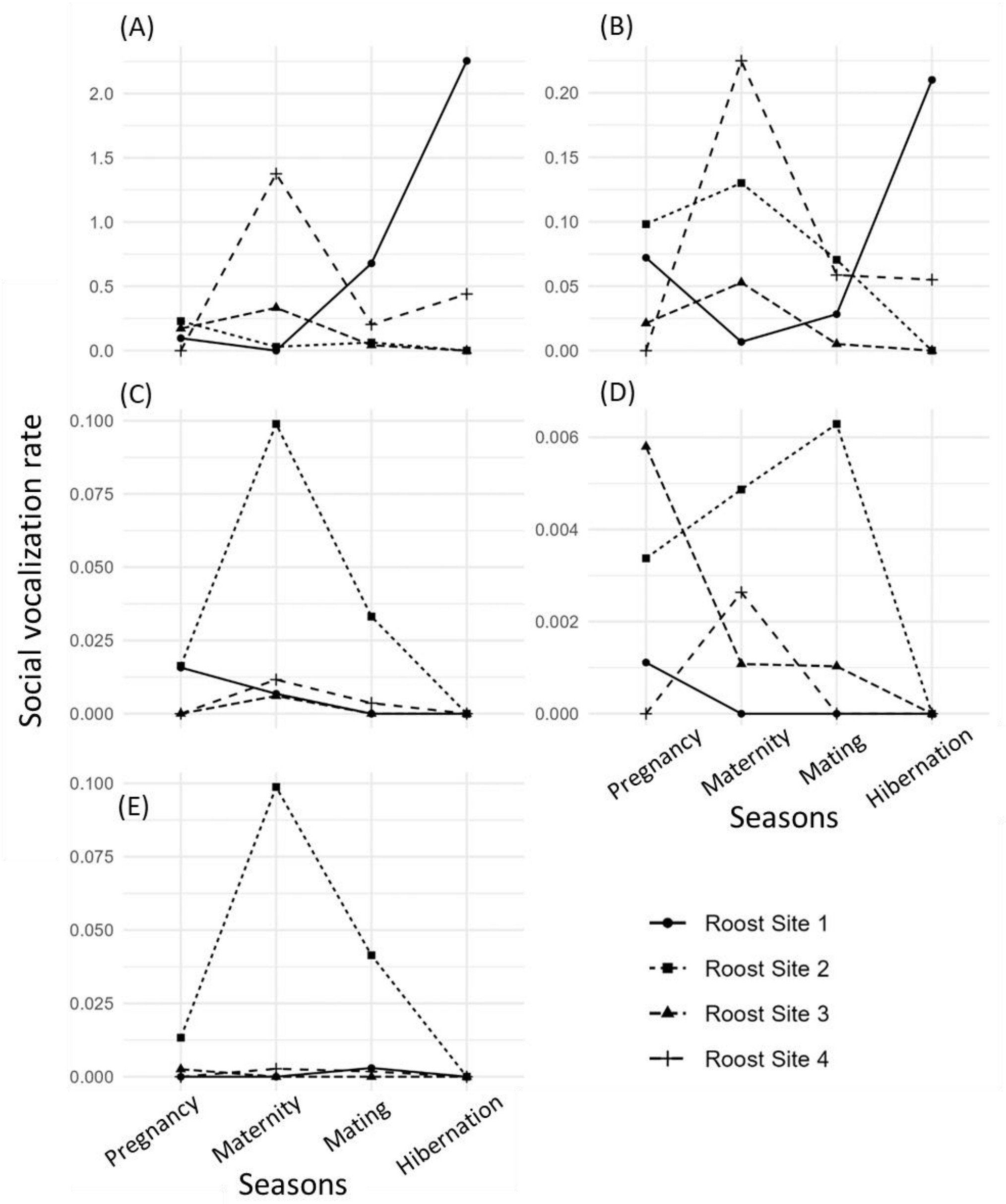


Figure 2.7. The five types of social vocalization rate (the number of social vocalization syllables/the total activity) change across the four life-cycle periods at four roosting sites. (A) Syllable 1; (B) Syllable 2; (C) Syllable 3; (D) Syllable 4; and (E) Syllable 5. Note: The y-axis levels vary in each chart to visualize the difference in the range of data values.

Discussion

This study examined the social vocalizations of a widely distributed Australian bat, *Chalinolobus gouldii*, at both foraging and roosting sites across the four life-cycle periods (i.e., pregnancy, nursing, mating and hibernation). *C. gouldii* produced at least five distinct syllables, identified by using HAC, plus broadband chatting sounds and syllable sequences which were manually identified. *Chalinolobus gouldii* produced syllable sequences during the pregnancy, nursing, and mating periods at foraging sites, along with complex sequences of over five syllables found during the pregnancy and mating periods. The number of *C. gouldii* social vocalizations per night was positively related to its total vocal activity. Adjusting for nightly activity, the social vocalization rate at foraging sites was increased during the pregnancy, nursing and mating periods, and the social vocalization rate at roosting site was increased high during the nursing period. The composition of *C. gouldii* social vocalizations did not vary across the four life-cycle periods. I suggest that these syllables in *C. gouldii* may be important for their daily communication, given that *C. gouldii* are flexible in a variety of environments across the Australian continent (Reinhold et al. 2001) though further studies are needed to understand the functions of social vocalizations.

Methods for studying vocal repertoire

The features of dual function sounds in bats, navigation (echolocation calls) and communication (social vocalizations), may contribute to the degree of vocal gradations and create a challenge in isolating social vocalizations. The existence of gradation between sounds in mammalian acoustic communication introduces difficulty in defining the boundary and separation of each sound, which may be due to variation in the environment, groups, and individuals. With notable exemptions (e.g., ghost bats *Macroderma gigas* (Hanrahan 2020), little brown bats *Myotis lucifugus* (Melendez et al. 2006)), most bat vocal repertoire studies have been conducted in a laboratory setting, using subjective visual classification of sound shapes in spectrograms (Lin et al. 2015, Nardone et al. 2017, Guo et al. 2019, Lattenkamp et al. 2019, Springall et al. 2019). This practice may make the characterization of social vocalizations difficult to replicate and to annotate those gradation vocalizations. I used HAC to categorize the social vocalizations based on the vocalization measurements and assessed the quality of clustering result through visual verification, which efficiently obtained objective classification (Hanrahan 2020). This process can be reproducible, impartial and minimize artificial bias except where visual verification introduces observer-dependent errors. Our results showed a slight degree of gradation which may result from nonlinear vocalization structures (Figure 2.2). There are potentially more types of syllables that went undetected using this method, because the complexity of vocalization structure cannot be fully reflected by the call measurements we took, and the finer differences among social vocalizations may be masked by echolocation calls or other sounds.

The potential motivation and functions of C. gouldii social vocalizations

I made preliminary assessments of the motivation and functions of *C. gouldii* social vocalizations based on call structures although our study did not record behaviors. We compared other species social vocalizations and applied vocal motivation-structural rules to interpret the potential functions of *C. gouldii* social vocalizations. Motivation-structural rules have been applied in the contexts of animal vocalizations, indicating that an animal’s emotional state can be encoded in its vocalizations (Morton 1977). Studies on bat social vocalizations that integrate both acoustic and behavioral recordings have summarized a general pattern in bat social vocalizations: wide bandwidth is associated with hostility, whereas narrow bandwidth reflects affiliative relationships or appeasement (Gadziola et al. 2012, Lattenkamp et al. 2019). Sounds with broadband noise-like, steep frequency modulation and high entropy (i.e., disorder) features tend to be accompanied by agonistic displays such as baring of teeth or snapping, representing hostility, while syllables with narrow bandwidth and downward frequency modulation tend to indicate appeasing states without showing agonistic displays, interpreted as appeasement (Gadziola et al. 2012, Lattenkamp et al. 2019). Furthermore, a comparative analysis generalized the structure and variability of bat social vocalizations into four distinct types (Pfalzer and Kusch 2003), giving an insight into the potential functions of *C. gouldii* social vocalizations. Type A – Aggressive/Threatening, broadband structure, noise-like and human-audible sounds; B – Distress, steep frequency-modulated calls; C - Mother-infant bat interaction calls (i.e., isolation calls) and group calls (i.e., contact calls), curved frequency-modulated calls; and D – complex songs including advertisement for mating and resource defense, comprising the sequences with mono- or multi- syllable types. I interpreted the possible functions of *C. gouldii* social vocalizations using the above information and observations.

Syllable 1 and 2

In agreement with the motivation-structure rules above and Pfalzer and Kusch (2003) categories, Syllable 1 and 2 in *C. gouldii* might be in accordance with affiliative relationship or cooperation features in vocalizations, curved-downward frequency modulation and relatively narrow bandwidth, and these structures are similar with the Type C (Pfalzer and Kusch 2003). Common social vocalizations with curved frequency-modulated structure are associated with personal information identity and usually occur in a single syllable in the echolocation call sequence during flight in many bat species. Species with similar vocalization structures function in individual recognition and group cohesion, as observed in white-winged vampire bats *Diaemus youngi* (Carter et al. 2009), pallied bats *Antrozous pallidus* (Arnold and Wilkinson 2011), and greater spear-nosed bats *Phyllostomus hastatus* (Boughman 1997, Boughman and Wilkinson 1998). Therefore, I suspected that these syllables possibly encode personal information for group connection.

Syllable 3, 4, and 5

The social vocalizations, Syllable 3, 4, and 5, in *C. gouldii* are steep frequency modulation, broad bandwidth and short duration, which may act as alert or distress signals, matching Type B (Pfalzer and Kusch 2003). Species with similar call structures, such as Peters's sheath-tailed bats *Emballonura atrata*, Malagasy mouse-eared bats *Myotis goudoti*, Major's long-fingered bats *Miniopterus majori*, and Manavi long-fingered bats *Miniopterus manavi* (Russ et al. 2004), produce these sounds when disturbed and have been observed at roosts (Pfalzer and Kusch 2003). These syllables in *C. gouldii* were found at both foraging and roosting sites. However, the potential functions of these syllables need to be investigated due to their occasional use.

Broadband, noise-like ‘chatting sounds'

I recorded many *C. gouldii* ‘chatting sounds’ near their roosts, but this sound was not included in the analysis due to disorder and lack of structure, which may affect the HAC accuracy. The features of broadband disorder chatting sounds have been described as aggressive or threatening associated with invasion behaviors or intruder encounters and are observed near roosts in other species, matching Type A (Pfalzer and Kusch 2003). This category of vocalizations is found in species such as greater mouse-eared bats *Myotis myotis* (Walter and Schnitzler 2019), big brown bats *E. fuscus* (Gadziola et al. 2012), and pale spear-nosed bats *Phyllostomus discolor* (Lattenkamp et al. 2019). *Chalinolobus gouldii* chatting sounds can be loud and low frequency, allowing the sounds to travel long distances. These sounds may be produced in response to or in anticipation of agonistic behaviors resulting from intruders. On the other hand, these sounds encode individual signatures in Seba's short-tailed bats *Carollia perspicillata* (Fernandez et al. 2014) and are correlated with aggression levels (Fernandez et al. 2014, Walter and Schnitzler 2019) which may enable roost member identification. This is relevant in *C. gouldii* roosts with non-random associations (Godinho et al. 2015), because it may allow this species to either discriminate intruders or identify social group members.

Syllable sequences

Chalinolobus gouldii also produced complex sequences, constructing more than one syllable, with mono-syllable (i.e., a sequence of repetition of the same syllables) or multi-syllable sequences (i.e., a sequence of different syllables). Complex sequences encode specific information (Bohn et al. 2008). For example, courtship songs contain dual functions either as attracting females or defending territory from males or agonistic behaviors (Gadziola et al. 2012, Smotherman et al. 2016, Knörnschild et al. 2017, Toth et al. 2018). Complex sequences in *C. gouldii* occurred more frequently during the pregnancy, nursing, and mating periods, with sequences containing more than five syllables recorded during the pregnancy and mating periods. These sequences also showed site-specific variation, which may be related to habitat use in these areas. For example, the increased recording of multi-syllable sequences at Foraging Sites 1 and 2 (supplementary information S2.7) may suggest spatial proximity to roosting sites within the same patch of bushland. At these sites, social vocalizations and complex sequences may function in territorial defense and facilitate maternity group cohesion during the breeding seasons. At other foraging sites, I observed more multi-syllable sequences during the mating periods, potentially functioning in mate attraction. However, further individual identity, such as sex and social groups, are needed to confirm the functions of these sequences.

Seasonality of social vocalizations

The composition of social vocalizations in *C. gouldii* did not vary over time. Bat activity in temperate regions, in general, follows seasonal and climate patterns to match life-cycle requirements. For example, bats swarm and vocalize courtship songs or increase social vocalizations for mate attraction in autumn before hibernation (Jahelková and Horáček 2011, Furmankiewicz et al. 2013, Bartoničková et al. 2016). I did not observe an increase in the rate of social vocalizations by *C. gouldii* during the mating period. These social vocalisations may be used for daily communication. I did observe a higher occurrence of more complex syllable sequences and speculated that sequences with more than five syllables may be used for courtship communication. For example, the songs of bats follow a hierarchical structure and are composed of multi-syllables at swarming sites, including courtship songs of Nathusius' pipistrelles *Pipistrellus nathusii* (Jahelková and Horáček 2011) and multi-syllable displays of brown long-eared bats *Plecotus auritus* during the mating season (Furmankiewicz et al. 2013).

On the other hand, the multi-syllable sequences of *C. gouldii* in this study revealed site-specific responses across seasons, suggesting that multi-syllable sequences may convey different functions across seasons, such as mate attraction or group identification (Knörnschild et al. 2017). In this study, a high rate of multi-syllable sequences at Foraging Site 5 and 7 during the nursing period and at Foraging Site 6 during the mating period may facilitate maternity group aggregation and mate attraction, respectively (supplementary information S2.7).

The possibility of other courtship songs in *C. gouldii* may exist owing to an unclear pattern of seasonality in social vocalizations. *Chalinolobus gouldii* potentially move to specific areas for courtship song lekking and swarming, with song display sites potentially located in open habitats or near hibernation sites at certain times. Those sites and research periods may not be included in this study. Further research and observation are needed to elucidate the association of multi-syllables and the courtship songs in *C. gouldii*.

Social vocal repertoire in bats

Habitat use and social complexity affect the size of social vocalization repertoire (Knörnschild et al. 2020). I categorized at least five types of social vocalization in *C. gouldii*, suggesting those social vocalizations may be important for social connections. Across the literature, echolocating bat social vocalization repertoire size has been reported to range from five to 18 types (Melendez et al. 2006, Gadziola et al. 2012, Nardone et al. 2017, Guo et al. 2019, Springall et al. 2019, Wilkinson and Boughman 1998, Lattenkamp et al. 2019, Milne et al. 2023). The social vocalisation repertoire size depends on species-specific requirement (Knörnschild et al. 2020). *Chalinolobus gouldii* is a widespread and urban-tolerant species across the Australian continent (Milne et al. 2023), having similar habitat use to an urban-tolerant species big brown bat *Eptesicus fuscus* in North America with at least 18 types of social vocalisations (Gadziola et al. 2012, Springall et al. 2019). *Eptesicus fuscus* are gregarious and form modest-sized colonies (< 100 individuals) in roosts (Kurta and Baker 1990). Social vocalisations in *E. fuscus* allow them to adjust associations and attract conspecifics (Wright et al. 2013). Given that *C. gouldii* roosts in groups with related roosting members (Godinho et al. 2015, Eastick 2022) and their social vocalisations did not vary over time, their social vocalisations may be crucial for their daily social interactions. These vocalisations may facilitate non-random associations in roosts (Godinho et al. 2015) though studies which further reveal the ecological significance of their social vocalizations are needed.

Limitations and further directions

Although our field recordings reflect true ecological interactions and behaviors of free-living animals, there are several limitations of this approach that restrict our interpretation of the vocalizations recorded. Firstly, the recording approach used in this study allowed to capture complex acoustic sequences, including multi-syllable sequences; however, I could not control the individual interactions, or even the interactions between species. Additionally, recording quality could not be easily controlled, affected by the ambient environmental conditions and the presence of multiple visiting individuals. Also, the social vocalizations are louder and lower in frequency than echolocation calls, potentially drawing both conspecific and predator attention, which may also lead to site-specific behaviors that were not assessed. The lack of seasonal patterns in social vocalization rates may reflect limited power of the study to detect such patterns due to field recording data and the unpredictability of bat behaviors. Increasing sampling effort and recording sites may increase the chance of social vocalization observation in each season, such as more social vocalization during ephemerally swarming behaviors in the mating season, that has been reported elsewhere (Russ et al. 2003, Voigt-Heucke et al. 2016, Dorrestein et al. 2024).

Communication is the process by which information is transmitted between signallers and receivers (Seyfarth and Cheney 2003, Kastein et al. 2013, Gokcekus et al. 2021). Future studies can focus on specific individual interactions by using microchips in the field or laboratory-based experiments. Individuals from the same and different social groups may respond differently to contact calls due to the distinct calls between groups (Sagot et al. 2018). The potential courtship songs of *C. gouldii*, composed of syllable sequences, may lead to the different responses between genders. For example, courtship songs in greater sac-winged bats *Saccopteryx bilineata* interact with male and female in different ways (Knörnschild et al. 2017). The interpretations of these interactions rely on individual identification and controlled experimental designs to exclude unwanted influences. Call playback experiments with individual identification are warranted to observe specific behavioral interactions, providing further insight into the ecological significance of vocalizations in bats.

Potential artificial effects associated with recording devices may have influenced the results. Differences in microphone sensitivity could affect call measurements, such as duration and acoustic frequency, particularly for higher-frequency components that are more prone to attenuation (Starbuck et al. 2024). In this study, three types of recording devices were used, and device type contributed to variation in some call measurements among social vocalisation types. This issue should be considered when interpreting the results, and the use of a consistent recording device is recommended for future studies.

Conclusion

This study gave an insight into *C. gouldii* social vocal repertoire, revealing at least five types of syllables, syllable sequences and other broadband 'chatting sounds', though the composition of social vocalisations did not vary over time with life cycle. I interpret that these social vocalisations may be related to grouping behaviours allowing individuals to adjust member associations. Also, high variation between recording sites potentially results from distinct strategies used to support resource acquisition in a variety of environments. Further studies should focus on the landscape features among sites, as well as on call playback behavioral responses, to examine the motivations behind the production of specific call types.

Acknowledgements

I thank Selina Kosak and Elsa Kohane for their assistance with device deployment and fieldwork. I also thank Tim Liston, Helen Pollard, Bradley Lloyd, Adam Ward, Nathan Lindsay, Tina Hsu, Ben Robb, Amara Glynn, and the site manager of Brownlow Hill for permitting me to conduct acoustic monitoring in the reserves and parklands.

Supplementary information

Supplementary information S2.1

The device deployment information includes dates and device types.

Table S2.1. The locations, device usage, and sampling periods of the 11 foraging sites are listed, with device types for each sampling date shown in brackets. The abbreviations used are: Anabat Swift (SW), Chorus (CH), and AudioMoth (AM)**.**

Site name	Location	Nursing	Mating	Hibernation	Pregnancy
Foraging Site 1	Cumberland State Forest	6-10 Dec 2022 (SW)	9-13 May 2023 (SW)	14-18 Jul 2023 (SW)	16-20 Sep 2023 (SW)
Foraging Site 2	Moxham Park	9 Nov (AM); 15-18 Dec 2022 (AM)	4-8 May 2023 (SW)	14-18 Jul 2023 (SW)	15-19 Sep 2023 (SW)
Foraging Site 3	Centennial Park – Duck Pond	19-21 Dec 2022 (SW)	20-24 Mar 2023 (SW)	7-11 Jul 2023 (SW)	8-12 Sep 2023 (SW)
Foraging Site 4	Centennial Park – Busby Pond	19-21 Dec 2022 (SW)	20-24 Mar 2023 (SW)	7-11 Jul 2023 (SW)	8-11 Sep 2023 (SW)
Foraging Site 5	Sydney Olympic Park – Wentworth control Pound	15-18 Dec 2022 (AM)	21-25 Mar 2023 (CH)	14-18 Jul 2023 (SW)	15-19 Sep 2023 (SW)
Foraging Site 6	Sydney Olympic Park – Haslams Creek	15-18 Dec 2022 (SW)	21-25 Mar 2023 (SW)	14-18 Jul 2023 (SW)	15-19 Sep 2023 (SW)
Foraging Site 7	Sydney Olympic Park – Haslams Pier	15-18 Dec 2022 (SW)	21-25 Mar 2023 (SW)	14-18 Jul 2023 (SW)	15-19 Sep 2023 (SW)
Foraging Site 8	Brownlow Hill – dam 1	1-5 Nov 2022 (SW)	21-25 Mar 2023 (SW)	No recording data	29 Aug – 2 Sep 2023 (SW)
Foraging Site 9	Brownlow Hill – dam 2	1-5 Nov 2022 (SW)	21-25 Mar 2023 (SW)	No recording data	29 Aug – 2 Sep 2023 (SW)
Foraging Site 10	Brownlow Hill – dam 3	1-5 Nov 2022 (SW)	21-25 Mar 2023 (SW)	No recording data	29 Aug – 2 Sep 2023 (SW)
Foraging Site 11	Brownlow Hill – dam 4	1-5 Nov 2022 (SW)	21-25 Mar 2023 (SW)	No recording data	29 Aug – 2 Sep 2023 (SW)

Table S2.2. The locations, device usage, and sampling periods of the four roosting sites are listed, with device types for each sampling date shown in brackets. The abbreviations used are: Anabat Swift (SW), Chorus (CH), and AudioMoth (AM).

Site name	Location	Nursing	Mating	Hibernation	Pregnancy
Roost Site 1	Cumberland State Forest	9 ,11, 13 Nov 2022 (AM)	30 Mar; 9,10 Apr 2023 (CH)	14, 15, 17 Jul 2023 (CH)	15, 20, 21 Sep 2023 (CH)
Roost Site 2	Moxham Park	15-16, 19 Dec 2022 (SW)	17, 19, 22 Mar 2023 (CH)	14, 15, 18 Jul 2023 (CH)	15-18 Sep 2023 (CH)
Roost Site 3	Bradleys Head	16-18 Nov 2022 (AM)	20-22 Mar 2023 (AM)	7, 9, 11 Jul 2023 (CH)	8, 11, 12 Sep 2023 (CH)
Roost Site 4	Chowder Bay	16-18 Nov 2022 (AM)	21, 22, 25 Mar 2023 (AM)	7, 10, 11 Jul 2023 (CH)	7, 9, 11 Sep 2023 (CH)

Supplementary information S2.2

Moran's I for spatial autocorrelation test

Parts of the foraging sites were clustering together. Moran's I test was used to test the social vocalization rate and spatial autocorrelation at foraging sites to assess if the social vocalization rate was affected by the proximity sites. A k-nearest neighbor spatial weighting scheme was set at 3, which was less than one-third of the number of data points. Regrading to foraging sites, the social vocalization rate didn't show spatial autocorrelation in the pregnancy (Moran's I value = 0.111, $p = 0.102$), nursing (Moran's I value = -0.230, $p = 0.785$), and hibernation (Moran's I value = -0.083, $p = 0.201$) periods, while the social vocalization rate in the mating period showed significant spatial autocorrelation (Moran's I value = 0.321, $p = 0.006$). The only one of recording sites at Brownlow Hill, Brownlow Hill Site 3, showed a spatial pattern of dispersion, where the Brownlow Hill Site 3 with the lower social vocalization rate was surrounded by the other sites at Brownlow Hill with high social vocalization rate (Moran's I value = -0.816, $p = 0.009$). However, it might result from the difference of microhabitat features. That site was opener than others.

Regarding roosting sites, the social vocalization rate in the four life-cycle periods didn't show spatial autocorrelation: pregnancy (Moran's I value <0.001, $p = 0.5$), nursing (Moran's I value < 0.001, p = 0.5), mating (Moran's I value <0.001, $p = 0.5$) and hibernation (Moran's I value = -1.299, $p = 0.903$) periods.

Supplementary information S2.3

Device variation

There may be some variation among devices due to the different microphone sensitivity, which may reflect on the call measurements. To assess this, I compared the confidence intervals of call measurements across devices for the five social vocalization types. Some variation was observed, particularly in frequency-related measurements such as peak frequency, and minimal frequency (e.g., the Swift device showed higher frequency measurements compared to the other two devices). The overall impact of device variation appears minimal because the HAC incorporated multiple call measurements to generate the clusters, ensuring a robust classification that accounts for potential measurement discrepancies.

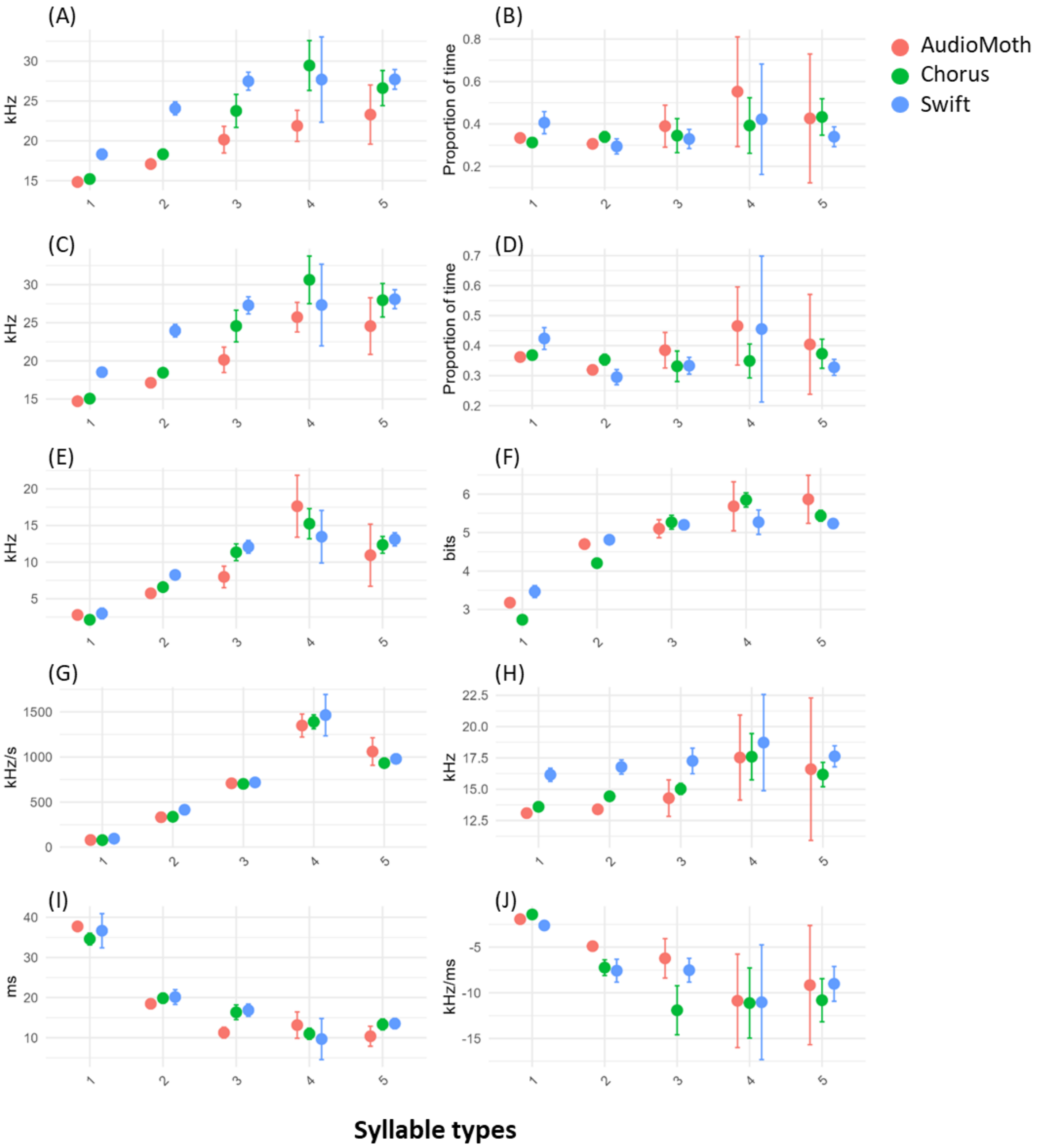


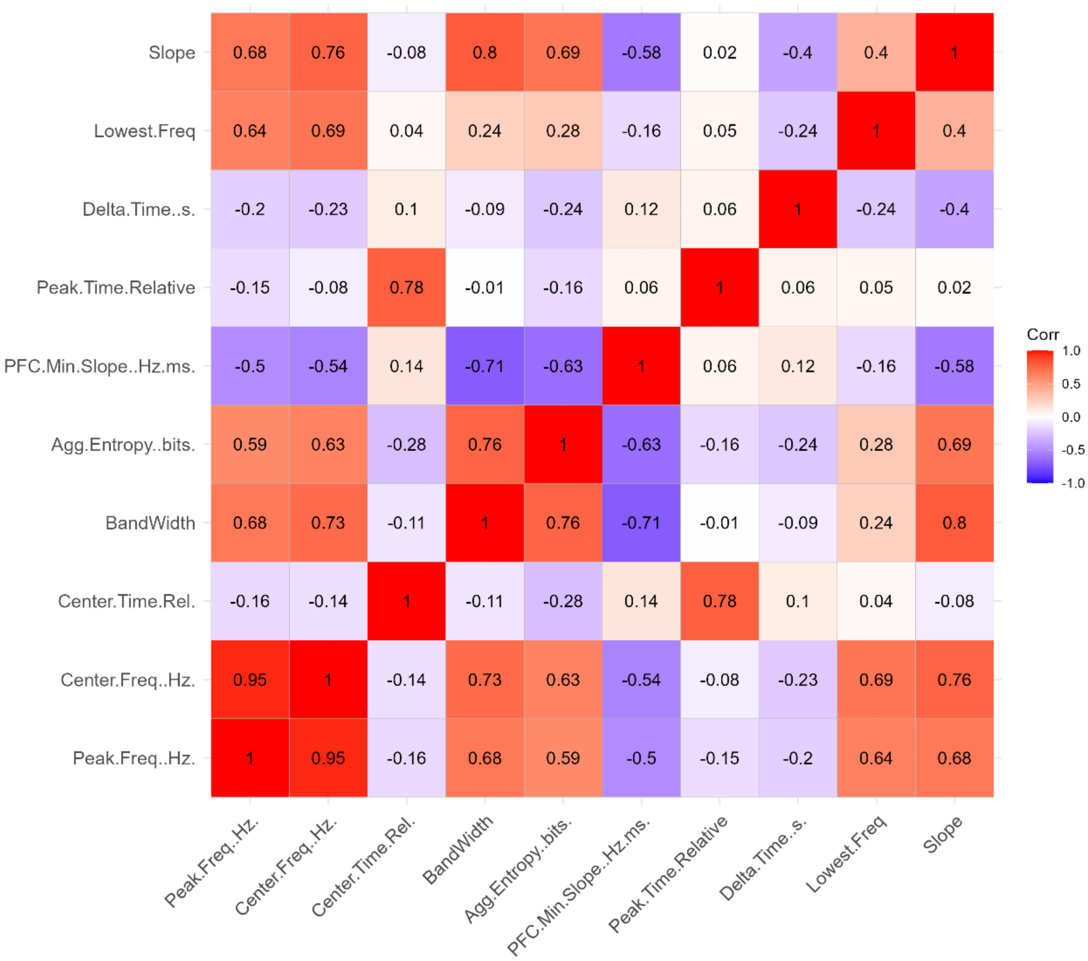
Figure S2.3. Confidence intervals of call measurements between devices across the five social vocalizations.

(A) Peak frequency; (B) The proportion of time reaching peak frequency; (C) Center frequency; (D) The proportion of time reaching 50% of the total energy; (E) Bandwidth; (F) Aggregate entropy; (G) Slope (bandwidth/duration); (H) Minimal frequency; (I) Duration; and (J) Peak frequency contour slope.

Supplementary information S2.4

The social vocalization processing

To assess the key call measurements, 30 temporal-frequency measurements of selected calls were taken from either Raven Pro 1.6 default or calculated based on Raven default measurements. Measurements from Raven Pro 1.6 default were peak frequency contour (PFC) maximum Frequency (kHz), PFC minimum frequency (kHz), aggregate entropy (bits), average entropy (bits), bandwidth 50% (kHz), bandwidth 90% (kHz), centre frequency (kHz), proportion of time reaching 50% of the total energy in the selection, duration 50% (ms), duration 90% (ms), frequency 25% (kHz), frequency 5% (kHz), frequency 75% (kHz), frequency 95% (kHz), maximum entropy (bits), minimum entropy (bits), PFC average slope (kHz /ms), PFC maximum slope (kHz/ms), PFC minimum slope (kHz/ms), proportion of time reaching peak frequency, proportion of time reaching 5% of the total energy in the selection, proportion of time reaching 25% of the total energy in the selection, proportion of time reaching 75% of the total energy in the selection, proportion of time reaching 95% of the total energy in the selection, delta time (ms), and peak frequency (kHz). Maximal frequency and minimal frequency were taken from the maximum and minimum frequency in the frequency contour 5%. Bandwidth was calculated as the difference between maximal frequency and minimal frequency. The definitions of measurements see the Raven pro user guide (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology 2025). Slope was calculated as the ratio of bandwidth to delta time.



	Peak.Freq..Hz.	Center.Freq..Hz.	Center.Time.Rel.	BandWidth	Agg.Entropy..bits.	PFC.Min.Slope..Hz.ms.	Peak.Time.Relative	Delta.Time..s.	Lowest.Freq	Slope
Slope	0.68	0.76	-0.08	0.8	0.69	-0.58	0.02	-0.4	0.4	1
Lowest.Freq	0.64	0.69	0.04	0.24	0.28	-0.16	0.05	-0.24	1	0.4
Delta.Time..s.	-0.2	-0.23	0.1	-0.09	-0.24	0.12	0.06	1	-0.24	-0.4
Peak.Time.Relative	-0.15	-0.08	0.78	-0.01	-0.16	0.06	1	0.06	0.05	0.02
PFC.Min.Slope..Hz.ms.	-0.5	-0.54	0.14	-0.71	-0.63	1	0.06	0.12	-0.16	-0.58
Agg.Entropy..bits.	0.59	0.63	-0.28	0.76	1	-0.63	-0.16	-0.24	0.28	0.69
BandWidth	0.68	0.73	-0.11	1	0.76	-0.71	-0.01	-0.09	0.24	0.8
Center.Time.Rel.	-0.16	-0.14	1	-0.11	-0.28	0.14	0.78	0.1	0.04	-0.08
Center.Freq..Hz.	0.95	1	-0.14	0.73	0.63	-0.54	-0.08	-0.23	0.69	0.76
Peak.Freq..Hz.	1	0.95	-0.16	0.68	0.59	-0.5	-0.15	-0.2	0.64	0.68

Figure S2.4.1. The correlation coefficient matrix of 10 measurements

Table S2.4.2. The definition of night selected measurements

Measurement	Unit	Definition
Proportion of time reaching 50% of the total energy in the selection	Non-available	Proportion of selection at which 50% of the total signal energy
Center frequency	kHz	Frequency at the midpoint of the total acoustic energy
Duration	ms	The total time of the signal.
Minimal frequency	kHz	The minimum frequency in the signal that selected from the lowest frequency in the peak frequency contour.
Bandwidth	kHz	The difference between the highest and lowest frequency in the peak frequency contour.
Peak Frequency Contour (PFC) Min Slope (Hz/ms)	kHz/ms	The smallest slope value of the peak frequency contour across the duration of the call.
Peak Frequency	kHz	The frequency with the highest energy in the signal.
Proportion of time reaching peak frequency in the selection	Non-available	Proportion of selection at which the timing of peak frequency in the total signal energy
Aggregate (Agg) Entropy	bit	A value of the complexity or randomness of the signal across its spectrum and time. High entropy indicates a more uniform energy distribution; low entropy indicates more concentrated or tonal energy patterns.
Slope	kHz/ms	The frequency changes through the time: bandwidth divides to the duration.

Note: Peak frequency contour: the trajectory of the frequency with the highest energy over time within a signal.

Supplementary information S2.5

Hierarchical Agglomerative Clustering method determination

To determine the optimal number of *C. gouldii* vocalization types, Hierarchical Agglomerative Clustering (HAC) was used. The '*NbClust*' from NbClust package was used and it provided 30 indices to determine the optimal number of cluster results by varying the combinations of number of clusters and distance between clusters (Charrad et al. 2014). I employed the original measurements, using *complete* linkage which maximized the distance between two points. The number of optimal clusters in this study was determined by visually validating the rationality of syllable spectrogram within and between clusters.

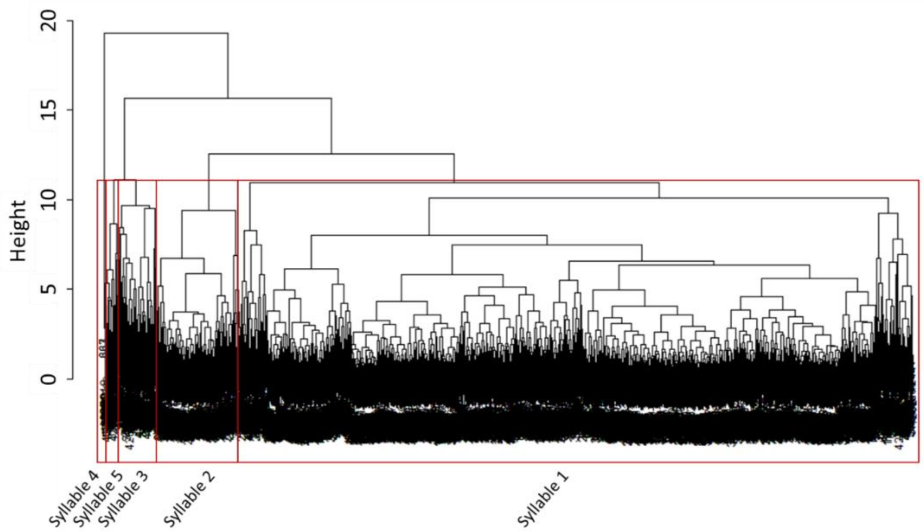


Figure S2.5 Dendrogram resulting from hierarchical clustering of the ten measurements**.** The complete linkage method and Euclidean distance were used. Each branch represents a syllable, and the vertical height at which two branches merge reflects the dissimilarity between them. Cutting the dendrogram at a height that yields five clusters (k = 5) determined by NbClust, indicated by rectangles.

Supplementary information S2.6. The information of ten measurements of five social vocalization syllables.

Table S2.6. The mean and standard deviation in the brackets of five social vocalization syllables

Syllable types	Description	Peak frequency (kHz)	Proportion of time reaching out peak frequency	Center frequency (kHz)	Proportion of time reaching out center frequency	Bandwidth (kHz)	Aggregate entropy (bits)	Slope (kHz/ms)	Minimal frequency (kHz)	Duration (ms)	PFC min slope (kHz/ms)
1	Quasi-constant frequency with a variety of duration	15.1 ^{d} (2.23)	0.33 ^{a} (0.23)	14.9^{d} (2.01)	0.37 ^{a} (0.15)	2.55 ^{d} (1.74)	3.03 ^{d} (0.91)	0.079 ^{e} (0.049)	13.4 ^{e} (1.65)	36.6 ^{a} (20.93)	-1.766 ^{a} (2.02)
2	Curved frequency-modulation descending with a variety of duration	18.8 ^{c} (5.10)	0.32 ^{a} (0.21)	18.8^{c} (4.57)	0.33 ^{b} (0.14)	6.49 ^{c} (3.31)	4.55 ^{c} (0.72)	0.349 ^{d} (0.115)	14.40^{d} (2.67)	19.2 ^{b} (9.31)	-6.192 ^{b} (5.86)
3	Steep narrowband frequency modulation with short duration	24.9 ^{b} (5.67)	0.35 ^{a} (0.21)	25.1^{b} (4.73)	0.34 ^{ab} (0.13)	11.07 ^{b} (4.12)	5.20 ^{b} (0.50)	0.712 ^{c} (0.068)	16.0 ^{c} (3.49)	15.6 ^{c} (5.77)	-8.614 ^{c} (6.50)
4	Steep broadband frequency modulation with extremely short duration	27.4 ^{a} (5.39)	0.43 ^{a} (0.22)	28.8^{a} (3.75)	0.40 ^{ab} (0.15)	15.29 ^{a} (3.90)	5.67 ^{a} (0.42)	1.400 ^{a} (0.150)	17.9 ^{a} (3.06)	11.1 ^{d} (3.25)	-11.045 ^{d} (5.65)
5	Steep broadband frequency modulation intergrading between Syllable 3 and 4	27.1 ^{ab} (5.46)	0.38 ^{a} (0.22)	27.9^{a} (3.79)	0.35 ^{ab} (0.12)	12.72 ^{a} (4.07)	5.34 ^{a} (0.46)	0.966 ^{b} (0.098)	17.0 ^{b} (3.19)	13.3 ^{cd} (4.48)	-9.691 ^{cd} (7.05)

Note: Superscript letters show the significant.

Supplementary information S2.7. The frequency of syllable sequence occurred at eight of the 11 foraging sites, and the remaining three sites did not record any social vocalizations.

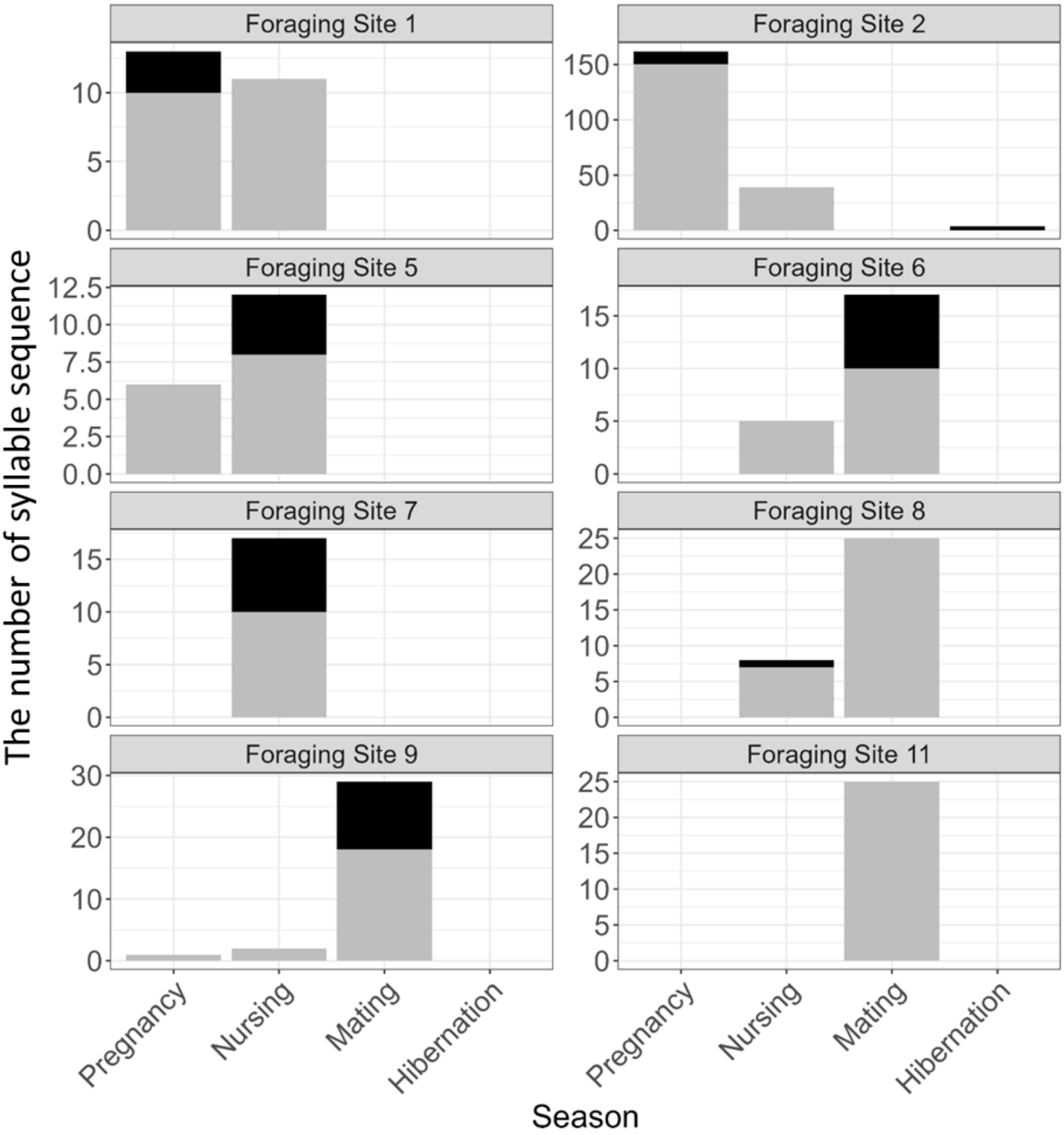


Figure S2.7. The frequency of syllable sequence occurrence in each site. Grey represents syllable counts ranging from two to five; black represents syllable counts exceeding five.

Chapter 3

Social vocalisations of the widely distributed species, *Chalinolobus gouldii*, attract conspecific and heterospecific bats

Note: This chapter is formatted as a paper for *Austral Ecology*.

Abstract

Social recognition is central to guiding behavioural responses during social interactions. Echolocating bats possess exceptional auditory systems and produce diverse vocalisations, including echolocation calls for navigation and foraging, feeding buzzes for prey capture, and social vocalisations used for various social interactions. However, the functions of and responses to social vocalisations vary both within and across species and depend on the social contexts. The aim of this study was to investigate the associations between the vocalisations of an Australian common bat species *Chalinolobus gouldii* and the behavioural responses of both conspecific and heterospecific individuals to these vocalisations. I conducted field-based playback experiments using six acoustic treatments: three categories of *C. gouldii* social vocalisations, echolocation calls, feeding buzzes, and ambient control sounds. Bat responses were recorded via acoustic detectors and video cameras. Responses were analysed both within treatments – comparing activity before, during, and after playback – and across treatments to assess differential responses. In the acoustic data, *C. gouldii* responded only to their own social vocalisations both within and across treatments. The predominant heterospecific detected, *Miniopterus orianae oceanensis*, responded significantly to only one of the three social vocalisations within treatments. The presence of individuals near the speaker before playback significantly increased responses across all treatments. Contrary to acoustic recordings where both conspecifics and heterospecifics were recorded approaching the three social vocalisations, the video recordings did not reveal explicit behavioural responses, which may be due to bats exhibiting behavioural dynamics at a distance beyond the video field of view. These findings suggest that *C. gouldii* vocalisations may not only convey information for conspecific communication but also serve as informative cues for heterospecific eavesdropping or the elicitation of curiosity. Understanding responses to social vocalisations provides valuable insight into conspecific communication and heterospecific interactions in bat communities.

Keywords

Bats, call broadcast, call playback, Chiroptera, echolocation, feeding buzz, social behaviour, social calls, social communication

Introduction

Communication is a fundamental component of social interactions and relies on social recognition (Wilson 1972, Tibbetts and Dale 2007, Tumulty and Sheehan 2020). Social recognition refers to an individual's ability to identify other individuals through the perception of signals, traits that have evolved specifically for communication, such as vocalisations and movement, as well as non-signal traits such as chemical cues, which may incidentally convey identity-related information (e.g., Tumulty and Sheehan 2020). Effective communication leads to both short-term and long-term relationships, including kin and non-kin relationships within species, or relationships across species, and confers numerous benefits (Tibbetts and Dale 2007, Tumulty and Sheehan 2020). These benefits range from cooperative breeding to the establishment of social bonds, territories within species (Yadav et al. 2023, Briefer et al. 2024), and to warn conspecifics and heterospecifics against danger (Magrath et al. 2015). Echolocating bats (hereafter 'bats') are highly social animals (Chaverri et al. 2018). They roost in groups (Kerth 2008, Chaverri et al. 2018) and exhibit a diverse range of social behaviours facilitated via acoustic signals, including within species group cohesion calls and across species alarm calls (Gillam and Fenton 2016, Chaverri et al. 2018). These traits make bats an excellent model for studying acoustic social interactions.

A long history of studying bat vocal behaviours, primarily echolocation, has demonstrated that bats use echolocation calls to acquire spatial orientation and locate prey (Schnitzler et al. 2003, Bohn and Gillam 2018, Denzinger et al. 2018). The search phase of echolocation calls can also serve as public information (Valone and Templeton 2002), which incidentally convey information, such as species, sex, age, and social status of the call producers

(Dechmann et al. 2009, Schuchmann and Siemers 2010, Voigt-Heucke et al. 2010, Jones and Siemers 2011, Bohn and Gillam 2018). In addition to this, the terminal phase of echolocation before a bat attacks prey, known as feeding buzzes, provides a reliable cue for individuals to eavesdrop on prey locations and potential prey abundance (Lewanzik et al. 2019). By exploiting cues in the form of echolocation calls and feeding buzzes, bats can enhance foraging efficiency (Gillam 2007, Kohles et al. 2020, Kohles et al. 2022), assess local conspecific and heterospecific density and competition level (Lewanzik et al. 2019, Krivoruchko et al. 2024), and adjust foraging movement, potentially to reduce niche overlap or avoid interspecific aggression (Voigt-Heucke et al. 2016, Marggraf et al. 2023). Altogether, the ability to eavesdrop on and integrate information from both conspecific and heterospecific echolocation calls and feeding buzzes enhances foraging efficiency.

In contrast to echolocation calls, social vocalisations in bats are produced for communication and often characterised by lower frequencies and higher amplitudes (Gillam and Fenton 2016). These vocalisations are functionally diverse and serve explicit social purposes within species, enabling individuals to recognise and respond to those sounds (Pfalzer and Kusch 2003). For example, group-living bats use contact calls to facilitate individual recognition and maintain group cohesion (Wilkinson and Boughman 1998, Arnold and Wilkinson 2011, Carter et al. 2012, Chaverri et al. 2012, Vrtilek et al. 2025); mother bats recognise their own pups' sounds, known as isolation calls, for individual recognition (e.g., Scherrer and Wilkinson 1993, Bohn et al. 2007); bats produce aggressive vocalisations to reinforce territorial borders (Fernandez et al. 2014) and use distress/threatening sounds to announce the presence of predators (Russ et al. 2004). Advertisement songs, comprising multiple syllables, are used in mating contexts or to signal territorial occupancy (e.g., Jahelková et al. 2008, Knörnschild et al. 2017). Eavesdropping on heterospecific social vocalisations has also been observed in bats. For example, pipistrelles respond to congeneric species distress calls as potential danger warnings (Russ et al. 2004, Chaverri et al. 2018) and reduce their activity upon hearing congeneric species territorial songs to avoid resource competition (Voigt-Heucke et al. 2016). Thus, vocal communication can benefit both within and between species; however, its ecological roles and consequences remain understudies in the field.

Investigating bat social interactions in the field is a challenge due to bats' rapid flight and nocturnality. Acoustic monitoring has emerged as a practical and non-invasive method for studying both echolocation and social vocalisations. While video recordings offer detailed insights into behavioural responses, for bats, this method is more commonly assessed in controlled environments due to limited visibility and tracking range at night (Fernandez et al. 2014, Schmidbauer and Denzinger 2019). In contrast, acoustic monitoring enables the detection of natural behaviours across broad spatial and temporal scales and has been used to assess bat activity and social interactions across landscapes (Hanrahan 2020, Starik and Göttert 2022). Hence, acoustic monitoring offers new opportunities to investigate bat social interactions under natural conditions.

Gould's wattled bats, *Chalinolobus gouldii*, are widely distributed across diverse habitats in Australia (Reinhold et al. 2001, Threlfall et al. 2012b, Milne et al.2023). It exhibits complex social behaviours near roosts and selects roosting members with which to form non-random associations during the maternity season (Godinho et al. 2015, 2019). Recent work has identified this species as producing at least five distinct social vocalisation syllables in addition to a broadband chatting sound (Chapter 2) though the function of these vocalisations is unknown. The aim of this study is to evaluate whether *C. gouldii* vocalisations elicit responses from conspecifics and heterospecifics, and to interpret the potential communicative functions. I conducted a call playback experiment in which *C. gouldii* vocalisations were broadcast, and bat responses were recorded using acoustic detectors and a video camcorder. I hypothesised that (1) *C. gouldii* would respond differently to conspecific vocalisations depending on the type of social information conveyed. Specifically, I predicted that *C. gouldii* would approach and increase activity in response to affiliative calls (e.g., group cohesion or roost-finding information; (Wilkinson and Boughman 1998, Furmankiewicz et al. 2011, Chaverri et al. 2012, Bohn and Gillam 2018)) but avoid and reduce activity in response to agonistic calls during conflicts (e.g., food or space; (Barlow and Jones 1997, Bohn and Gillam 2018)). I then used these predictions to interpret the potential functions of *C. gouldii* social vocalisations, either affiliative or aggressive signals. Given that the widespread distribution of *C. gouldii* across landscapes, I further hypothesised that (2) heterospecifics with overlapping ecological niches may eavesdrop on *C. gouldii* social vocalisations to exploit information on resource discovery or acquisition. Alternatively, heterospecifics may approach all *C. gouldii* vocalisations due to novelty. Accordingly, I predicted that heterospecifics would selectively approach *C. gouldii* social vocalisations if they use similar resources, such as prey or roosts.

Materials and Methods

I assessed responses by conspecific and heterospecific bats to *C. gouldii* vocalisations at Cumberland State Forest (Pennant Hills, New South Wales, Australia) in Autumn 2024 (Permit No. RES100216). Cumberland State Forest is located in northwestern Sydney, containing 40 hectares of native forest, and is surrounded by housing (around 500 houses per kilometre). The surrounding area is home to bat species, including *Austronomus australis*, *C. gouldii*, *C. morio*, *Falsistrellus tasmaniensis*, *Miniopterus australis*, *M. orianae oceanensis*, *Mormopterus norfolkensis*, *Nyctophilus geoffroyi*, *Ozimops ridei*, *Scoteanax rueppellii*, *Scotorepens orion*, and *Vespadelus vulturnus* (Velasco et al. 2023). To test whether conspecific and heterospecific bats respond to *C. gouldii* vocalisations in line with the two hypotheses, I used a range of sound exemplars. The preparation of these sounds and experimental setup is described below. Data collection was approved by Animal Research Authority (2023/2386) of The University of Sydney.

Study species, call preparation and experimental design

I recorded *C. gouldii* vocalisations at Cumberland State Forest at both foraging and roost sites from November 2022 to September 2023. Using these recordings, two of the five social vocalisation types, Syllable 1 and 2, classified using Hierarchical Clustering Analysis (HAC) plus *C. gouldii*'s broadband chatting sounds, which are frequently used by *C. gouldii* at these sites (Chapter 2). However, both Syllable 1 and 2 showed high levels of within-syllable variation, so two subgroups were defined within each syllable based on syllable duration: long and short duration syllables. A total of eight sound treatments were used: the two subgroups of Syllable 1, the two subgroups of Syllable 2, broadband chatting sounds, *C.*

gouldii search-phase echolocation calls, *C. gouldii* echolocation sequences containing feeding buzzes (i.e., indicative of prey attack), and ambient control sounds which were used as a negative control without any bat social vocalisations or echolocation calls (Figure 3.1). Eight exemplars were selected for each sound treatment, for a total of 64 exemplars (8 treatments x 8 exemplars). To minimise bias from selecting sounds produced by a single individual or recorded under similar environmental conditions, exemplars were selected from different recording nights and locations. The duration of the sound exemplars was set to 1.5 seconds, considering the quality of sound as it entered and exited the microphone's recording range. All sound exemplars had good signal-to-noise (>25 dB) and showed no evidence of clipping, as determined visually in Kaleidoscope Lite (Version 5.6.3, Wildlife Acoustic, Inc, USA).

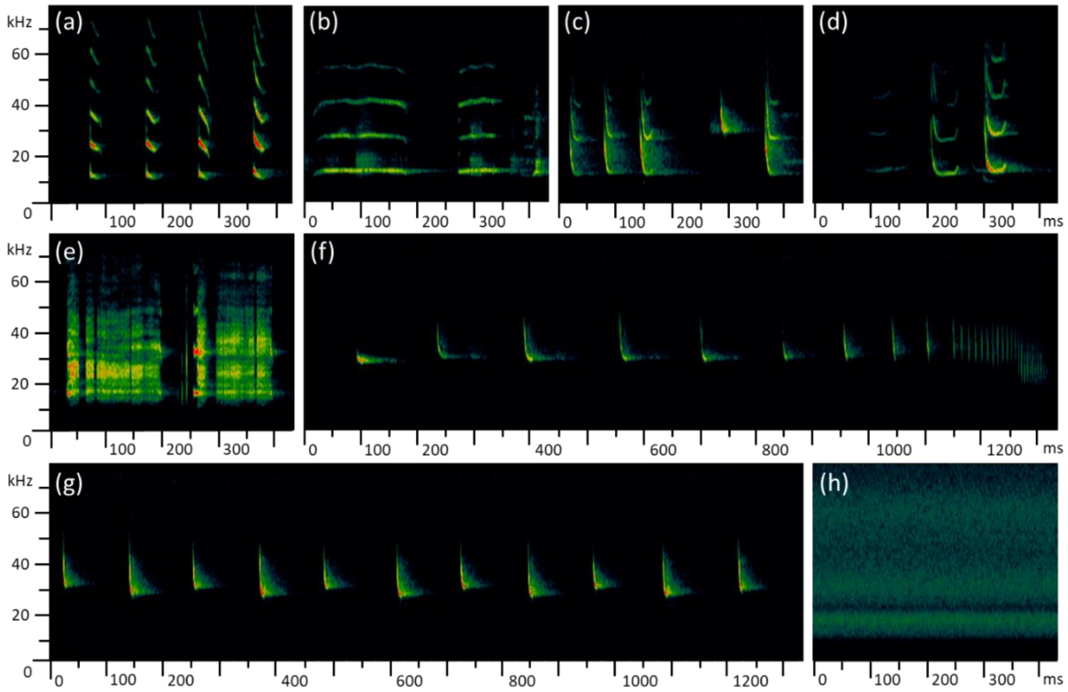


Figure 3.1. The example exemplars of the eight sound treatments. (a) Syllable 1 – short duration, (b) Syllable 1 – long duration, (c) Syllable 2 – short duration, (d) Syllable 2 – long duration, (e) a broadband chatting sound, (f) feeding buzz, (g) echolocation call sequence, and (h) ambient sound. The spectrograms were created in Kaleidoscope Lite (Version 5.6.3) with brightness set to -18 dB gain and contrast set to -50 dB dynamic range (except for (h) where the contrast is -75 dB for easy visualisation). Note: only part of 1.5 seconds spectrogram of each sound is shown here. All spectrograms are in the same scale as shown in (h).

Each treatment sequence was broadcast continuously for one minute, consisting of a 1.5-second exemplar repeated 40 times. A three-minute observation period was allocated for each treatment, including one minute before, during, and after the sound broadcast. Eight treatments constituted a block, with a 30-second transition period between treatments. During the 30-second transition period, no sound was broadcasted. Eight blocks were broadcasted per night (Figure 3.2). The order of treatments and blocks was arranged using a Latin square to minimise any association between time of night and treatments (supplementary information, Table S3.1). On the first night, the broadcast began with the first block. Each subsequent night, started with the next block in sequence, completing the full rotation over eight nights. All sound sequences were broadcast at the original track amplitude without adjustment.

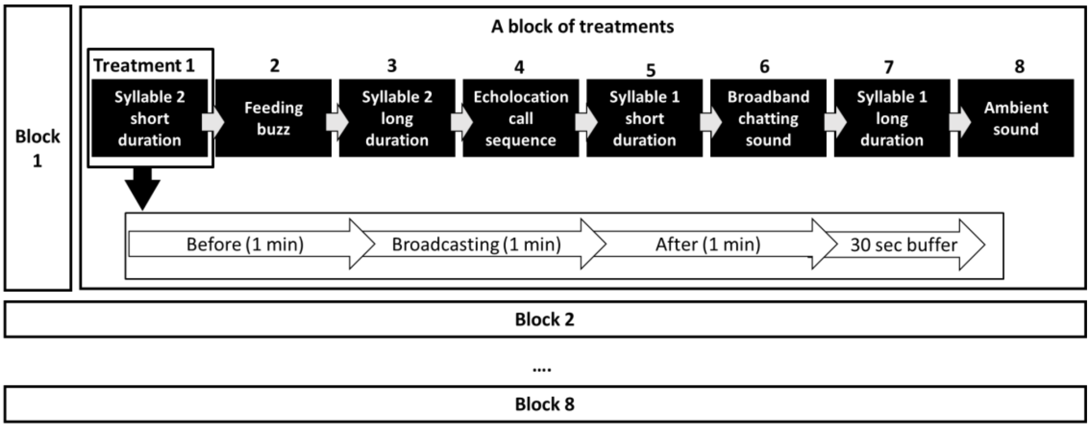


Figure 3.2. An example of the call broadcast process used in the experiment. Each block consisted of eight treatments with three observation periods. Eight blocks were broadcast per night, with each subsequent night beginning with the next block in sequence.

I conducted the experiment at the edge of bushland within and adjoining Cumberland State Forest, which supports known *C. gouldii* colonies throughout all seasons (Figure 3.3 (a)). Eight broadcast locations were selected; each situated at least 50 metres from main paths or roads. To minimise carry-over effects, adjoining broadcast locations were maximally spaced from those used on the consecutive night, ensuring the greatest possible distance between locations on successive nights, thereby reducing the likelihood that individuals from one location influenced subsequent treatments at another (range: 1 – 2.02 km; median = 1.14 km). The order of experimental locations is shown in Figure 3.3 (b). To avoid affecting *C. gouldii* behaviours during the pregnancy and nursing seasons, from late spring to summer (Eastick et al. 2022), the experiment was conducted in the middle of autumn 2024, with playback trials carried out over eight days: 8, 10, 11, 12, 24, 25, 26, and 27 April 2024. The experiment started at 30 minutes after sunset and ran for four and a half hours per night.

Equipment setup

A full-spectrum speaker (L400 Ultrasound Speaker, Pettersson Elektronik AB, Sweden) was used to broadcast the exemplars at 192 kHz sampling rates. The speaker amplitude was standardised using an ultrasonic microphone (M500 USB Ultrasound Microphone, Pettersson Elektronik AB, Sweden) to reach -25 dB full-scale digital level in the oscillogram when Syllable 1 was broadcast at five metres from the speaker. The sound amplitude was a reasonable volume typically emitted by bats living in roosts when the ultrasonic microphone was placed at five metres away. The speaker was positioned at a height of 1.5 metres and placed three metres from the forest edge. A camcorder capable of recording in near infra-red (Sony AX53 4K Handycam, Sony, Japan) was mounted on a tripod at a height of 1.5 metres, facing the speaker from five metres away. Two ultrasonic detectors (Anabat Swift, Titley Scientific, Australia) were positioned on either side of the speaker and camcorder. The same detectors were used throughout the experiment to minimise variation in microphone sensitivity. To help improve the clarity of the video recordings, two infrared illuminators, powered by external power banks, were positioned along the recording path, approximately two-thirds of the way between the speaker and the camcorder, and oriented toward the speaker (Figure 3.3 (c)). The angles of the illuminators were adjusted slightly to accommodate the local experimental environments.

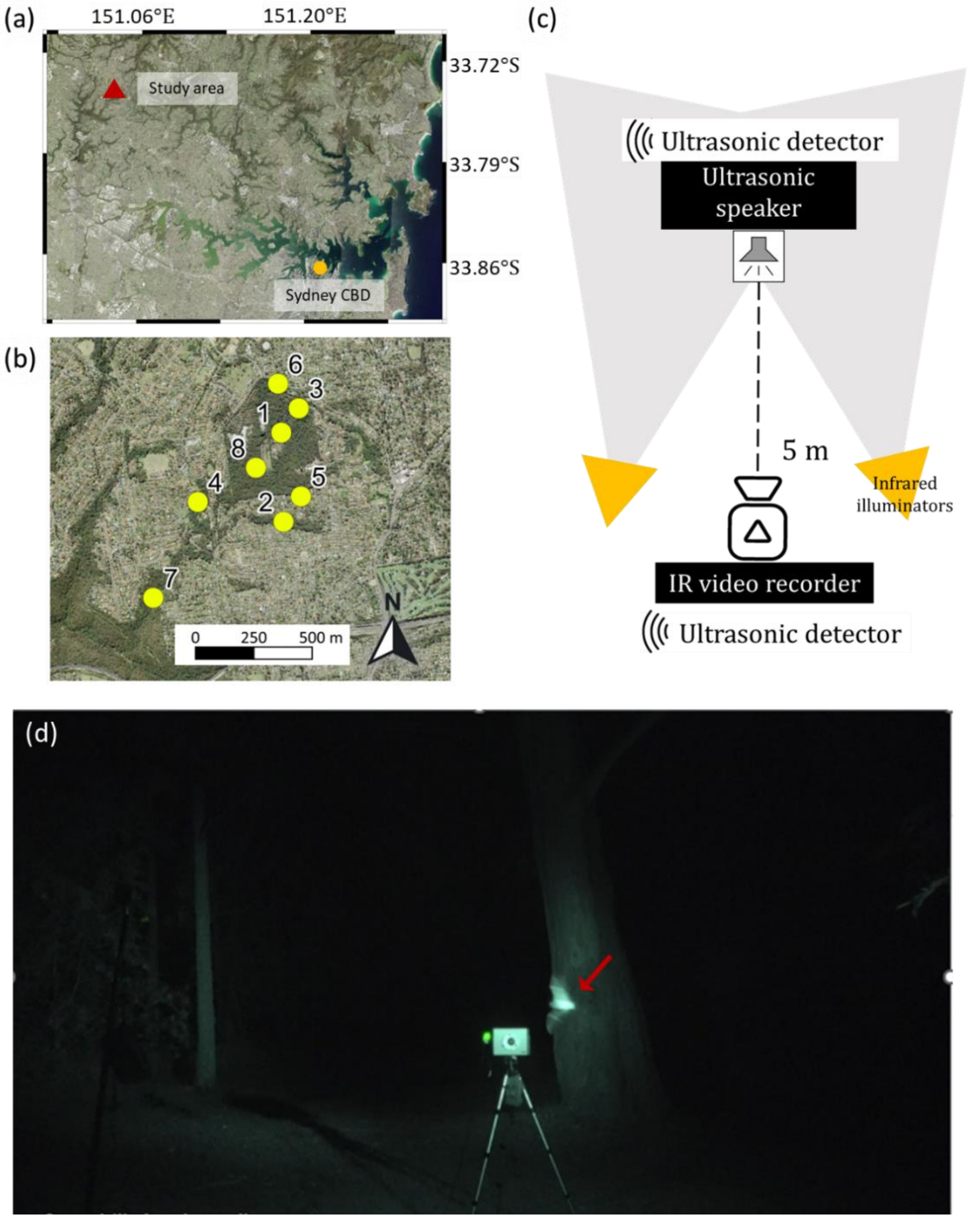


Figure 3.3. (a) Map showing the relative location of Sydney and study area (distance: 20 km). (b) Map of the eight experimental sites; (c) Equipment setup, including an ultrasonic speaker, detectors, infrared (IR) video recorder, and two infrared illuminators; (d) Field of view of the footage. The speaker is positioned at the centre, and the red arrow indicates a bat flying within the recording field. Numbers in (b) indicate the order in which the experiments were conducted: the first night at location 1, the second night at location 2, and so on.

Behavioural responses

I analysed acoustic and video recordings separately, assessing the behavioural responses within three-observation periods: 1-min before, 1-min during and 1-min after the sound broadcast (Figure 3.2).

I identified the responding species through echolocation call sequences (Adams et al. 2010). Two species dominated the responses recorded, the conspecific *C. gouldii* and the heterospecific *Miniopterus orianae oceanensis*. I listed other species responding to the playback in the supplementary information, Text S3.1 and Table S3.2.

For the acoustic recording, I analysed the detector on the speaker side and estimated the distance between speaker and bats based on the oscillogram amplitude. Bat echolocation calls produced while approaching the speaker may overlap with the broadcast sound. In this case, I checked for irregular peaks in the oscillogram that did not correspond to the broadcast signal and confirm bat responses using the video recordings. The amplitude of ultrasound may vary with direction (Jakobsen et al. 2013); therefore, the amplitude of echolocation calls can serve as a response indicator when bats are oriented toward the speaker. Additionally, video footage can be used to corroborate the acoustic recordings, as described in ‘bat response distance’ below. I used three sound levels to estimate bat response distance: level 1 was recorded as bats in the surrounding area but at a moderate distance from the speaker (< 50% of overall amplitude in full-scale digital level in the waveform); level 2 was recorded as bats in vicinity of the speaker but typically outside the video recording field (between 50 and 99% of overall amplitude in full-scale digital level in the waveform); level 3 was recorded as bats flying around approaching the speaker and within the video recording field (reaching 100% of overall amplitude in full-scale digital level in the waveform and oscillogram overloading and clipping) (supplementary information, Figure S3.1). No echolocation calls were recorded, as no bats approaching. I only analysed vocal sequences with strong amplitude, classified as level 2 and 3, which correspond to approach behaviours. The following response variables were analysed: (1) binary responses – whether level 2 or 3 bat calls were recorded as present or not; (2) latency to arrival (seconds) – the time taken for the first strong bat sound to be recorded; (3) response duration (seconds) – the length of time bats remained near the speaker; and (4) social vocalisation response – whether non-echolocation calls were recorded as present or not.

For the video recordings, I analysed (1) binary responses – whether bats flew into the video recording field or not (Figure 3.3(d)); (2) latency to arrival (seconds) – the time taken for the first bat to fly into the video recording field; (3) response duration (seconds) – the length of time bats remained and flew around the speaker within the video recording field; and (4) whether two types of behavioural responses were observed: bats flying toward and circling around the speaker, defined as ‘approaching’; bats attempting to touch or land on the speaker, defined as ‘landing’. If bats flew past the speaker without altering their flight path, the behaviour was defined as ‘no response’.

Statistical analysis

I first analysed whether bats responded differently to the two subgroups of the two social vocalisations, Syllable 1 and 2. I found no significant differences between the subgroups in the binary responses, latency to arrival, and response duration (supplementary information Text S3.2 and Table S3.3). Hence, the two subgroups within each social vocalisation syllable were pooled into two main syllables, Syllable 1 and 2, for subsequent analyses, resulting in a reduction from the original eight to six treatments: Syllable 1, Syllable 2, broadband chatting sounds, echolocation sequences, echolocation sequences with feeding buzzes, and ambient control sounds.

Generalised Linear Mixed Models (GLMMs) were used, implemented using the g*lmmTMB* package (Brooks et al, 2024). The family used in each model was selected based on the distribution of the response variable. I also used the *DHARMa* package (Hartig 2020) to perform diagnostic tests and overdispersion tests to assess model fit. The locations were set as the random effect to control for site differences in bat activity.

Within treatment comparisons

For the acoustic data, I first analysed responses across the three observation periods to examine whether there was a difference in bats approaching the speaker during the sound broadcast period compared to before or after the sound broadcast period. The binary responses of *C. gouldii* were used as the response variable. The fixed variables were used as the three observation periods, with the before the sound broadcast period set as the reference level, and the presence/absence of *C. gouldii* (in conspecific responses) or *M. orianae oceanensis* (in heterospecific responses) within a proximity distance (i.e., sound level 1, 2 and 3) before the sound broadcast. The variance explained by the before- and after-observation periods in echolocation sequence, feeding buzz, and ambient control sound treatments was estimated as zero due to the absence or rarity of responses, resulting in a singular fit, so I excluded these three treatments in this analysis. For the video data, no bat was filmed before and after the sound broadcast, so the analysis of the responses across the three observation periods were unavailable.

Between treatment comparisons

Hereafter, I focused on the responses ‘during’ the sound broadcast observation period in both the acoustic and video data to examine the difference in behavioural response across the six treatments. The response variable was the presence or absence (0/1) of individuals (either *C. gouldii* or *M. orianae oceanensis*, a binary response). Ambient control sound treatment was set as the reference level. The *binomial* family was used for examining binary responses. On the occasions when bats approached the broadcast, I extracted the time of latency to arrival and response duration, comparing these across sound treatments. Here, Kruskal-Wallis rank sum tests were used in both the acoustic and video recordings to compare treatment ranks. Statistical analysis was performed in R (Version 4.3.1, R Code Team, 2025).

Results

Conspecific responses

Binary responses within treatment comparison

I first examined the responses of each sound treatment before, during, and after the sound broadcast periods through acoustic and video datasets. The results based on acoustic recordings revealed that *C. gouldii* individuals were significantly attracted to the broadcast of Syllable 1 and 2 (Table 3.1). *Chalinolobus gouldii* individuals also responded to broadband chatting sounds, although this response was only marginally significant (Table 3.1). Additionally, the presence of *C. gouldii* prior to sound playback significantly increased responses whether they approached the speaker in Syllable 1, 2 and chatting sound treatments (Table 3.1 and Figure 3.5). *Chalinolobus gouldii* was recorded approaching ambient control sounds on two occasions and echolocation call sequence on two occasions, although the sample size was too low for formal analyses of these data. *Chalinolobus gouldii* did not approach the feeding buzzes during broadcasting (Figure 3.5).

Table 3.1. Generalised Linear Mixed Model results for *Chalinolobus gouldii* presence/absence responses before, during, and after the broadcast of sound treatments.

Treatment	Estimate	SE	*z*-value	*p*-value
Model 1: Syllable 1				
Intercept	-5.735	0.912	-6.287	<0.001
During	2.372	0.833	2.848	**0.004**
After	2.013	1.083	1.859	0.063
C. gouldii existence before the sound broadcast	3.441	0.665	0.665	**<0.001**
Model 2: Syllable 2				
Intercept	-5.741	1.071	-5.359	<0.001
During	3.344	1.056	3.167	**0.002**
After	2.020	1.220	1.655	0.098
C. gouldii existence before the sound broadcast	2.276	0.537	4.236	**<0.001**
Model 3: Chatting sound				
Intercept	-6.619	2.246	-2.947	0.003
During	3.014	1.548	1.946	0.052
After	1.501	1.845	0.814	0.416
C. gouldii existence before the sound broadcast	4.513	2.079	2.170	**0.030**

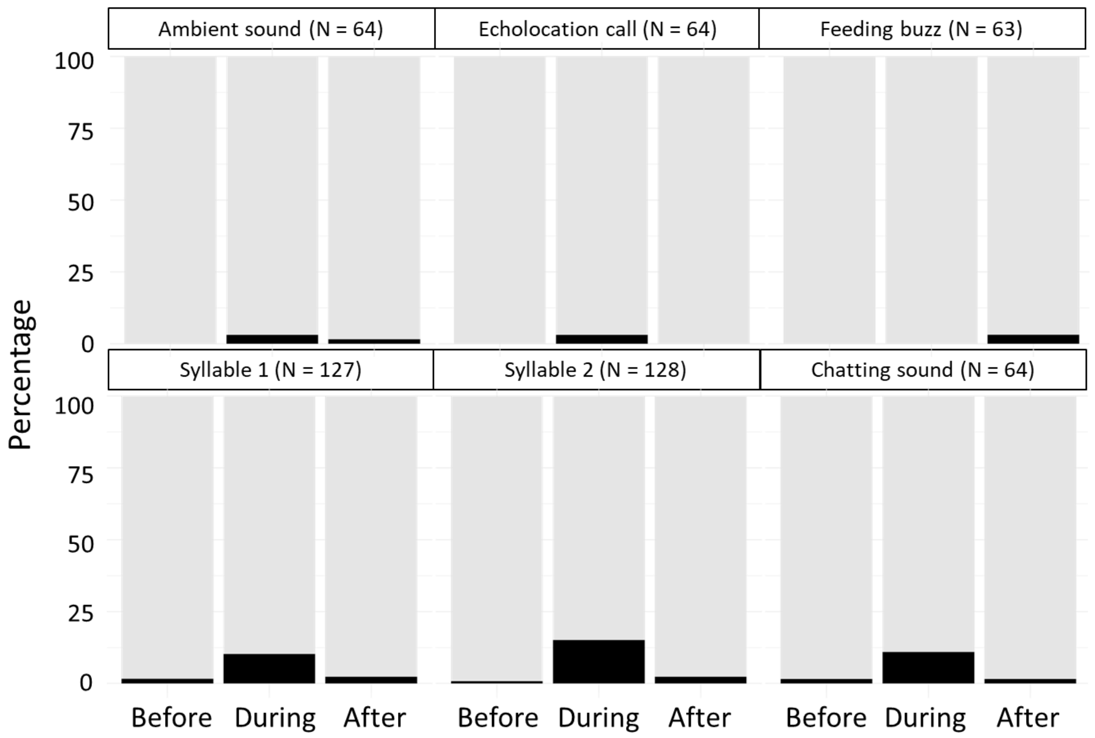


Figure 3.5. The percentage of trials where *Chalinolobus gouldii* was detected by acoustic recorders, before, during, and after the sound playback. The graphs present the percentage of trials where responses were detected (black) compared to trials without responses (grey) across the three observation periods. N is the number of trials. Note: Missing data occurred in the feeding buzz and Syllable 1 treatments on one occasion due to equipment malfunction.

For the video dataset, bats were only filmed approaching during the broadcast of Syllable 1, Syllable 2, and broadband chatting sounds. No bat was filmed before and after the sound broadcast, so no analyses across the three observation periods were conducted. The number of approaches recorded during broadcasts was seven for Syllable 1, 17 for Syllable 2, and 4 for chatting sounds (Figure 3.6).

Figure 3.6. The percentage of trials where *Chalinolobus gouldii* was recorded by video camera, before, during, and after the sound playback**.** The graphs present the percentage of trials where responses were detected (black) and compared to trials without responses (grey) across the three observation periods. N is the number of trials. Note: Missing data occurred in the feeding buzz and Syllable 1 treatments on one occasion due to equipment malfunction.

Binary responses among the six-treatment comparison

I then compared the responses during the sound broadcast periods across the six treatments. I also included whether *C. gouldii* were present prior to sound broadcast using the acoustic data. *Chalinolobus gouldii* approached Syllable 2 and broadband chatting sounds significantly more often compared to the ambient control sounds (see pairwise treatment comparisons in supplementary information Table S3.4). Additionally, the presence of *C. gouldii* prior to sound playback significantly increased responses (Table 3.2 and Figure 3.5).

Table 3.2. Generalised Linear Mixed Model results for *C. gouldii* presence/absence responses among treatments and the presence of conspecific before sound broadcast.

Treatment	Estimate	SE	*z*-value	*p*-value
Intercept	-4.315	0.773	-5.581	<0.001
Syllable 1	1.467	0.808	1.815	0.070
Syllable 2	1.864	0.793	2.350	**0.019**
Chatting sound	1.769	0.865	2.044	**0.041**
Echolocation call	0.134	1.048	0.128	0.898
C. gouldii existence before the sound broadcast	2.403	0.363	6.620	**<0.001**

Note: 'Feeding buzz' treatment was removed due to no response.

For the video data, I examined responses during the sound broadcast periods across the six treatments and did not consider the presence of *C. gouldii* prior to sound broadcast because *C. gouldii* never flew near the ground and no bat was filmed before and after the sound broadcast. Responses to the five vocalisation treatments did not differ from the ambient control sound (Figure 3.6 and supplementary information Table S3.5).

The latency to arrival and response duration between the three social vocalisations

I extracted the approaching responses during Syllable 1, 2, and broadband chatting sound broadcast from the acoustic and video data to examine the time to arrival and response duration among treatments. The results from both acoustic and video data indicated that *C. gouldii* responses did not differ among the three social vocalisations for latency to arrival and response duration (Kruskal-Wallis rank sum test: acoustic data: latency to arrival: chi-square = 0.111, *df* = 2, *p* = 0.946, response duration: chi-square = 1.207, *df* = 2, *p* = 0.751; video data: latency to arrival: chi-square = 0.801, *df* = 2, *p* = 0.670, response duration: chi-square = 0.760, *df* = 2, *p* = 0.684).

Other behavioural responses in the acoustic and video data

In the acoustic data, a sequence of free-flying *C. gouldii* echolocation calls with social vocalisations was recorded on one occasion after Syllable 1 broadcast. In the video data, *C. gouldii* attempted to land on the speaker on four separate occasions: twice for Syllable 1, once for Syllable 2, and once for chatting sounds.

Heterospecific responses

At least six species approached the speaker, however I analysed the predominant heterospecific *M. orianae oceanensis* behavioural responses, as this species provided a sufficient effective sample size (for details on responses from other heterospecifics, see supplementary information Test S3.1 and Table S3.2).

Binary responses within treatment comparison

I examined the *M. orianae oceanensis* responses to each sound treatment before, during, and after the sound broadcast periods through acoustic and video datasets. The results based on acoustic recordings revealed that *M. orianae oceanensis* was significantly attracted to *C. gouldii* Syllable 2 social vocalisations six times compared to before the sound broadcast (GLMM: estimate = -1.533, SE = 0.674, z = -2.276, p = 0.023), and the presence of *M. orianae oceanensis* prior to sound playback significantly increased responses whether individuals approached the speaker in Syllable 2 (GLMM: estimate = 1.925, SE = 0.856, z = 2.749, p = 0.025). For the other *C. gouldii* vocalisations, the statistical analysis did not show significant responses to these vocalisations and ambient sounds (supplementary information Table S3.2 and Table S3.6).

For the video dataset, *M. orianae oceanensis* individuals were only filmed approaching during the sound broadcast. *Minopterus orianae oceanensis* individuals never flew near the ground and was not filmed before and after the sound broadcast, so no analyses across the three observation periods were conducted. The number of approaches observed during the sound broadcasts were three for Syllable 1, twice for Syllable 2, once for chatting sounds, three for echolocation calls, and once for feeding buzzes. *Minopterus orianae oceanensis* did not respond to the ambient control sound.

Binary responses among the six-treatment comparison

I compared the *M. orianae oceanensis* responses during sound broadcast periods across the six treatments. I also included whether *M. orianae oceanensis* were present prior to sound broadcast using the acoustic data. The binary responses of *M. orianae oceanensis* did not differ among the six sound treatments in the acoustic data, despite approach responses observed. Interestingly, the presence of *M. orianae oceanensis* prior to sound broadcast significantly increased the likelihood of bat responses during the sound broadcast in the acoustic data (GLMM: estimate = 2.080, SE = 0.690, z = 3.015, p <0.001; supplementary information Table S3.7).

For the video data, I examined responses during the sound broadcast periods across the six treatments; however, there was no significant differences in their response compared to ambient control sounds (supplementary information Table S3.2 and Table S3.8). Notably, *M. orianae oceanensis* attempted to land on the speaker on one occasion during *C. gouldii* broadband chatting calls broadcast.

Discussion

Information transfer through vocalisations has the potential to convey benefits to conspecifics and heterospecifics. However, this process has been poorly studied in Australian bats. In this study, *C. gouldii* appeared to perceive and respond specifically to conspecific social vocalisations, Syllable 1, 2 and broadband chatting sounds, potentially representing affiliative social information and ignoring echolocation calls or feeding buzzes. *Miniopterus orianae oceanensis* approached all *C. gouldii* vocalisations during the sound broadcast. These responses did not differ from those of the control treatments, and the presence of *M. orianae oceanensis* prior to the sound broadcast strongly influenced the likelihood of responses. This finding suggests that *M. orianae oceanensis* may show a generalised response to any *C. gouldii* vocalisations. In the case of *C. gouldii*, conspecific social vocalisations may facilitate social information transfer, allowing coordination among group members or finding resources, such as prey or roosts. In the case of *M. orianae oceanensis*, they may respond to *C. gouldii* vocalisations due to the novel sounds instead of a similar foraging niche.

Conspecific responses

Results of this study suggest that *C. gouldii* perceived and responded to their own social vocalisations. I recorded bats moving toward the speaker when *C. gouldii* social vocalisations were broadcast, where the speaker was set at 1.5 metres above the ground and was not in a ‘typical’ flight path. I also observed the response differences in *C. gouldii* during these three social vocalisation broadcasts, suggesting that these vocalisations may represent slightly different social information, further discussed below.

Syllable 1 and 2 may function as contact calls, reflecting affiliative (e.g., cooperative and grouping) or neutral signals, as previous call playback studies in other bat species indicate that bats more likely approach affiliative signals and avoid aggressive or agonistic signals (Barlow and Jones 1997, Wilkinson and Boughman 1998, Furmankiewicz et al. 2011, Chaverri et al. 2012, Bohn and Gillam 2018). I did not observe overt agonistic behaviours; instead, the most common responses involved bats circling and inspecting the speaker in flight, with three recorded instances of landing. Syllable 1 and 2 were frequently recorded when *C. gouldii* were at roosts (Chapter 2). Given that *C. gouldii* co-habits with familial individuals (Godinho et al. 2015, Eastick 2022), individuals may produce these syllables to advertise their location to roost mates while non-roost mate conspecifics obtain and interpret the social information to decide whether to approach (Furmankiewicz et al. 2011). Although previous studies show that bats can use social vocalisations, such as contact calls, to coordinate social foraging mates (Wilkinson and Boughman 1998, Egert-Berg et al. 2018), whether *C. gouldii* produces social vocalisations for cooperative foraging still needs to be investigated. While these findings suggest that Syllable 1 and 2 are affiliative signals, further research is required to determine their functions in the social interactions of *C. gouldii*.

Broadband sounds in bats, in contrast to contact calls or affiliative signals, have been suggested to function as warning or aggressive calls (Russ et al. 1998, Carter et al. 2015, Eckenweber and Knörnschild 2016, Hörmann et al. 2021, Hanrahan et al. 2022) comparable to the broadband chatting sounds of *C. gouldii*. These sounds are produced to warn conspecifics during threatening situations, such as periods of increased predation risk (Russ et al. 1998, Carter et al. 2015, Eckenweber and Knörnschild 2016, Hörmann et al. 2021), and to provoke receiver inspection flights (Carter et al. 2015, Eckenweber and Knörnschild 2016). Aggressive calls possibly happen during conflict, such as fighting over roost or food resources, or during unwanted mating attempts (Fernandez et al. 2014). In this study, *C. gouldii* approached the speaker significantly more often during the broadband chatting sounds broadcast in the acoustic data rather than the video data, suggesting that receivers may have been within the proximity of the broadcast area but remained at least two metres away, i.e., outside the camcorder's field of view. Receivers potentially inspected the area surrounding the speaker instead of approaching it directly, possibly to avoid potential risks or to assess the identity of the sound signallers before deciding whether to approach. Therefore, I interpret that the broadband chatting sound is likely used to convey a warning, and that *C. gouldii* may respond by inspecting the area to assess the threat.

Heterospecific responses

Sympatric species with overlapping niches can eavesdrop on heterospecific social information to obtain potential benefits (Russ et al. 2004). The predominant heterospecific in this study was *M. orianae oceanensis*, which overlaps with *C. gouldii* in foraging niches, as both are aerial-hawking edge foragers that primarily feed on Lepidoptera (Vestjens and Hall 1977, McKenzie and Rolfe 1986, Fullard et al. 1991). Within sound treatments, *M. orianae oceanensis* were attracted to *C. gouldii* Syllable 2, and the presence of *M. orianae oceanensis* prior to the sound broadcast increased their responses. Between treatments, *M. orianae oceanensis* were more likely to approach any *C. gouldii* vocalisations including echolocation and feeding buzzes when they were present around the speaker prior to the broadcast. This may imply that the ability of *M. orianae oceanensis* to discriminate *C. gouldii* social vocalisations is limited, but that they can extract explicit information from Syllable 2, prompting them to scan the sound more closely (Moss and Surlykke 2010). Many studies indicate that bats approach and eavesdrop on heterospecific social vocalisations, for example for locating roosts (Bergmann et al. 2022b) or detecting predators (Russ et al. 2004, Huang et al. 2018). Also, heterospecific social vocalisations can be used as acoustic lures to increase capture or detection rates (e.g., Hill et al. 2014, Hill et al. 2015, Aylen et al. 2022, Davidson-Watts and O'Donnell 2023), potentially eavesdropping on social information or merely responding to the novel sounds (Aylen et al. 2022). Alternatively, *M. orianae oceanensis* may unselectively approach *C. gouldii* vocalisations due to curiosity and novel sounds because *M. orianae oceanensis* responded to not only *C. gouldii* social vocalizations but also ambient sounds. The frequency range of echolocation calls in *C. gouldii* and *M. orianae oceanensis* are 25-34 kHz and 43-48 kHz, respectively (Adams et al. 2010). Given that the acoustic frequency of social vocalisations is lower than that of echolocation calls, *C. gouldii* vocalisations potentially overlap with the social vocalisations of *M. orianae oceanensis* and draw their attention. The ecological significance of heterospecific responses still requires investigation, but factors that may influence their occurrence include the perceptual capacity of the heterospecific and the fitness or energetic benefits derived from this behaviour.

The cue of echolocation calls and feeding buzzes

Echolocation calls provide reliable indicators of activity, whereas feeding buzzes represent public information of foraging (Dorado-Correa et al. 2013). *Chalinolobus gouldii* did not respond to conspecific echolocation calls and feeding buzzes, while heterospecific *M. orianae oceanensis* responded to these vocalisations, consistent with a previous playback study on *C. gouldii* echolocation calls (Velasco 2018). Previous work on other bats has indicated that echolocation activity has a negative effect on conspecific echolocation activity, potentially due to competition (Lewanzik et al. 2019), but in other studies, bats have been observed approaching conspecific echolocation calls to facilitate group hunting (Dechmann et al. 2009, Dechmann et al. 2010, Gager 2019) and heterospecific echolocation calls when species share similar foraging ecology (Arlettaz et al. 2000, Hügel et al. 2017), particularly in edge-foragers (Velasco 2018). Compared with echolocation calls, bat responses to feeding buzzes are more complex depending on species-specific foraging strategies and population density of both conspecifics and heterospecifics in the environment (Gager 2019, Krivoruchko et al. 2024). Such responses either improve feeding efficiency (Gillam 2007, Dorado-Correa et al. 2013, Kohles et al. 2022) or avoid competition (Voigt-Heucke et al. 2016, Lewanzik et al. 2019, Marggraf et al. 2023). Given that *M. orianae oceanensis* and *C. gouldii* overlap in their foraging niches, eavesdropping on *C. gouldii* echolocation calls and feeding buzzes may either enhance foraging efficiency or avoid competition.

The sensitivity of audition in bats

Hearing ability may influence how bats respond to broadcast sounds. Bats exhibit species-specific auditory perception, which reflects interactions among sound amplitude and frequency, echolocation calls, and social vocalisations (Lattenkamp et al. 2021). Weather conditions, such as humidity and temperature, also affect sound transmission, particular for high-frequency components of sounds, which are easily lost due to atmospheric attenuation (Chaverri and Quirós 2017, Goerlitz 2018). Previous studies indicate that changes in call frequency and bandwidth can convey different information and elicit different behavioural responses in bats (Russ et al. 2005). In this broadcast study, the relative importance of acoustic frequency and sound amplitude was not explicitly accounted for, as the hearing sensitivities of *C. gouldii* and *M. orianae oceanensis* are currently unknown. This limitation could be addressed in future research through well-controlled laboratory-based experiments.

Conclusion

Chalinolobus gouldii vocalisations can elicit response from both conspecifics and heterospecifics. While these calls are known to attract bats, the specific benefits and costs to the responding individuals remain unclear. In this study, most bats were detected by ultrasonic recorders when they approached the speaker, but they were not always visible on the video footage, likely because individuals remained at a distance to inspect the sounds. Integrating acoustic and video recordings in field studies of highly mobile, nocturnal animals can allow to obtain a broader range of behavioural responses. Together, these findings suggest that vocal communication plays a key role in mediating conspecific and heterospecific interactions. Future research should explore the ecological significance of these interactions, including the benefits associated with social information use in bat communities.

Acknowledgments

I thank Tim Liston from the Forestry Corporation of NSW at Cumberland State Forest for enabling us to conduct my work in the evening after hours, and John Macris, biodiversity adviser at Macquarie University, for allowing us to carry out the pilot test on campus. I am also grateful to the Lab of Animal Ecology at Western Sydney University for providing equipment, including video camcorders, infrared illuminators, external power sources, and an ultrasonic speaker (Pettersson L400).

Supplementary information

Table S3.1. The order of treatments and blocks arranged with Latin square design. Each treatment has eight exemplars.

	Order of treatment							
Block	1	2	3	4	5	6	7	8
1	A	B	H	C	G	D	F	E
2	B	C	A	D	H	E	G	F
3	C	D	B	E	A	F	H	G
4	D	E	C	F	B	G	A	H
5	E	F	D	G	C	H	B	A
6	F	G	E	H	D	A	C	B
7	G	H	F	A	E	B	D	C
8	H	A	G	B	F	C	E	D

A: Syllable 2 – short duration, B: feeding buzz, C: echolocation call sequence, D: broadband chatting sound, E: ambient control sound, F: Syllable 2 – long duration G: Syllable 1– short duration, and H: Syllable 1 – long duration.

Text S3.1. Heterospecific responses

Miniopterus orianae oceanensis and at least five species including *Nyctophilus* species*, Vespadelus vulturnus*/*C. morio* complex*, Falsistrellus tasmaniensis, M. australis*, and *Scotorepens orion* were identified in the study site through the echolocation call sequences. Heterospecifics responded to all five types of *C. gouldii* vocalisations, including three social vocalisations, echolocation calls, and feeding buzzes. I also recorded *Nyctophilus* species trying to land on the speaker twice during *C. gouldii* Syllable 1 broadcast.

Table S3.2. The number of heterospecific approaches observed during the sound broadcast in the acoustic and video data

Species	Syllable 1	Syllable 2	Chatting sound	Feeding buzz	Echolocation calls	Ambient sound
Acoustic data						
M. orianae oceanensis	4	6	2	3	4	2
Nyctophilus species	3	1	0	0	5	0
V. vulturnus/ C. morio complex	0	1	1	0	1	0
F. tasmaniensis	0	2	0	0	0	0
S. orion	1	0	0	0	0	0
M. australis	2	0	0	1	1	0
Video data						
M. orianae oceanensis	3	2	1	1	3	0
Nyctophilus species	3	1	0	0	2	0
V. vulturnus/ C. morio complex	0	1	1	0	1	0
F. tasmaniensis	0	0	0	0	0	0
S. orion	1	0	0	0	0	0
M. australis	1	0	0	0	0	0

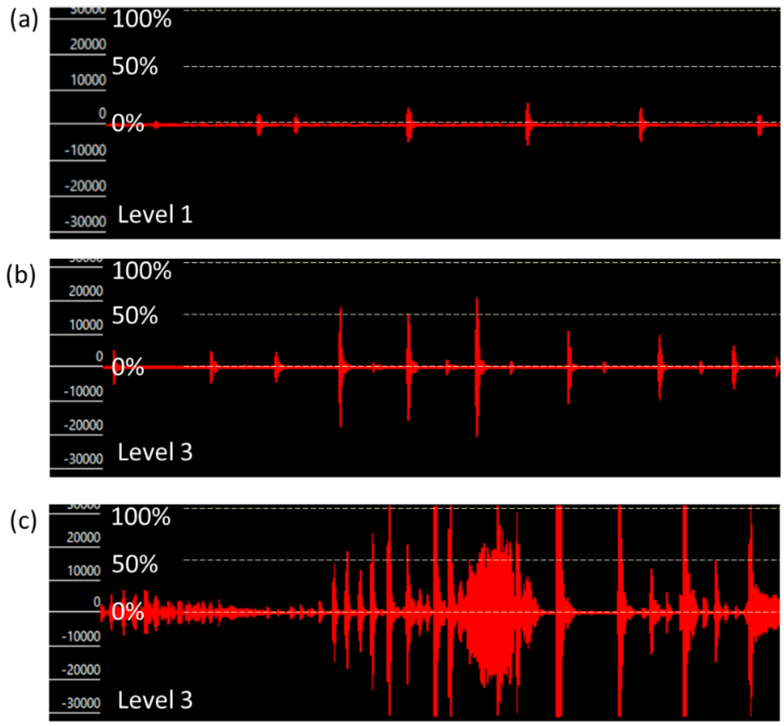


Figure S3.1. The illustration of sound amplitude and bat distance assessment. (a) Level 1; (b) Level 2; (c) Level 3.

Text S3.2. The gradation of syllables within treatments test

Syllable 1 and 2 showed high gradation within syllables; therefore, I selected the extreme exemplars within Syllable 1 and 2 treatments. I picked up the shorter and longer syllables within treatments as the subset. I used a generalised linear mixed model (GLMM) to analyse if bats showed different responses to the two extreme exemplars within the treatments. The response variable (approaching speaker or not, yes/on) in both acoustic and video dataset was modelled using binomial distribution with a logit link function. The exemplar was a fixed variable, and the location was a random effect to account for repeated measures. Models were fitted using the glmmTMB package in R.

The GLMM revealed a non-significant effect of the exemplars on bat responses in each treatment in both acoustic and video data. The results were summarised in the table below. I then pooled the two extreme subsets from the two syllables together, respectively.

Table S3.3. The test of the two extreme subsets within Syllable 1 and 2 in both acoustic and video dataset

Treatment	Estimate	SE	*z*-value	*p*-value
Acoustic data				
(intercept)	-3.119	0.462	-6.752	<0.001
Syllable 1 (short vs. long duration)	-0.224	0.491	-0.456	0.649
(intercept)	-2.711	0.321	-8.435	<0.001
Syllable 2 (short vs. long duration)	-0.098	0.431	-0.227	0.820
Video data				
(intercept)	-3.869	0.638	-6.068	<0.001
Syllable 1 (short vs. long duration)	-0.277	0.771	-0.359	0.720
(intercept)	-3.418	0.415	-8.238	<0.001
Syllable 2 (short vs. long duration)	0.634	0.518	1.223	0.221

Table S3.4. Results of pairwise treatment comparisons for *C. gouldii* acoustic responses.

Contrast	Estimate	SE	*z*-value	*p*-value
Control – Echo	-0.1343	1.05	-0.128	0.898
Control – Feeding buzz	19.0774	10000.00	0.002	0.999
Control – Syllable 1	-1.4668	0.81	-1.815	0.070
Control – Syllable 2	-1.8647	0.79	-2.35	**0.019**
Control – Chatting	-1.7685	0.87	-2.044	**0.041**
Echo – Feeding buzz	19.2117	10000.00	0.002	0.999
Echo – Syllable 1	-1.3325	0.81	-1.65	0.099
Echo – Syllable 2	-1.7304	0.79	-2.184	**0.029**
Echo – Chatting	-1.6343	0.86	-1.895	0.058
Feeding buzz – Syllable 1	-20.5442	10000.00	-0.002	0.998
Feeding buzz – Syllable 2	-20.9421	10000.00	-0.002	0.998
Feeding buzz – Chatting	-20.8459	10000.00	-0.002	0.998
Syllable 1 – Syllable 2	-0.3979	0.42	-0.946	0.344
Syllable 1 – Chatting	-0.3018	0.54	-0.561	0.575
Syllable 2 – Chatting	0.0962	0.51	0.187	0.852

Table S3.5. The summary of video data of *C. gouldii* binary responses among treatments.

Fixed variable	Estimate	SE	*z*-value	*p*-value
Intercept	-22.677	10498	-0.002	0.998
Syllable 1	19.835	10499	0.002	0.998
Syllable 2	20.819	10499	0.002	0.998
Chatting sound	19.969	10499	0.002	0.998
Echolocation call	-4.037	79702	0	1
Feeding buzz	-4.193	86730	0	1

Table S3.6. The summary of *M. orianae oceanensis* binary responses before, during and after sound broadcast of sound treatments.

Treatment	Estimate	SE	*z*-value	*p*-value
Model 1: Syllable 1				
Intercept	-2.552	0.482	-5.292	<0.001
During	-0.620	0.522	-1.188	0.235
After	-0.462	0.486	-0.951	0.343
Conspecific existence before sound broadcasted	0.105	1.135	0.093	0.926
Model 2: Syllable 2				
Intercept	-2.690	0.657	-4.093	<0.001
During	-1.533	0.674	-2.276	**0.023**
After	-0.527	0.465	-1.133	0.257
Conspecific existence before sound broadcasted	1.925	0.856	2.749	**0.025**
Model 3: Chatting sound				
Intercept	-2.176	0.608	-3.582	<0.001
During	-0.980	0.718	-1.365	0.172
After	-0.716	0.614	-1.166	0.244
Conspecific existence before sound broadcasted	1.521	0.996	1.528	0.127
Model 4: Feeding buzz				
Intercept	-2.650	0.854	-3.104	<0.001
During	-0.834	0.713	-1.170	0.242
After	-0.617	0.651	-0.948	0.343
Conspecific existence before sound broadcasted	-0.213	1.422	-0.150	0.881
Model 5: Echolocation call				
Intercept	-2.676	0.569	-4.700	<0.001
During	0.143	0.674	0.212	0.832
After	0.822	0.594	1.383	0.164
Conspecific existence before sound broadcasted	1.548	1.117	1.386	0.166
Model 6: Ambient sound				
Intercept	-2.435	0.754	-3.228	0.001
During	-0.509	0.674	-0.754	0.451
After	-0.158	0.563	-0.281	0.779
Conspecific existence before sound broadcasted	-0.055	1.065	-0.051	0.959

Table S3.7. The summary of acoustic data of *M. orianae oceanensis* binary responses among treatments and the presence of conspecific before sound broadcast.

Treatment	Estimate	SE	*z*-value	*p*-value
Acoustic data				
Intercept	-3.128	0.698	-4.482	<0.001
Syllable 1	-0.207	0.649	-0.319	0.750
Syllable 2	-0.349	0.633	-0.552	0.581
Chatting sound	0.340	0.678	0.590	0.555
Echolocation call	0.413	0.665	0.621	0.535
Feeding buzz	-0.127	0.717	-0.177	0.840
Conspecific existence before sound broadcast	2.080	0.690	3.015	**<0.001**

Table S3.8. The summary of video data of *M. orianae oceanensis* binary responses among treatments.

Fixed variable	Estimate	SE	*z*-value	*p*-value
Intercept	-24.17	17741	-0.001	0.999
Syllable 1	20.03	17741	0.001	0.999
Syllable 2	19.63	17741	0.001	0.999
Chatting sound	19.60	17741	0.001	0.999
Echolocation call	20.75	17741	0.001	0.999
Feeding buzz	19.63	17741	0.001	0.999

Chapter 4

Greater canopy cover in urban areas enhances social interactions in an urban-dwelling bat, *Chalinolobus gouldii*, in Australia

Note: This chapter is formatted as a paper for *Urban Ecosystem*

Abstract

Urbanisation is a major ecological stressor, driving habitat degradation and subsequently, altering wildlife behaviours. Bats are known for their sophisticated vocal production, producing high-frequency echolocation calls for navigation and low-frequency, non-navigational sounds for social communication. While the effect of habitat attributes on urban bat activity has been widely studied, predominantly through analyses of echolocation calls, comparatively little is known about how changes in urban habitats influence social communication in bats. I investigated how urbanisation affects social vocalisation in the Gould’s wattled bat, *Chalinolobus gouldii*, a widespread and urban-dwelling species in Australia that produces at least five syllable types for social communication. Using acoustic recordings from 21 rural and urban sites in the Greater Sydney region, I examined social vocalisation rates in relation to canopy cover and urbanisation within a 1-km radius buffer and whether *C. gouldii* adjust their vocalisation in response to urbanisation. Social vocalisations increased with conspecific echolocation activity, so the nightly frequency of social vocalisations was corrected for by dividing by conspecific echolocation activity, expressed as a rate. Overall, the effect of habitat attributes on social vocalisation rates depended on the urban category. In urban areas, the rate of total social vocalisation increased rapidly as the size of canopy cover increased. At the syllable level, the rates of two of the five syllable types (Syllable 1 and 3) used for social communication increased with canopy cover irrespective of urbanisation level, whereas the rate of Syllable 2 increased with canopy cover only in urban areas. Given that greater canopy cover can increase social vocalisation rates, this may reflect the use of social vocalisations to transmit information about resources such as swarming prey and roosts in habitats with greater canopy cover.

Additionally, *C. gouldii* shifted its social vocalisations toward higher frequencies and shorter durations in urban areas, potentially in response to impervious surfaces such as obstacles or noise. These findings broaden the understanding of bat social communication in urban areas and highlight the importance of looking beyond echolocation to assess habitat use and resource requirements of urban fauna.

Keywords

Bats, biological urbanisation, *Chalinolobus gouldii*, Chiroptera, foraging, social communication, social vocalisation, syllable

Introduction

Urban growth results in widespread alterations of natural environments, including natural habitat loss, degradation, fragmentation, and increased exposure to artificial light and noise (Theodorou 2022, Moreno-García et al. 2025). Such environmental changes impose novel selective pressures on wildlife (Moreno-García et al. 2025). While many species fail to adapt and disappear from disturbed areas (McDonnell and Hahs 2015, Piano et al. 2020), others persist due to their broad physiological tolerance (Bonier et al. 2007) or behavioural flexibility (Lowry et al. 2013, Ritzel and Gallo 2020). Flexibility in activity patterns, foraging strategies, movement behaviours, and social interactions may even enable some species to thrive in urban environments (Lowry et al. 2013, Jung and Threlfall 2018, Ritzel and Gallo 2020, Hahs et al. 2023). Understanding how urban-tolerant species respond to urban pressures is critical for predicting the ecological consequences of ongoing urbanisation—not only for common species, but also for those already in decline.

One of the most prominent environmental consequences of urbanisation is habitat fragmentation and habitat loss (Theodorou 2022, Moreno-García et al. 2025, Sgarlata et al. 2025). Habitat fragmentation and loss lead to resource decline, which in turn alter animal social interactions by reducing habitat availability and subsequently affecting population size (Luck and Smallbone 2010, Theodorou 2022, Moreno-García et al. 2025). As a result, animals may change how they interact with conspecifics and heterospecifics. For example, common pipistrelles *Pipistrellus pipistrellus* in urban areas show more aggressive interactions for food resources (Starik and Göttert 2022). In contrast, striped field mice *Apodemus agrarius* in urban areas display increased social tolerance to minimise the physiological costs of higher population densities, such as fighting (Łopucki et al. 2021).

A key feature of urban landscapes is anthropogenic noise, generated by transportation, construction, industry, public activities, and residential activities (Leaffer et al. 2025). Urban noise can mask animal acoustic signals (Fisher et al. 2021) and reduce sound transmission distance (Grabarczyk and Gill 2020). Because acoustic communication plays a central role in many species in coordinating social interactions, many species adapt their vocal strategies in response to noise (Patricelli and Blickley 2006). Certain bird species reduce their singing rate in urban habitats (Gross et al. 2010, Önsal et al. 2022), shift to higher frequencies (Nemeth and Brumm 2009, Gross et al. 2010, Narango and Rodewald 2016) or increase amplitude (Halfwerk et al. 2018) to avoid noise masking and signal jamming. Beyond altering animal acoustic signals themselves, urban noise can change behavioural responses, as seen in reduced mobbing behaviour (Ewing et al. 2025). However, relatively few studies have investigated how vocal communicators who use acoustic and ultrasonic signals, such as echolocating bats, adjust vocal communication to respond to urbanisation.

Bats (Chiroptera) are a highly diverse mammalian order, with over 1,500 species (Simmons and Cirranello 2025). Their ecological niches are shaped by species-specific traits such as echolocation call structure and wing morphology, and interactions with habitat features (Denzinger and Schnitzler 2013, Denzinger et al. 2018). Approximately 70% of bat species primarily rely on vocalisations, using echolocation for navigation and social calls for communication (Fenton 2003, Kanwal 2021). Bats' ability to fly, combined with their varied ecological traits, makes them particularly useful for studying how urbanisation affects wildlife (Russo et al. 2012, Denzinger and Schnitzler 2013, Russo and Ancillotto 2015, Russo and Jones 2015). Whilst species-specific responses exist, increased canopy cover generally enhances bat diversity and activity by providing a greater diversity of food and roosting resources, such as tree hollows, cavities or crevices (Russo and Ancillotto 2015, Russo and Jones 2015), whereas impervious surfaces, including buildings and concrete infrastructures as well as artificial light at night, often have negative impacts (e.g., Threlfall et al. 2011, Dixon 2012, Luck et al. 2013, Silva de Araújo and Bernard 2016, Straka et al. 2016, Haddock et al. 2019a, Wolf et al. 2022, Callas et al. 2024, Parsons et al. 2025). These contrasting effects highlight the importance of urban habitat composition in shaping bat communities and underscore the need for targeted urban planning to support bat diversity and ecological function.

Despite a growing body of research linking bat diversity and activity to habitat attributes, relatively little is known about how social interactions can change in response to urbanisation. Social vocalisations in bats facilitate foraging group cohesion, roost interactions, territorial defence, and mate attraction (Pfalzer and Kusch 2003, Chaverri et al. 2018). As seen in birds, bats in urban environments may adjust their calls, shifting to higher frequencies or shorter durations, to likely avoid noise masking and signal jamming (Starik and Göttert 2022). In addition, bats change the compositions of their vocal vocalisations in response to urbanisation. For example, common pipistrelles *Pipistrellus pipistrellus* in Berlin produce relatively more agonistic calls and advertisement calls in urban areas compared to rural areas, potentially resulting from resource competition and territorial defence, while other sympatric species, serotine bats *Eptesicus serotinus* and common noctules *Nyctalus noctula*, do not show similar increase in agonistic calls in urban areas (Starik and Göttert 2022). Thus, these findings suggests that bat responses to urbanisation are species-and context-dependent.

To broaden understanding of how bat vocal repertoires respond to urbanisation, this study focuses on the Gould's wattled bat, *Chalinolobus gouldii*, in the Greater Sydney region of Australia. Sydney currently supports 4.9 million residents (2024), with projections exceeding 6.3 million by 2041 (NSW Population Projections 2024), with annual urban expansion rates of approximately 1.5% (Atlas of Urban Expansion 2025). *Chalinolobus gouldii* is one of the most common urban-dwelling bats in Australia, capable of inhabiting diverse habitats (Scanlon and Petit 2008, Threlfall et al. 2011, Threlfall et al. 2012b, Godinho et al. 2019). In addition to its echolocation call (the characteristic frequency of call sequences ranged from 26.8 kHz to 31.9 kHz, alternating pulses; Reinhold et al. 2001, Adams et al. 2010), this species produces at least five distinct social vocalisations in roosts and foraging contexts (Chapter 2). However, little is known about how its social vocalisation changes with habitat variables across urban-rural landscapes.

The aims of this study were (1) to examine the association between *C. gouldii* social vocalisation occurrence and echolocation activity per night; (2) to investigate the influence of habitat attributes on the rates of overall and syllable-specific social vocalisations ; and (3) to test whether *C. gouldii* adjusts its vocalisation frequencies and duration in both echolocation calls and social vocalisations across the urban-rural landscape. I investigated the association between echolocation activity and the number of social vocalisations. I hypothesised that bats would produce social vocalisations at different rates to potentially reflect differences in resource availability, such as prey and roosts, in urban versus rural areas. Alternatively, the social vocalisation rates did not change, instead the number of social vocalisations produced might reflect conspecific activity rather than habitat attributes. I further hypothesised that *C. gouldii* would adjust their social vocalisations to mitigate masking from increased impervious surfaces or increased noise in urban areas.

Materials and Methods

Study area and sites

This study was conducted within the Greater Sydney region, New South Wales, Australia. Sites in this study were located across Greater Sydney (Figure 4.1). This region is characterised by a temperate climate, sandstone-derived soils, and a heterogeneous landscape of urban development interspersed with remnant dry sclerophyll forests, riparian corridors, and parklands (Tozer 2003), providing a range of roosting and foraging habitats for echolocating bats.

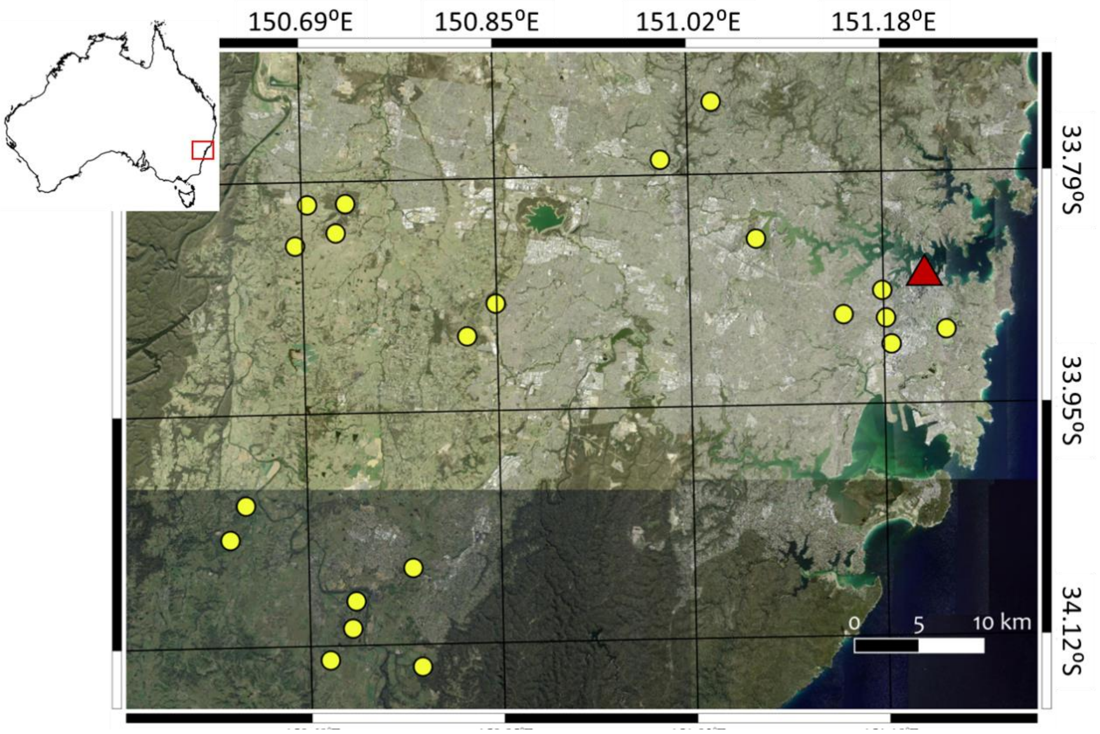


Figure 4.1. Map of the recording sites**.** Recording locations are shown as yellow circles, with the red triangle indicating Sydney CBD.

Sampling sites were selected from a large pool of monitoring sites, totalling 56 sites, established for bat acoustic monitoring in 2023 (Amjah 2023, Sharpley 2023). From these, 21 sites were selected that were at least 2 km apart, and that spanned the urban – rural gradient present, to maximise independence among sampling sites (Figure 4.1).

Habitat attributes

Habitat attributes were quantified within a 1-km radius buffer centred on each recorder using QGIS (Version 3.32.1; QGIS.org 2025). I chose a 1-km radius buffer because it captures the foraging ranges of multiple bat species and covers the habitat attributes that may affect bat activity (Dixon 2012, Gallo et al. 2018, Comparato 2023). *Chalinolobus gouldii* is considered an edge-space forager (Fullard et al. 1991) and is capable of foraging not only in the edge of vegetated habitats but also in urban areas (Threlfall et al. 2012b, Haddock et al. 2019a, Milne et al. 2023), allowing it to exploit a range of habitats. Given the high habitat flexibility of *C. gouldii*, three variables were assessed to simplify habitat attributes: tree canopy cover (km^2, hereafter called canopy cover), where trees and vegetation are defined as occurring > 3 m in height (Sweeney et al. 2021); the area (km^2) of open water; and human dwelling density (as documented in the Census of Population and Housing, detailed below). All measurements were made in QGIS. All GIS layers used were the latest available versions.

Canopy cover was derived from the Native Vegetation of the Sydney Metropolitan Area dataset (Office of Environment and Heritage Sydney 2016), extracting polygons classified as vegetation > 3 m in height (*'Canopy'*). This layer was successfully used in previous studies (e.g., Haddock et al. 2019a). The area of the buffer that contained canopy was then calculated in hectares (ha) and was converted to km^2 for further analyses.

Waterbodies were extracted from the Geoscience Surface Hydrology dataset (1:250,000 scale), including natural and man-made features such as water courses. A plugin function from AusMap was used in QGIS to select the 'Watercourse Area' layer within the 'Natural Environment – water' dataset, including categories of major perennial, major non-perennial, minor perennial, and minor non-perennial watercourses. Additional waterbodies that were omitted in these data were digitised manually using the 'NSW Imagery' layer (1:150,000, a limited accuracy of at best 2 metres). The area of the buffer that contained water was then calculated in km^2.

Human dwellings were calculated using the Mesh Block layer (MB_2021_AUST_GDA2020) from the Australian Statistical Geography Standard (ASGS) digital boundaries (Edition 3) and a joint layer of the Census of Population and Housing (Mesh block counts, 2021) from Australian Bureau of Statistics to assess the number of dwellings (km^2, '*mesh_block_NSW_Dwelling*' in the attributes) in each block. This layer included all land-use categories.

For each buffer, I calculated the intersected area of the meshblock within the 1-km radius buffer zones. The amount (area of canopy (ha) or dwellings/ha) of canopy and dwellings per meshblock were then summed across the buffer area, to represent the amount of the urban footprint with dwellings or with tree canopy.

Sites were classified as urban or rural following one of the criteria in 'urban Statistical Areas Level 1 (SA1)' from Australian Bureau of Statistics: The SA1 has a population density ≥ 100 persons/km^2 and a dwelling density ≥ 50 dwellings/km^2 (Australian Bureau of Statistics 2022). Considering the local context in this study, one of the sites was within a vegetated area between two suburbs with a dwelling density of 90.64, which might overestimate the effect of urbanisation. Therefore, sites with < 90.64 dwelling density were categorised as rural. Based on the criteria above, 10 sites were classified as urban and 11 as rural.

Bat acoustic monitoring

I deployed ultrasonic recorders (Anabat Swift and Chorus; Titley Electronics, Australia) between March and May 2023 (autumn). Each site was monitored for at least four consecutive nights from 30 minutes before sunset to 30 minutes after sunrise. At least four-recording nights were used as this was sufficient to reduce within-site variability (Fischer et al. 2009). Microphones were mounted 1.5 meter above the ground at a 45^o angle, positioned in open spaces, vegetation gaps, or at vegetation edges depending on local habitat structure.

Recordings were collected in full-spectrum format at a sampling rate of 256 kHz, using omnidirectional ultrasonic microphones (Omni-directional Ultrasonic Microphone: US-O V3 or Low-Profile Ultrasonic Microphone, Titley Electronics, Australia). The high-pass filter was disabled, and sensitivity was set to 16. File lengths ranged from a minimum of two seconds to a maximum of 15 seconds. When the maximum length was reached, files were re-triggered automatically. Data collection was approved by Animal Research Authority (2023/2386) of The University of Sydney.

Social vocalisations, echolocation calls, and activity

All recordings were manually screened using Kaleidoscope Lite (Version 5.6.3, Wildlife Acoustics, USA). Files containing *C. gouldii* social vocalisations were extracted (Chapter 2). Each social vocalisation was manually selected to obtain call measurements in Raven Pro 1.6

(Version 1.6.5, Cornell Lab of Ornithology, US). Analyses were conducted in full spectrum with Hann function, window size 1024 samples, 75% overlap, 256 hop size, and 1024 discrete Fourier transform size. Ten measurements were used including peak frequency, centre frequency, bandwidth, minimal frequency, aggregate entropy, duration, the proportion of time reached peak and centre frequency, slope, and peak frequency contour slope. To avoid species misidentification, only social vocalisations surrounded by the *C. gouldii* echolocation calls were analysed. I used a linear model with ten call measurements as predictors to obtain syllable types developed in previous work (Chapter 2).

To analyse the vocalisation adjustment in rural versus urban areas, including social vocalisations and echolocation calls, I also sub-sampled 20 *C. gouldii* echolocation calls at each site. Specifically, four pulses were selected from search-phases of each sequence due to the characteristic alternating call shapes in *C. gouldii* echolocation call sequences (Reinhold et al. 2001), with five sequences analysed per site. I further examined the results of four common call measurements only, including duration, peak frequency, minimum frequency, and bandwidth of the three syllables (Syllable 1, 2, and 3) and echolocation calls separately, in response to urbanisation.

For each site, I quantified (1) the average number of each syllable type per hour and (2) the average number of total social vocalisations per hour. (3) Bat vocal activity was measured as the number of 15-second files containing *C. gouldii* echolocation or social vocalisations per night. AnaScheme (Version 1.0, Titley Electronics, Australia) were used to obtain species identification (Adams et al. 2010), with additional manual inspection of echolocation calls. (4) The social vocalisation rate was calculated as the average number of social vocalisations per hour divided by the average bat vocal activity per hour.

Statistical analysis

I used Linear Regression Models implemented in the glmmTMB package (Bolker 2019). I assessed (1) the association between presence or absence of *C. gouldii* social vocalisation and echolocation activity per night using a binomial distribution. Next, I assessed the effects of habitat attributes on (2) vocal activity per hour using a Gaussian distribution and (3) the rates of total social vocalisations and three common syllable types using Tweedie distributions. Habitat attributes were analysed with canopy cover, waterbody area (square-root log-transformed), and urban category (urban versus rural) as fixed variables. No correlation occurred between canopy cover and transformed-waterbody area (Spearman's rank correlation: rho= -0.205, *p* = 0.372). I examined the combination of the three fixed variables including interactions between variables. Model selection was based on lowest Akaike's information criterion (AIC) with delta AICc >2 (Burnham and Anderson 2002) (supplementary information Table S4.1-S4.6). Waterbody area was excluded from all four social vocalisation rate models, as it contributed little to explaining variance in AICc.

To examine whether *C. gouldii* adjusted its vocalisations in response to urbanisation based on call measurements, I analysed the ten measurements mentioned above of Syllable 1, 2, and echolocation calls, separately. A non-parametric multivariate analysis of variance test test (np-MANOVA) based on ranked data and Euclidean distance with 999 permutations was applied. Where np-MANOVAs revealed significant effects, Wilcoxon rank-sum tests were applied to urban-rural comparisons for each call measurement, and *p*-values were adjusted for multiple testing across call measurements using the Holm’s method. I analysed only the vocalisations recorded by Anabat Swift to avoid variation between devices.

All statistical analyses were conducted in R (Version 4.5.1; R core team, Austria) within the RStudio environment (Version 2025.05.1; Posit Team, US).

Results

I collected 852 *C. gouldii* social vocalisations from 21 sites, including 516 Syllable 1, 236 Syllable 2, 55 Syllable 3, 27 Syllable 4, and 18 Syllable 5. These five syllables were produced by *C. gouldii* during foraging.

The probability of total social vocalisation was positively correlated with nightly echolocation activity in *C. gouldii* (GLM: estimate = 0.043, standard error = 0.011, $z = 3.902$, $p < 0.001$, Figure 4.2).

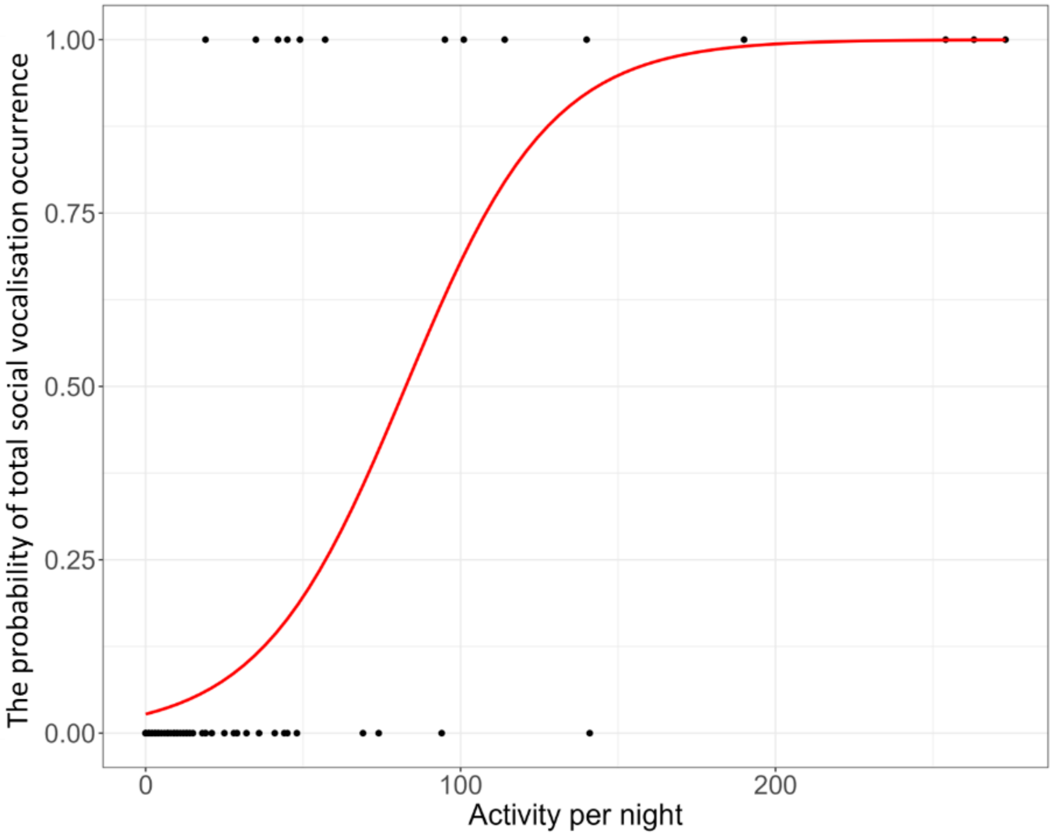


Figure 4.2. Logistic regression analysis of *Chalinolobus gouldii* total social vocalisation occurrence (presence of a social call within any recorded file per night) positively associated with *C. gouldii* activity per night (sum of all 15-sec files containing *C. gouldii* echolocation calls per night) across the Sydney study area.

Areas classified as urban had a negative effect on *C. gouldii* vocal activity, while the size of canopy cover and waterbodies had a positive effect on their activity (Table 4.1).

Table 4.1. Results of GLM with habitat attributes as fixed effects on the average *Chalinolobus gouldii* vocal activity per hour as the response variable.

Parameter	Estimate	Standard error	*z*-value	*p*-value
Intercept	-0.129	0.213	-0.604	0.032
Urbanisation: urban vs. rural	-0.480	0.142	-3.374	**<0.001**
Waterbody area (transformed)	2.569	1.079	2.380	**0.017**
Canopy cover	1.298	0.249	5.212	**<0.001**

The nightly probability of occurrence of *C. gouldii* social vocalisations was positively associated with canopy cover, negatively associated with urbanisation, and unaffected by waterbody area (Table 4.2). The rate of total social vocalisation (defined as the number of social vocalisations divided by echolocation activity, measured as the number of 15-second files per night) was influenced by an interaction between urban category and canopy cover (Table 4.3). Specifically, greater canopy cover had higher social vocalisation rates in urban areas but not in rural areas (Figure 4.3).

Table 4.2. Results of GLM with habitat attributes as fixed effects and the nightly probability of occurrence (0/1) of *Chalinolobus gouldii* social vocalisation as the response variable.

Parameter	Estimate	Standard error	*z*-value	*p*-value
Intercept	-5.234	1.355	-3.864	<0.001
Urbanisation: urban vs. rural	-3.031	1.155	-2.625	**0.008**
Waterbody area (transformed)	8.292	5.520	1.502	0.133
Canopy cover	4.574	1.421	3.219	**0.001**

Rates of the three social vocalisation types (Syllables 1, 2, and 3) were also examined separately. All three were positively associated with increasing canopy cover. Urbanisation did not affect the rates of Syllable 1 and 3. The interaction between urban category and canopy cover was significant only for Syllable 2 (Table 4.3), with increasing canopy cover in urban areas, but not in rural areas, associated with higher Syllable 2 rates (Figure 4.4).

Table 4.3. Results of GLM with habitat attributes as fixed variables and response variables listed on the top of each model.

Parameter	Estimate	Standard error	*z*-value	*p*-value
Total social vocalisation rate (number of social vocalisations/activity)				
Intercept	-6.529	1.879	-3.474	<0.001
Urbanisation: urban vs. rural	-15.713	5.906	-2.661	**0.008**
Canopy cover	4.770	2.044	2.334	**0.020**
Urbanisation x Canopy cover	10.685	4.613	2.316	**0.021**
Syllable 1 rate (number of Syllable 1/activity)				
Intercept	-6.564	1.838	-3.571	<0.001
Urbanisation: urban vs. rural	-129.509	67417.869	-0.002	0.998
Canopy cover	4.159	1.964	2.117	**0.034**
Urbanisation x Canopy cover	89.925	46912.537	0.002	0.998
Syllable 2 rate (number of Syllable 2/activity)				
Intercept	-7.440	2.089	-3.561	<0.001
Urbanisation: urban vs. rural	-13.358	6.135	-2.177	0.029
Canopy cover	4.448	2.226	1.998	**0.046**
Urbanisation x Canopy cover	9.508	4.746	2.004	**0.045**
Syllable 3 rate (number of Syllable 3/activity)				
Intercept	-8.393	1.967	-4.266	<0.001
Urbanisation: urban vs. rural	-94.195	121525.267	-0.001	0.999
Canopy cover	3.987	1.982	2.012	**0.044**
Urbanisation x Canopy cover	64.993	84563.017	0.001	0.999

Note: Waterbody area was excluded from all four social vocalisation rate models, as it contributed little to explaining variance (see supplementary information, Table S4.3-S4.6).

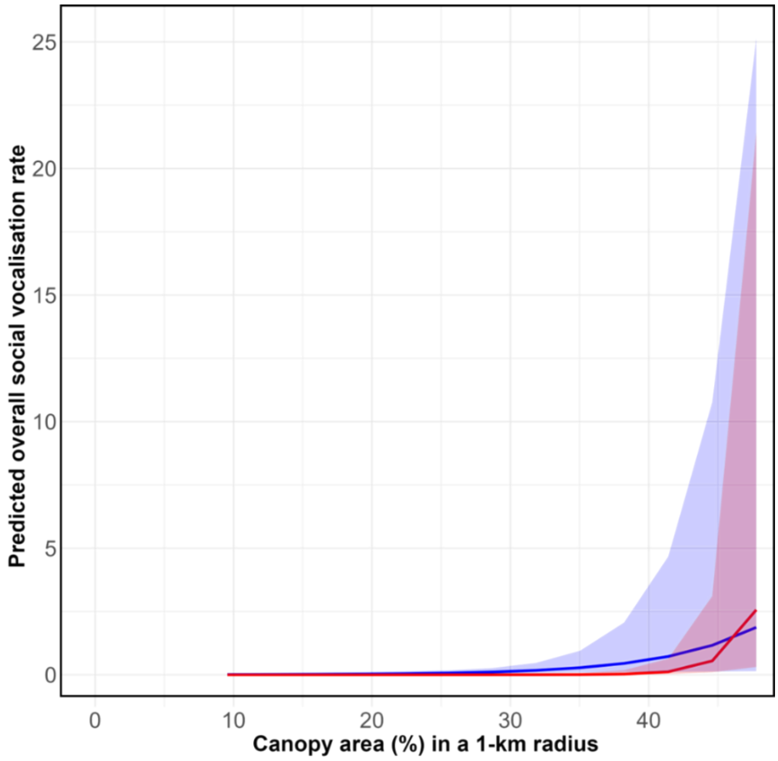


Figure 4.3. The interaction between canopy cover and urbanisation on *Chalinolobus gouldii* overall social vocalisation rate. Red line: urban areas; blue line: rural areas. Shaded polygons represent 95% confidence intervals.

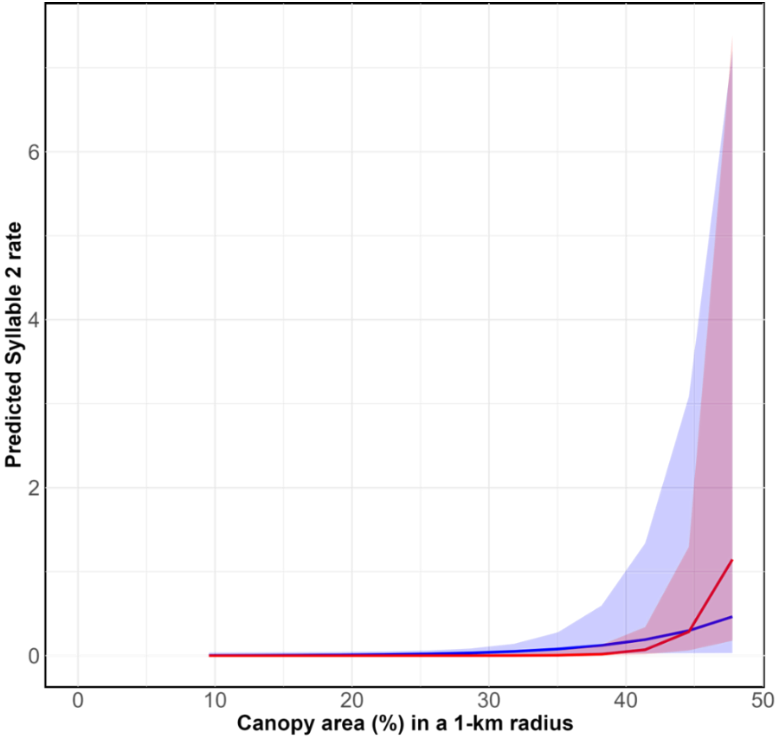


Figure 4.4. The interaction between canopy cover and urbanisation on *Chalinolobus gouldii* Syllable 2 rate. Red line: urban areas; blue line: rural areas. Shaded polygons represent 95% confidence intervals.

The structure of *C. gouldii* social vocalisations varied in response to urban category (urban vs. rural) for all three syllable types (MANOVA: Syllable 1, pseudo-$F = 10.117$, $R^2 = 0.020$, $p = 0.001$; Syllable 2, pseudo-$F = 13.733$, $R^2 = 0.057$, $p = 0.001$; Syllable 3, pseudo-$F = 24.468$, $R^2 = 0.029$, $p = 0.001$). Echolocation call structure also differed between urban and rural areas (MANOVA: pseudo-$F = 9.676$, $R^2 = 0.076$, $p = 0.001$). Across all three social vocalisation syllables, minimum and peak frequencies were higher, and call durations were shorter in urban areas than in rural areas (Table 4.4), with only Syllable 2 exhibiting a narrower bandwidth in urban areas. In contrast, echolocation calls in urban areas had lower minimum frequencies, broader bandwidths, and longer durations than those in rural areas, while peak frequency did not differ (Table 4.4; also see supplementary information Figure S1-S4).

Table 4.4. Median and interquartile range showing in the brackets for the three common social vocalisations and echolocation calls of *Chalinolobus gouldii* in rural and urban areas with adjusted *p*-value (Willcoxon signed-rank test).

	Syllable 1			Syllable 2			Syllable 3			Echolocation calls		
	Rural	Urban	Adjusted *p*-value	Rural	Urban	Adjusted *p*-value	Rural	Urban	Adjusted *p*-value	Rural	Urban	Adjusted *p*-value
Minimum frequency (kHz)	16.25 (2.19)	**17.81 (3.67)**	**0.006**	17.50 (3.13)	**19.69 (3.13)**	**<0.001**	16.56 (2.50)	**18.75 (4.22)**	**<0.001**	**30.00 (1.56)**	28.88 (1.88)	**<0.001**
Peak frequency (kHz)	17.50 (2.81)	**19.69 (2.03)**	**<0.001**	19.69 (4.69)	**20.94 (3.67)**	**0.002**	18.13 (3.75)	**20.31 (3.15)**	**<0.001**	31.25 (1.64)	30.63 (2.5)	0.107
Bandwidth (kHz)	3.44 (2.81)	3.75 (3.20)	0.112	**5.93 (3.44)**	4.69 (1.56)	**0.002**	4.38 (3.44)	4.53 (2.50)	0.690	3.13 (1.33)	**4.38 (3.28)**	**0.030**
Duration (ms)	**37.8 (22.93)**	33.2 (25.33)	**0.014**	**16.6 (10.5)**	12.2 (3.7)	**0.001**	**26.6 (27.6)**	13.9 (16.18)	**<0.001**	7.90 (2.22)	**9.1 (2.73)**	**<0.001**

Note: Significant values are shown in bold.

Discussion

Urbanisation was associated with changes in *C. gouldii* social vocalisations, including increasing social vocalisation rates and shifting toward higher frequencies and shorter durations. I found that the presence of social vocalisations was positively correlated with *C. gouldii* activity. The size of canopy cover positively affected bat social vocalisation rates depending on urban category. The rates of total (corrected for activity) and Syllable 2 social vocalisations increased as the canopy cover increased in urban areas but not in rural areas, which support the hypothesis that bats produce social vocalisation at different rates in different environments. Greater canopy cover in urban areas potentially facilitate transmission of information about prey or roost locations. In rural areas, the social vocalisation rates may not have been affected by the extent of canopy cover. Bats produced more social vocalisations when vocal activity was higher, possibly reflecting passive information exchange among individuals. This finding potentially supports the idea that denser populations provide greater opportunities for encounters (Gurarie and Ovaskainen 2013), in addition to greater opportunities for communication that could improve foraging efficiency or information transfer. Furthermore, the three social vocalisations in *C. gouldii* shifted toward higher peak and minimum frequencies and shorter durations in urban areas compared with rural areas, suggesting the potential effects of anthropogenic noise or obstacles on their social vocalisation production, while the main mechanism still need to be investigated.

Canopy cover as a key habitat feature

Consistent with previous studies, canopy cover emerged as the strongest predictor of any bat species activity (e.g., Luck et al. 2013, Ancillotto et al. 2016, Silva de Araújo and Bernard 2016, Callas et al. 2024); however, the effect of canopy cover on social vocalisation rates in previous studies varied depending on species-specific responses (Silva de Araújo and Bernard 2016, Starik and Göttert 2022). Canopy cover provides multiple benefits including increased foraging and roosting resources for species such as *C. gouldii* (Hanspach et al. 2012, Threlfall et al. 2012a). *Chalinolobus gouldii* can also forage within the interior of vegetation patches where prey abundance is higher (Haddock et al. 2019), potentially enhancing social interactions due to high activity.

Hollows and crevices associated with mature trees serve as indicators of roost resources for tree roosting bat species (Lunden et al. 2022, Parsons et al. 2025). In bats, roost-based societies with non-random associations are often characterised by the production of social vocalisations that facilitate group cohesion and recruitment (e.g., Chaverri et al. 2010). Many bat species use social vocalisations to attract conspecifics to roosting locations, particularly in species that switch roosts frequently or form stable groups (Chaverri and Gillam 2010, Schöner et al. 2010, Furmankiewicz et al. 2011). It has not been assessed whether *C. gouldii* uses social vocalisations for roost advertisement, but this species lives in groups with familial associations (Godinho et al. 2015, Eastick 2022) and exhibits higher activity around roosts (Velasco et al. 2023), suggesting a potential role of social vocalisations in roost advertisement. Thus, greater canopy cover may facilitate more frequent social interactions and activity in urban areas.

Negative effects of urbanisation

Urbanisation had a negative effect on *C. gouldii* echolocation activity and social vocalisation rates despite *C. gouldii* being considered an urban-tolerant species (Scanlon and Petit 2008, Threlfall et al. 2011). This contrasts with findings for *Pipistrellus pipistrellus*, which often produces more agonistic or advertisement calls in urban areas due to competition for limited resources (Starik and Göttert 2022). In my study, social vocalisation rate increased faster in urban areas with greater canopy cover, particularly when canopy cover exceeded 40% within the 1-km radius buffer (Figure 4.3). This finding suggests that sufficient tree cover can mitigate the effect of urbanisation on bat activity (Dixon 2012), which may in turn facilitate social interaction among bats.

In rural areas with patchy prey distributions, some bat species have been shown to increase their use of group foraging to increase successful prey capture (Chaverri et al. 2018, Egert-Berg et al. 2018). At fine scales, prey availability can be unpredictable, even in areas with high canopy cover (Kohles et al. 2022). Thus, it is possible that bats employ a strategy of group facilitation to increase foraging efficiency by using contact calls for coordinating social foraging behaviours (Wilkinson and Boughman 1998, Egert-Berg et al. 2018). Conversely, in areas with more predictable prey distributions, bats have been recorded to forage alone (Egert-Berg et al. 2018) with more agonistic calls, such as *P. pipistrellus* in urban areas (Starik and Göttert 2022). In my study, the probability of *C. gouldii* social vocalisation depended on conspecific vocal activity. In urban areas, where conspecific activity was low, *C. gouldii* likely foraged more solitarily, commuting to higher-quality habitats such as parklands or green spaces where prey is predictable (Silva de Araújo and Bernard 2016). In contrast, higher activity with the high probability of social vocalisations in rural areas likely reflected unpredictable prey distributions, with social vocalisation facilitating connections among individuals and forming foraging networks (Wilkinson and Boughman 1998; Egert-Berg et al.

2018).

Limited role of waterbodies on C. gouldii social vocalisation rates

Increasing access to water (measured as waterbody area in this study) showed a positive effect on *C. gouldii* echolocation activity. The effect of waterbodies on increasing social vocalisation rates was weak, in comparison to the stronger effect of urbanisation and canopy cover on social vocalisation rates. Fresh water is an essential resource for drinking and foraging for bats and plays an important role in the life cycle of many insects (Fukui et al. 2006, Lintott et al. 2015, Blakey et al. 2018). *Chalinolobus gouldii* is primarily an edge-space forager (McKenzie and Rolfe 1986, Fullard et al. 1991) and may exploit a variety of open and gap habitats, including riparian zones for feeding (Lloyd et al. 2006). Therefore, I expected water to influence social vocalisation rates given high activity near water. One possible explanation for the null effect on social vocalisation rates is that water surfaces could increase echo or create a noisy background, negatively influencing the transfer of information through social vocalisations (Rydell et al. 1999, Russo et al. 2012). Alternatively, the waterbodies in a 1-km radius may not be used by *C. gouldii*, which may be relevant to water quality that I did not measure (Lloyd et al. 2006), or *C. gouldii* may interact near the waterbodies where I did not record. Consequently, waterbodies can enhance foraging (and/or drinking) activity for bats, including *C gouldii*, but the influences on *C. gouldii* social vocalisations need to be further investigated.

Adjustments in call structure

I found that *C. gouldii* social vocalisations but not echolocation calls shifted toward higher frequencies and shorter durations in urban areas. This pattern is consistent with acoustic adaptation to avoid masking by low-frequency urban noise and would help to maintain communication efficiency (Nemeth and Brumm 2009, Starik and Göttert 2022). A similar pattern indicates that bats exposed to chorusing insect background noise shift their calls to higher frequencies compared with bats in silent environments (Gillam and McCracken 2007). However, changes in call structure may result from other factors. For example, increased encounters with artificial obstacles (e.g., buildings and urban infrastructure) may lead bats to adjust calls to achieve finer spatial resolution (Starik and Göttert 2022). Additionally, smooth surfaces such as windows or walls in urban areas may reflect vocalisations, potentially impacting call measurements (Ratcliffe and Jakobsen 2018). Weather conditions can introduce non-linear variation in analysed call measurements, particularly in high-frequency components (Chaverri and Quirós 2017, Goerlitz 2018). These factors were not accounted for in this study. The mechanism leading to shifts in social vocalisation structure is likely context-specific and requires further investigation.

The importance of social vocalisations

These findings highlight the importance of natural habitat elements for bat communities within urban landscapes. Even in heavily urbanised areas, the results of this study reveal that increased canopy cover reduced negative effects of urbanisation on social interactions. This suggests that urban green spaces, particularly with mature trees, could support not only foraging and roosting but also social interactions in bat populations. Understanding how social vocalisations vary with habitat attributes provides insight into how bats persist in modified landscapes. As *C. gouldii* is one of the most widespread and adaptable Australian bats, its responses may offer general insights into managing bat populations against the backdrop of urban expansion. However, further work is needed to clarify the specific functions of distinct social vocalisations, their responses to urban noise, and their role in the transmission of social information, such as the location of resources.

Acknowledgements

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Supplementary information

Table S4.1. Summary of Akaike's Information Criterion models for the binary response of social vocalisations

Treatment	AIC	ΔAIC
Model 1: canopy cover	75.70	7.96
Model 2: waterbody	84.69	16.95
Model 3: urbanisation or not	77.98	10.24
Model 4: urbanisation + waterbody + urbanisation x waterbody	77.47	9.73
Model 5: urbanisation + canopy cover + urbanisation x canopy cover	69.74	2
Model 6: urbanisation + canopy cover + waterbody	67.74	0

Table S4.2. Summary of Akaike's Information Criterion models for echolocation activity

Treatment	AIC	ΔAIC
Model 1: canopy cover	237.50	3.6
Model 2: waterbody	248.69	14.79
Model 3: urbanisation or not	247.38	13.48
Model 4: urbanisation + waterbody + urbanisation x waterbody	246.63	12.73
Model 5: urbanisation + canopy cover + urbanisation x canopy cover	237.51	3.61
Model 6: urbanisation + canopy cover + waterbody	233.90	0

Table S4.3. Summary of Akaike's Information Criterion models for overall social vocalisation rate

Treatment	AIC	ΔAIC
Model 1: canopy cover	88.78	6.66
Model 2: waterbody	98.08	15.96
Model 3: urbanisation or not	100.05	17.93
Model 4: urbanisation + waterbody + urbanisation x waterbody	101.75	19.63
Model 5: urbanisation + canopy cover + urbanisation x canopy cover	82.12	0
Model 6: urbanisation + canopy cover + waterbody	87.11	4.99

Table S4.4. Summary of Akaike's Information Criterion models for Syllable 1 rate

Treatment	AIC	ΔAIC
Model 1: canopy cover	71.93	5.52
Model 2: waterbody	79.43	13.02
Model 3: urbanisation or not	81.92	15.51
Model 4: urbanisation + waterbody + urbanisation x waterbody	81.18	14.77
Model 5: urbanisation + canopy cover + urbanisation x canopy cover	66.41	0
Model 6: urbanisation + canopy cover + waterbody	71.04	4.63

Table S4.5. Summary of Akaike's Information Criterion models for Syllable 2 rate

Treatment	AIC	ΔAIC
Model 1: canopy cover	61.23	3.03
Model 2: waterbody	72.76	14.56
Model 3: urbanisation or not	74.05	15.85
Model 4: urbanisation + waterbody + urbanisation x waterbody	76.06	17.86
Model 5: urbanisation + canopy cover + urbanisation x canopy cover	58.20	0
Model 6: urbanisation + canopy cover + waterbody	62.35	4.15

Table S4.6. Summary of Akaike's Information Criterion models for Syllable 3 rate

Treatment	AIC	ΔAIC
Model 1: canopy cover	28.45	2.5
Model 2: waterbody	34.77	8.82
Model 3: urbanisation or not	35.59	9.64
Model 4: urbanisation + waterbody + urbanisation x waterbody	36.57	10.62
Model 5: urbanisation + canopy cover + urbanisation x canopy cover	25.95	0
Model 6: urbanisation + canopy cover + waterbody	28.26	2.31

Table S4.7. Results of the Generalised Linear Mixed Model examining vocalisation features of *Chalinolobus gouldii* echolocation calls. All vocalisation features and the urbanisation gradient were log-transformed prior to analysis. The urbanisation gradient was included as a fixed effect, and site was modelled as a random effect. All models assumed a Gaussian error distribution with an identity link function. There was no clear change in echolocation calls across habitats.

Vocalisation feature	Estimate	Std. error	*z*-value	*p*-value
(Intercept)	8.132	0.100	81.11	<0.001
Bandwidth	0.023	0.022	1.08	0.281
(Intercept)	10.290	0.010	949.6	<0.001
Minimum frequency	-0.001	0.002	-0.5	0.637
(Intercept)	<0.001	0.006	1521.6	<0.001
Peak Frequency	<0.001	<0.001	0.1	0.906
(Intercept)	-4.987	0.068	-73.43	<0.001
Duration	0.020	0.015	1.33	0.182

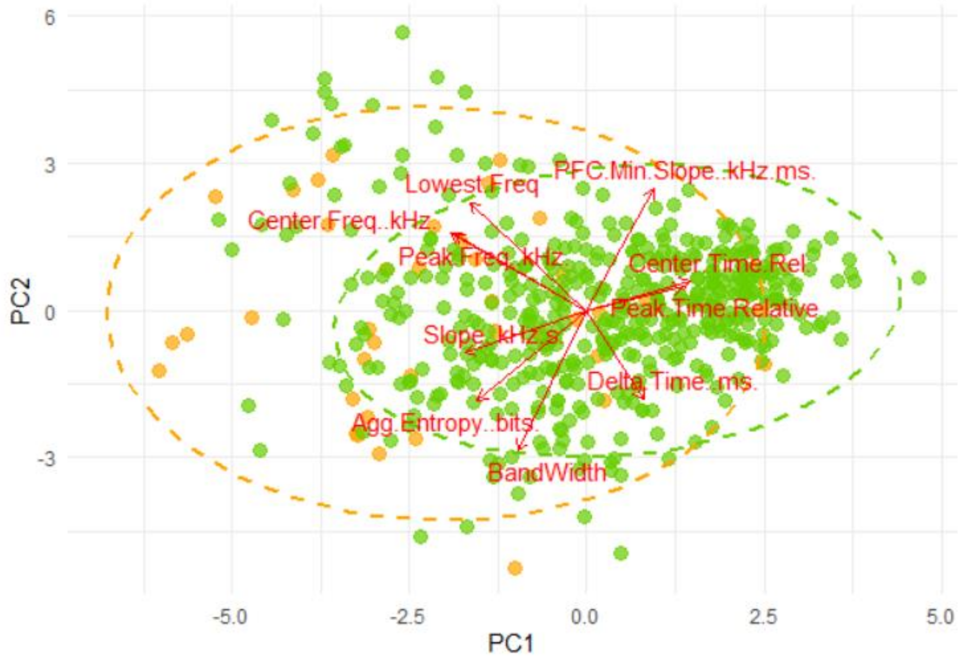

Figure S4.1. PCA biplot of Syllable 1 with 95% CI Ellipses. Green dot: rural area; orange dot: urban area.

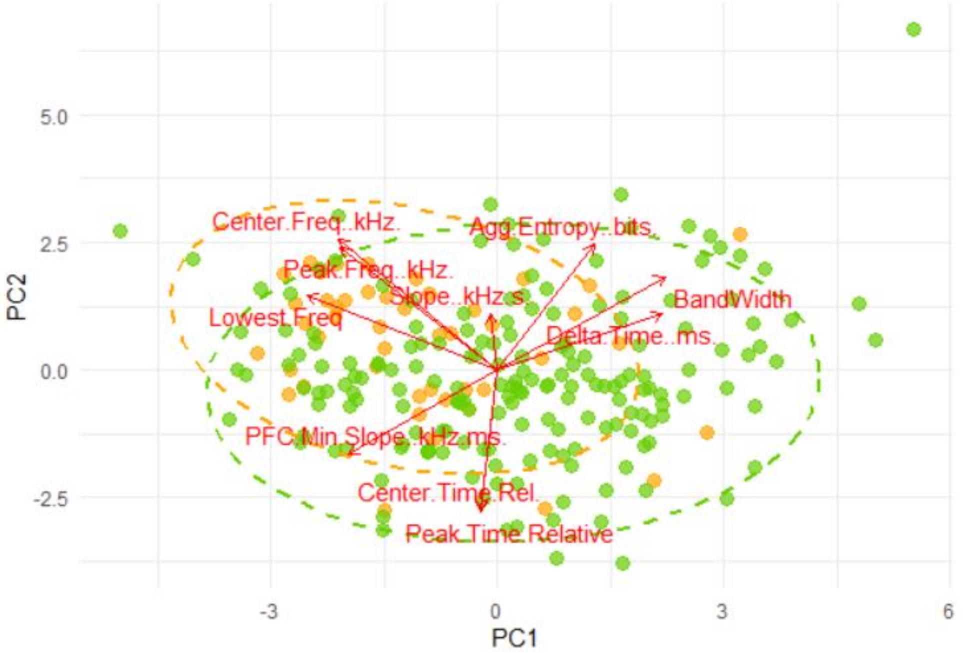

Figure S4.2. PCA Biplot of Syllable 2 with 95% CI Ellipses. Green dot: rural area; orange dot: urban area.

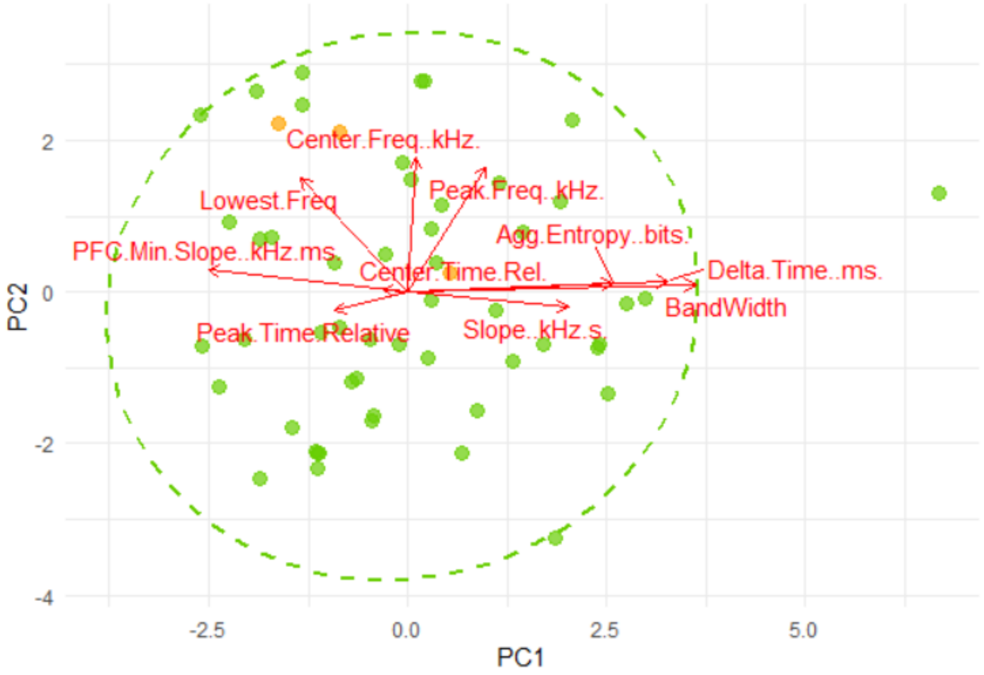

Figure S4.3. PCA Biplot of Syllable 3 with 95% CI Ellipses. Green dot: rural area; orange dot: urban area.

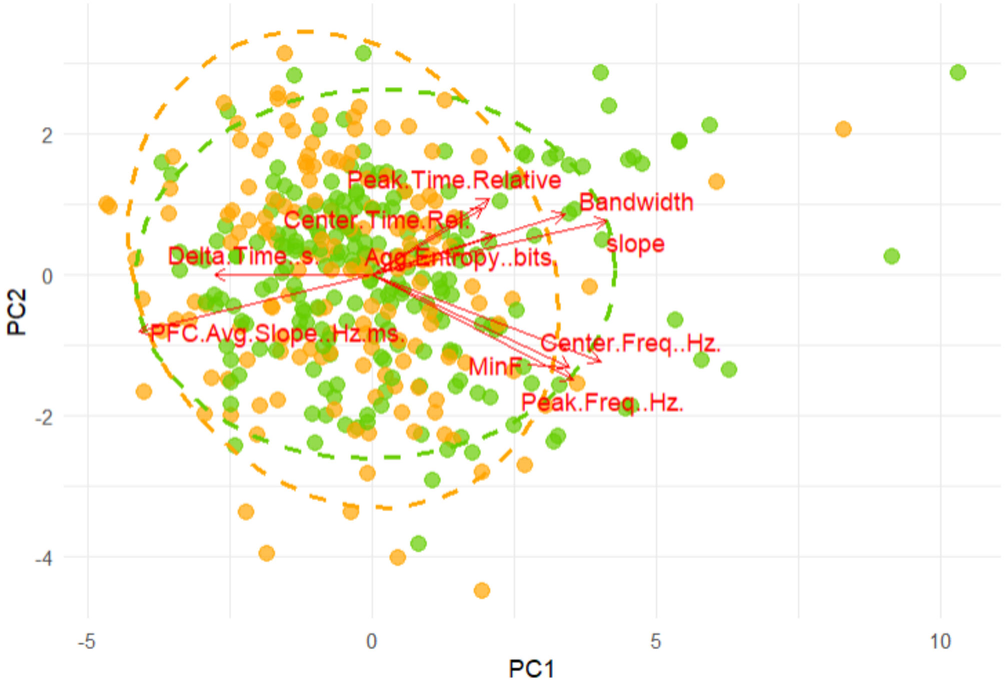

Figure S4.4. PCA Biplot of echolocation calls with 95% CI Ellipses. Green dot: rural area; orange dot: urban area.

Chapter 5

Investigating links between roost density, social networks, and vocal variation in a common urban-dwelling bat in urban ecosystem

Note: This chapter is formatted as a short note for *Austral Ecology*.

Abstract

Urbanisation generally leads to declines in the resources available for native wildlife and this can have consequences for animal social interactions and communication. Roost resources are a key factor shaping social networks in species that congregate colonially, yet the influence of decline of roost resources on bats' social communication remains poorly understood. The Gould's wattled bat, *Chalinolobus gouldii*, is a common urban species that roosts in tree hollows or bat boxes and typically congregates at roosts during the maternity season. I compared colonies roosting in three urban green spaces in Sydney that differed in roost density. Roost density was quantified through surveys of tree hollows and bat boxes, and social networks were constructed from banded individuals captured in bat boxes between 2020 and 2025. Colonies at the site with the lowest roost density exhibited higher network density but lower network modularity than colonies at the sites with higher roost density. High roost density potentially supported multiple subgroups with fewer connections between individual bats from other subgroups. Vocalisation analyses revealed greater distances among the most common social vocalisations, Syllable 1, at the site with low roost density compared with the sites with intermediate and high roost density. These findings imply that roost scarcity intensifies social connectivity, which in turn increases social vocalisation variation in *C. gouldii*, potentially to facilitate individual recognition. The results highlight the role of ecological constraints in shaping bat social organisation and communication in urban areas.

Keywords

Bats, Chiroptera, network modularity, social networks, biological urbanisation, social communication, social organisation

Introduction

Roost is one of the major constraints for socially roosting animals in urban areas (Moretto and Francis 2017). Habitat fragmentation and habitat degradation associated with urbanisation lead to declines in the availability and density of natural roosts, potentially altering social interaction patterns (Chaverri 2010, Russo and Ancillotto 2015). Social network analysis can provide insight into the association between animal social interactions and resource availability, broadening the understanding of how animals respond to urbanisation (Farine and Whitehead 2015).

The way in which groups roost together is influenced by both intrinsic and extrinsic factors, including population density, sex and relatedness, and habitat structure and roost availability and density, respectively (Kerth 2008, Johnson et al. 2013, Wilkinson et al. 2019). Roost density can directly affect animal social organisation, either promoting congregation or segregation of animals in space and time (Chaverri 2010). Highly social animals benefit from communal roosting with related or familiar individuals through reciprocal benefits such as information transfer and cooperative breeding (Wilkinson et al. 2016). To maintain social connection, acoustic communication can facilitate roost-mate recognition and locating roosts (Gokcekus et al. 2021, Vrtilek et al. 2025). Yet, few studies have examined the extent to which roost density shapes social networks and, consequently, communication in social roosting animals.

Social network analyses provide a quantitative framework for examining the dynamics of associations among individuals and their interactions with the environment (Johnson et al.

2013; Silvis et al. 2016). Using a set of metrics, these analyses allow researchers to characterise animal societies, including defining social groups, identifying social structure, and assessing the effects of anthropogenic disturbance (Wey et al. 2008; Zeus et al. 2018). For example, roost density influences bat social networks within day roosts (Chaverri 2010; Silvis et al. 2014). Social network analyses enable investigation of long-term relationships among individuals and groups across years or reproductive stages (August et al. 2014; Zeus et al. 2018). This tool provides valuable insights into the ecological and social drivers of animal behaviour.

The Gould's wattled bat *Chalinolobus gouldii* is one of the most common and adaptable urban-dwelling bats in Australia. It forages in urban green spaces and roosts in both tree hollows and artificial bat boxes. Previous studies indicate that *C. gouldii* predominantly roost with familial individuals (Godinho et al. 2015, Eastick 2022). Colonies are typically female-biased (Godinho et al. 2015), with mean colony sizes of 8.7 ± 1.4 individuals, forming maternity groups in tree hollows and artificial bat boxes during the breeding season (Dixon and Huxley 1989, Lumsden et al. 2002, Lumsden et al. 2020). Males and non-breeding females usually roost alone or in small groups of one to two individuals (Evans and Lumsden 2011). Additionally, females tend to present long-term residency at sites (Dixon and Huxley 1989). Roost group sizes also differ across roost types, with tree hollows often used by solitary individuals and bat boxes by multiple individuals (Evans and Lumsden 2011). Spatial subdivision of groups has been observed within roosting sites spanning 52 ha (Godinho et al. 2015). *Chalinolobus gouldii* produces a diverse range of communication sounds (i.e., social vocalisations) around roosts (Chapter 2). Of these social vocalisations, Syllable 1 can attract conspecifics to inspect sounds during call playback experiments (Chapter 3) and is the most predominant syllable recorded at roost sites (Chapter 2), although the functions of Syllable 1 still need to be investigated. Despite existing knowledge of roosting ecology, the links among roost density, social networks, and social communication in *C. gouldii* remain unclear.

This research note aimed to explore how ecological constraints shape social networks and drive variation in Syllable 1 in *C. gouldii* during the maternity season. I focused on the colonies roosting in three urban green spaces with differing roost density in the Greater Sydney region (Velasco et al. 2023) (Figure 5.1). Specifically, I quantified roost density, including tree hollows and artificial bat boxes, at the three sites to construct *C. gouldii* social networks and assess whether network structure affects variation in Syllable 1 shape and frequency. I hypothesised that roost density might affect *C. gouldii* roosting social networks, which in turn might drive increased social vocalisation variation, in Syllable 1 specifically, depending on the social networks.

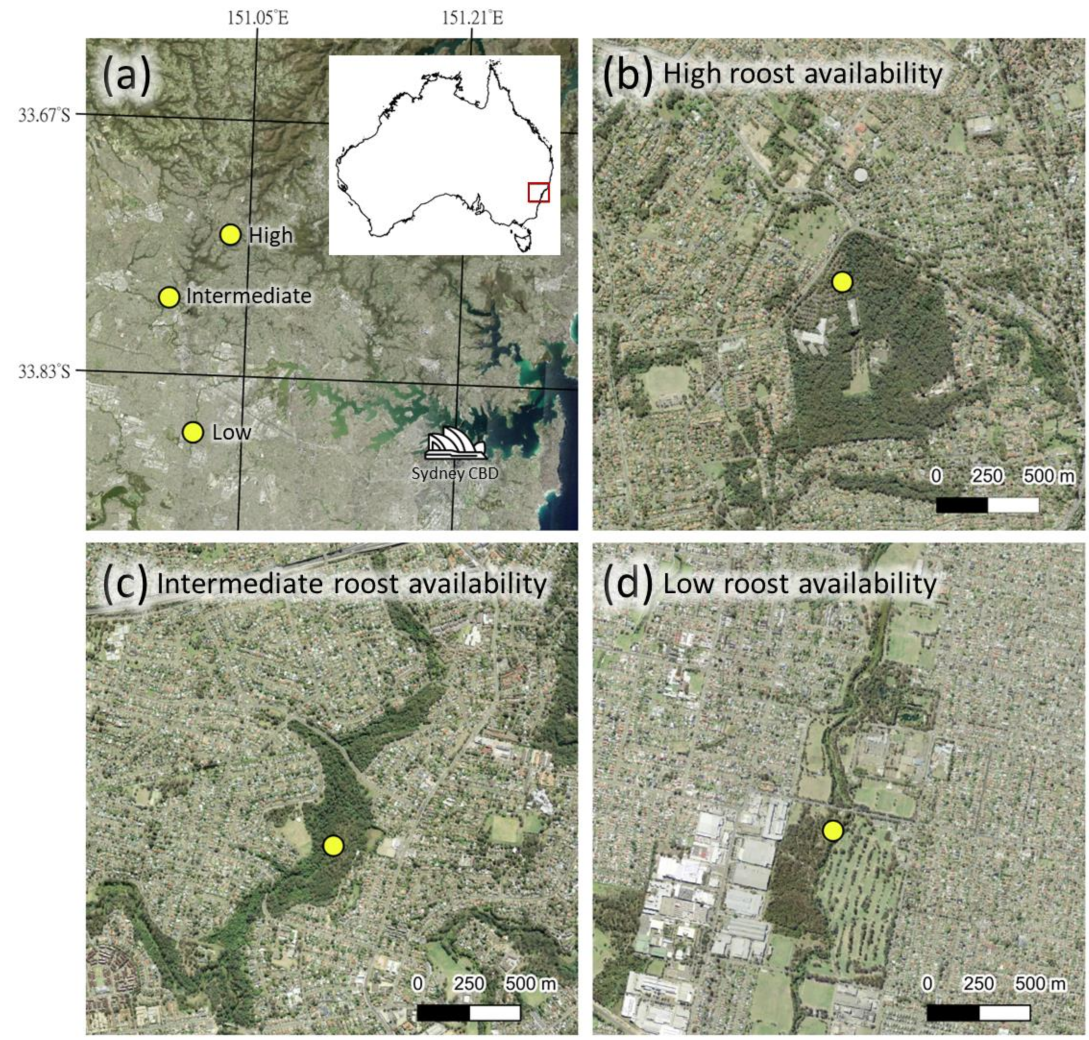

Figure 5.1. (a) Overview of the Sydney landscapes around three sites; (b) high roost density (Cumberland State Forest), as measured by relative abundance of tree hollow and bat boxes; (c) Intermediate roost density (Moxham Park); and (d) Low roost density (Wategora Reserve).

Materials and Methods

Study site

I conducted this study in the Greater Sydney region, Australia. Three green spaces were chosen: Cumberland State Forest (latitude: 33.742S; longitude: 151.036E), Moxham Park (33.782S, 150.993E), and Wategora Reserve (33.865S, 151.013E), where *C. gouldii* is known to roost in installed bat boxes and tree hollows (Velasco et al. 2023). The pairwise distances between sites were as follows: Cumberland State Forest–Moxham Park, 6.36 km; Cumberland State Forest–Wategora Reserve, 13.94 km; and Moxham Park–Wategora Reserve, 9.49 km, with an average distance of 9.96 km.

Roost density

I assessed the roost density at the three sites by establishing plots to estimate the relative abundance of tree hollows and by counting the absolute number of bat boxes.

To sample tree hollows, I conducted replicate 20 m x 50 m plots and counted tree hollows in every tree within plots. A plot was designated every 0.12 km^2, with the number of plots per site determined by the total site area. Any size of cavity or hole > 3 cm in diameter) was defined as a potential roost that bats can use, located within the trunk or branches of a living or dead tree with diameter at breast height > 10 cm (Threlfall et al. 2013). In Cumberland State Forest (approximately 0.45 km^2), four plots were established (mean number of hollows bearing trees per 1000 m^2 (HBTs), = 8.5, range: 5-17); Moxham Park (approximately 0.45 km^2) had four plots (HBTs = 7.25, range: 5-15), and Wategora Reserve (approximately 0.2 km^2) had three plots, where no tree hollows were found (HBTs = 0).

All three sites had bat boxes installed, and *C. gouldii* is known to roost primarily in the bat boxes during the maternity to the early mating season, from November to April (Velasco et al. 2023). In Cumberland State Forest, 14 bat boxes were installed, nine in Moxham Park, and six in Wategora Reserve.

Based on the relative abundance of tree hollows and the absolute number of bat boxes, I classified roost density as ‘high’ (Cumberland State Forest: HBTs = 8.5; bat boxes = 14), ‘intermediate’ (Moxham Park: HBTs = 7.3; bat boxes = 9), and ‘low’ (Wategora Reserve: HBTs = 0; bat boxes = 6) (Table 5.2).

Bat capture and social networks

Although *C. gouldii* also roosts in tree hollows (Lumsden et al. 2020), I restricted the investigation to bats roosting in bat boxes due to the inaccessibility of tree hollows. Bat captures were conducted at least once, or twice maximum, to avoid intense disturbance between September and April (i.e., maternity season) of each year from 2020 to 2025. During this period, bats form maternity colonies until juvenile independence, and most bats at these sites leave bat boxes at the late-March. Bats were obtained using a hand net with an extension pole, which fully covered the entrance of bat box as bats flew out. Boxes were visually inspected to confirm the absence of bats. Captured individuals were measured, marked, identified, and placed in soft cloth bags. Individuals already banded were recorded by band number, while non-banded individuals were fitted with an omega-shape aluminium band provided by the Australian Bird and Bat Banding Scheme (ABBBS) on the forearm. Researchers checked for injuries in all recaptured individuals, and newly banded individuals were monitored before release. All procedures were approved by Animal Research Authority

(2020/1825; 2023/2386) of The University of Sydney.

For captured individuals, I recorded the number of individuals in each box, counted the number of males and females per site, and calculated the sex ratio at each site (the number of males per 100 females). I also counted the number of banded individuals and the number of recaptured individuals at each site. Recapture rate was defined as the percentage of recaptured individuals relative to the total number of banded individuals.

To construct *C. gouldii* social networks at each site, I used the 'sna' Package in R (Butts 2008) and assessed three metrics through simple ratio index: (1) node size (number of individuals in the network), (2) density (the proportion of actual to potential connections, using the *edge_density* function), and (3) modularity (the extent to which the network is divided into subgroups, using the *cluster_fast_greedy* function). Only bats captured more than twice were included in social network analysis to avoid bias (Farine and Whitehead 2015).

Acoustic recordings

To explore whether social network structure influenced *C. gouldii* social vocalisation variation, I recorded *C. gouldii* vocalisations using Anabat Chorus (Titley Scientific, Australia) at bat box locations between December 2024 to April 2025. Ultrasonic recorders were positioned 3.5 m away from the selected bat boxes and tilted at a 45-degree angle up toward the box. I deployed ultrasonic recorders at boxes occupied by *C. gouldii* or at the most frequently used boxes if none were occupied. When multiple boxes were in use, recorders were deployed at as many boxes as possible. Specifically, three boxes were recorded at Cumberland State Forest, two at Moxham Park, and one at Wategora Reserve, where most bats congregated at a single box. If multiple boxes had recorders deployed, only one of the boxes was selected for social vocalisation analysis. The number of bats occupying each box was unknown as I did not capture bats during the recording period.

Files containing *C. gouldii* social vocalisations were extracted and screened in Kaleidoscope Lite (Version 5.6.3, Wildlife Acoustics, USA). To avoid misidentification, only social vocalisations surrounded by *C. gouldii* echolocation calls were analysed, as echolocation calls of *C. gouldii* can be unambiguously assigned to species level (Adams et al. 2010).

Social vocalisations that differed in spectrogram of *C. gouldii* echolocation calls were manually selected and ten acoustic measurements were obtained from each of the selections in Raven Pro 1.6 (Version 1.6.5, Cornell Lab of Ornithology, US). To assign the selected social vocalisations to the specific syllable types, which were identified in Chapter 2, a linear model was applied to the ten acoustic measurements. I focused on the most frequent, social vocalisations around roosts: Syllable 1 (Chapter 2; Figure 5.2 (d)).

To assess the variation in Syllable 1 among sites, I assessed the Mahalanobis distance, calculated from the ten acoustic measurements relative to the overall Syllable 1 centroid from a Principal Component Analysis. To balance sample sizes, 141 syllable 1 were selected from each site (141 was the number of Syllable 1 recorded in Moxham Park). For each recording night, no more than five Syllable 1 examples were selected, with time separation maximised to minimise the likelihood that vocalisations were produced by the same individuals. Differences in Mahalanobis distances among sites were examined using a Kruskal-Wallis rank sum test. Pairwise Wilcoxon rank-sum tests were conducted between sites where significant differences were found. Adjusted p-values were reported in multiple statistical tests to control the increased risk of false positives.

Results

In the *C. gouldii* capture and recapture data, no individuals were recorded roosting at more than one site. The year capture patterns of sites between 2020 and 2025 see Table 5.1. At the intermediate roost density site, no capture occurred in 2020. At the low roost density site, no capture occurred in 2020 and 2025.

Table 5.1. The year capture patterns of sites between 2020 and 2025

	Roost density					
	High		Intermediate		Low	
Year	Overall capture	Recapture	Overall capture	Recapture	Overall capture	Recapture
2020	27	Not available	Not available	Not available	Not available	Not available
2021	19	7	42	Not available	65	Not available
2022	6	0	21	2	35	17
2023	7	1	6	3	49	10
2024	9	0	36	9	9	7
2025	35	6	11	1	Not available	Not available

The number of times an individual was recaptured ranged from one to five. Recapture rate ranged from 19% to 27% across sites. Seventeen of 88 individuals in Cumberland State Forest were recaptured; 20 of 101 individuals in Moxham Park; and 34 of 125 individuals in Wategora Reserve (Table 5.2). Bat box occupancy and recaptured individuals were female biased at each site (Table 5.2).

Table 5.2. *Chalinolobus gouldii* capture and recapture data, including number of individuals by sex, sex ratio, and recapture rate.

	Roost density								
	High (Cumberland State Forest)			Intermediate (Moxham Park)			Low (Wategora Reserve)		
Number of individuals	M	F	Sex ratio	M	F	Sex ratio	M	F	Sex ratio
Banded	33	55	60	35	66	53	50	75	67
Recapture	4	13	31	1	19	5	5	29	17
Total banded individuals		88			101			125	
Recaptured individuals		17			20			34	
Recapture rate (%)		19.3			19.8			27.2	

Abbreviations: M, male; F, female. Note: Sex ratio refers to the number of males per 100 females. Recapture rate is defined as the percentage of recaptured individuals relative to the total number of banded individuals.

Social network metrics showed that sites with high and intermediate roost density had lower network density with fewer individuals recaptured, whereas the site with low roost density had high density with more individuals banded and higher capture-recapture rate (Table 5.2 and 5.3; Figure 5.3 (a)-(c)). Network modularity was highest at the high roost density site, followed by the intermediate site, and lowest at low roost density site (Table 5.3).

Vocalisation analyses revealed significant differences among sites (Kruskal-Wallis rank sum test: $H = 73.925$, $df = 2$, $p < 0.001$, n = 141 syllables per site). Syllable 1 exhibited larger Mahalanobis distances from the overall centroid at the low roost density site than at the high and intermediate sites, while no difference was detected between the high and intermediate sites (Pairwise Wilcoxon rank-sum tests, high versus intermediate: statistic: 10446, adjusted-$p > 0.05$; high versus low: statistic: 5376, adjusted $p < 0.001$; intermediate versus low: statistic: 4380, adjusted $p < 0.001$) (Figure 5.2 (d)-(e); supplementary information Figure S5.1).

Table 5.3. The summary of roost density and social network metrics: node, density and modularity at the three sites.

Roost density	High (Cumberland State Forest)	Intermediate (Moxham Park)	Low (Wategora Reserve)
Mean HBTs (Range)	8.5 (5-17)	7.25 (2-15)	0
Number of bat boxes	14	9	6
Average individuals in bat boxes (Standard deviation)	5.9 (6.4)	8.3 (6.5)	19.4 (15.8)
Social network metrics			
Node (individuals)	17	20	34
Density	0.36	0.38	0.66
Modularity	0.46	0.36	0.2

Note: number of hollows bearing trees per 1000 m^2 (HBTs).

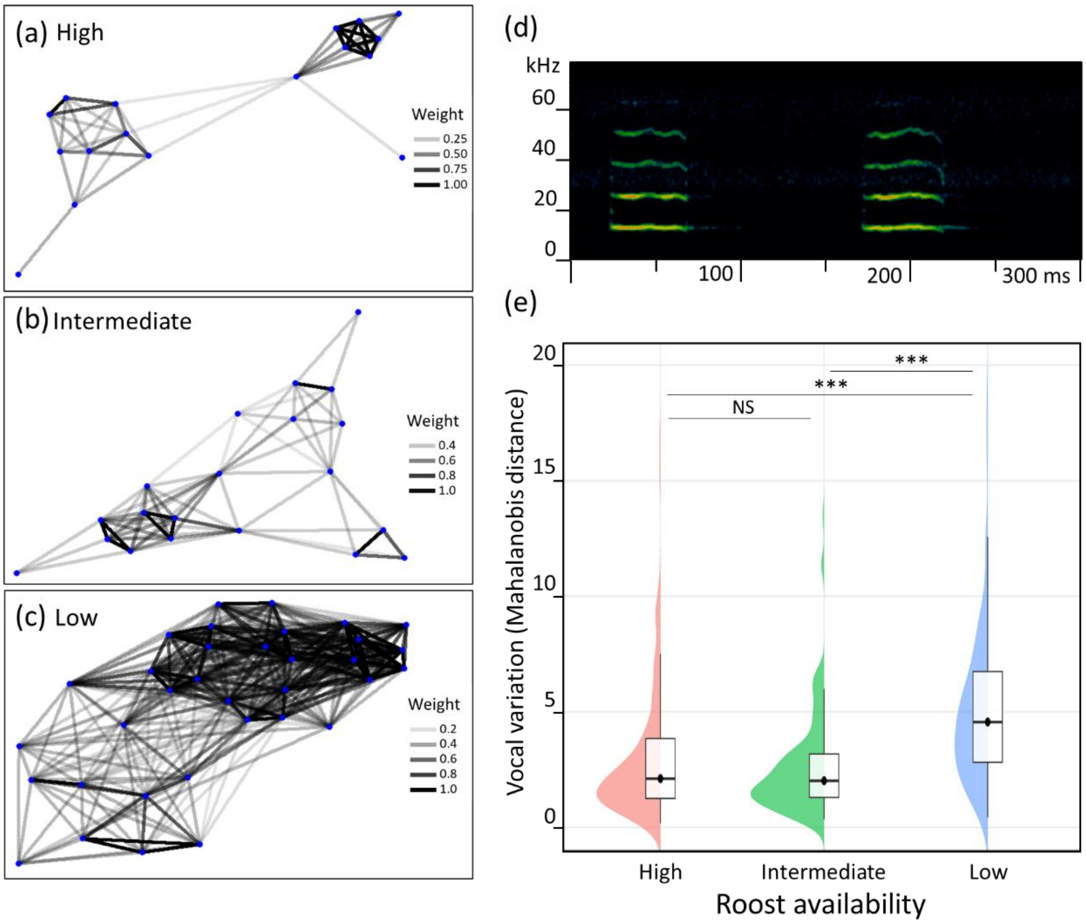

Figure 5.2. Social network of *Chalinolobus gouldii* at (a) high roost density (Cumberland State Forest), (b) intermediate (Moxham Park), and (c) low (Wategora Reserve). Dots represent individuals, and link colour indicates the frequency of co-roosting. (d) *C. gouldii* social vocalisation, Syllable 1. (e) Boxplots show variation in Syllable 1 across three levels of roost density. Shaded areas represent data density, and asterisks indicate significant differences in pairwise Wilcoxon signed-rank tests.

Discussion

Roost density can shape social networks of echolocating bats and potentially affect their acoustic communication. This study found that sites with low roost density had high network density and low network modularity, whereas sites with high roost density had low network density and high network modularity. This pattern may reflect the tendency of *C. gouldii* to congregate with social roosting mates: low roost density may concentrate individuals within fewer roosts (Chaverri 2010, Johnson et al. 2013). Moreover, sites with high network density and low network modularity had greater Syllable 1 variation, potentially reflecting strong demands for individual recognition. These findings are supported by the hypothesis that social complexity is linked to vocal complexity (Knörnschild et al. 2020). Thus, the results suggest a pathway in which low roost density leads to high network density, which in turn precipitates greater distance from the overall centroid in social vocalisations.

Not only roost density, but also physiological requirements can shape social networks (Kerth 2008). I compared three sites in urban areas with different absolute numbers of bat boxes and relative tree hollow abundance, suggesting roost density could affect *C. gouldii* social network density. However, several limitations prevent us from disentangling the effects of roost density on social networks. Tree hollows and bat boxes provide distinct microclimates (Evans and Lumsden 2011), and roost choice may depend on sex- and breeding stage-specific requirements. For example, solitary or male bats prefer cooler roosts for torpor to save energy, while breeding females require warmer roosts for pup rearing (Encarnaçao et al. 2005, Borkin and Parsons 2011, Evans and Lumsden 2011, Wilkinson et al. 2016, Wilkinson et al. 2019). This sex-dependence roosting behaviours may explain the female-biased use of bat boxes and the lower number of recaptured males at sites with low roost density and no tree hollows. Hence, a different pattern may be revealed if tree hollow-using individuals were sampled, or the roosting behaviours and physiological requirements may reflect different between sexes, which needs to be investigated.

Social complexity influences the complexity of communication across various taxon (Freeberg 2006, Knörnschild et al. 2019). Individual recognition is critical to social interactions (Gokcekus et al. 2021) and benefits group coordination and cohesion (Knörnschild et al. 2025). In group-living species, individuals in larger groups produce calls with greater complexity (measured as bits of information) than those in smaller groups (Freeberg 2006). In this study, individuals in larger group sizes at low roost-density sites exhibited larger distances from the overall centroid in social vocalisations than individuals in smaller groups at high roost-density sites, potentially indicating higher demands for individual recognition (Knörnschild et al. 2020). In contrast, areas with high roost density and lower population sizes supported higher modularity, which may facilitate spatially distinct subgroups with limited interactions due to non-overlapping home ranges (August et al. 2014). Consequently, reduced encounter rates among individuals may decrease the need for highly variable social vocalisations for recognition (Knörnschild et al. 2020), or alternatively, subgroups may develop their own group-specific signatures (Wilkinson et al. 2019; Carlson et al. 2020). The mechanisms underlying congregation and roost-mate recognition at the population, group, or individual level in *C. gouldii* presents a promising avenue for future research.

In conclusion, roost density is likely to be one of the major factors influencing *C. gouldii* social organisation, networks, and vocal variation in urban ecosystems. While the comparison was limited to three sites, future work should (1) increase the number of sampling sites to assess the relationship between roost density, network structure, and vocal variation; (2) assess the connectivity of urban green spaces to estimate potentially available roosts and possible bat movements outside of the site; and (3) evaluate the importance of vocal communication in mediating social interactions to cope with ecologically simplified areas, such urban environments. Understanding these factors will provide broader insights into *C. gouldii* roosting ecology and habitat requirements and inform management strategies for this and other social bat species in urban environments.

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Supplementary information

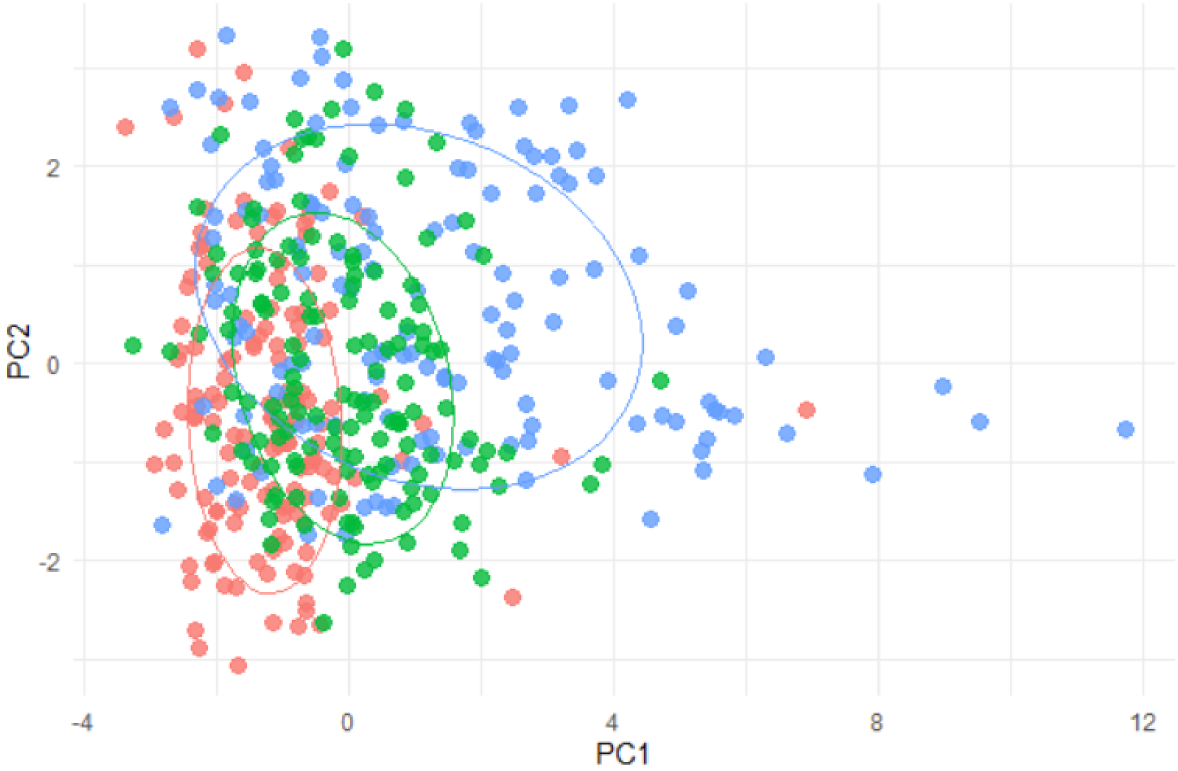


Figure S5.1. PCA Biplot of Syllable 1 across three sites with 95% CI Ellipses. Coral dot: high roost density (Cumberland State Forest); green dot: intermediate roost density (Moxham Park); blue dot: low roost density (Wategora Reserve).

Chapter 6. General discussion

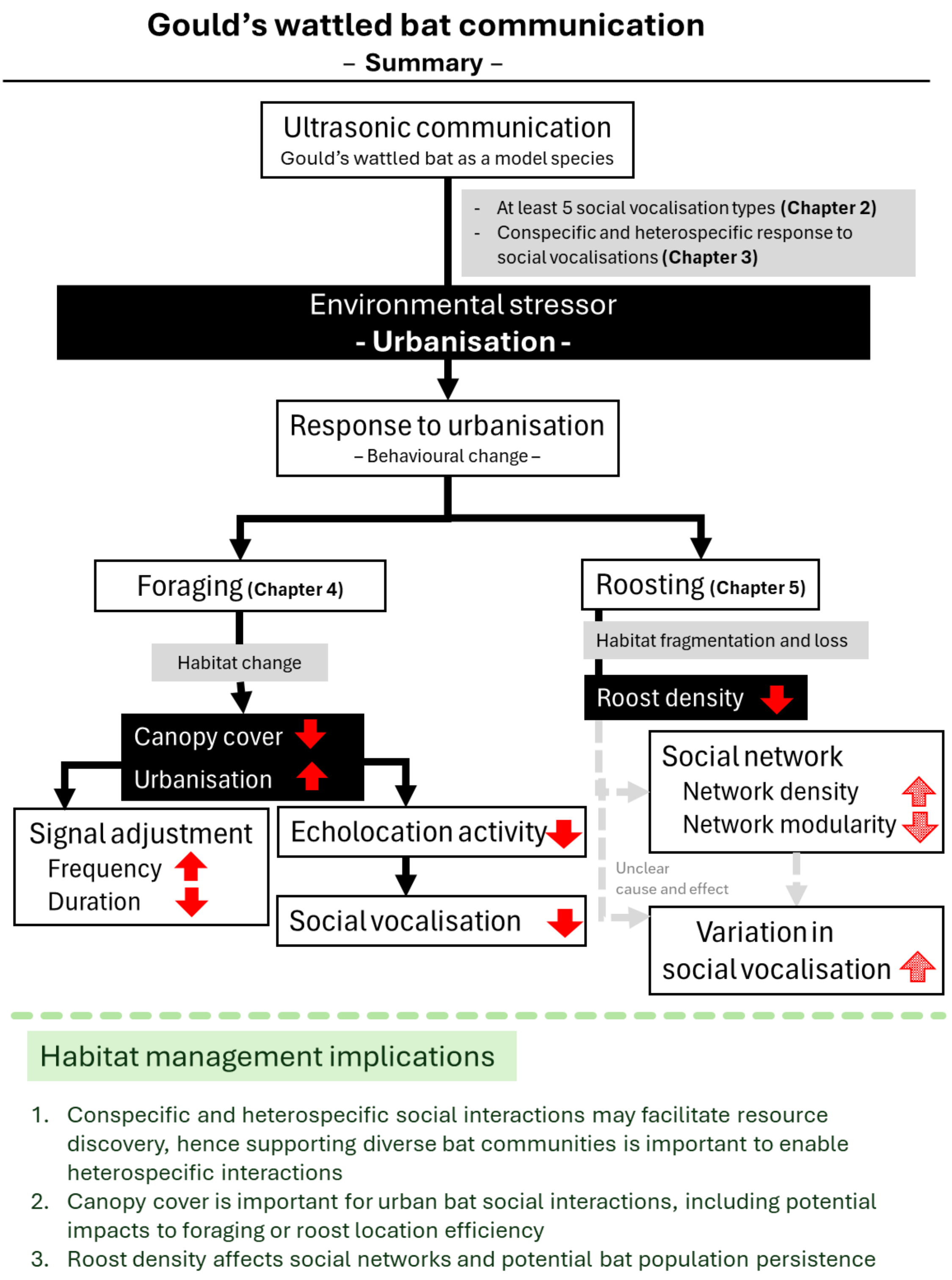
6.1 Overview of findings

Understanding how bat communication changes in urban areas can provide insight into ultrasonic communicators beyond the well-known audible communicators such as birds and amphibians. This thesis focused on the Gould's wattled bat *Chalinolobus gouldii* which inhabits a diverse range of habitats in Australia, from rural and natural habitats to human-induced urban areas. Given their widespread distribution, they are a valuable model species to address how ultrasonic communicators respond to artificial environments via behavioural and ecological research (Figure 6.1).

In Chapter 2, I identified at least five types of social vocalisations produced by *C. gouldii*. These vocalisations did not vary temporally, contrary to the initial hypothesis. In Chapter 3, *C. gouldii* responded differently to conspecific vocalisations, approaching social vocalisations but not echolocation calls and feeding buzzes. Additionally, the heterospecific *M. orianae oceanensis* approached *C. gouldii* vocalisations, including echolocation calls and feeding buzzes. In Chapter 4, social vocalisation rates of *C. gouldii* were higher in areas with greater canopy cover, particularly in urban areas. Furthermore, *C. gouldii* in urban areas adjusted their social vocalisations to higher frequencies and shorter durations compared with rural conspecifics, supporting the hypothesis that *C. gouldii* potentially mitigating acoustic masking from increased impervious surfaces or anthropogenic noise. In Chapter 5, within patches of urban bushland, *C. gouldii* exhibited high network density and low network modularity at sites with low roost density, forming a monocolonial social structure. In contrast, sites with higher roost density were characterised by lower network density and higher modularity, supporting the presence of multiple subgroups. These differences in social network structure, in turn, influenced social vocalisation variation among individuals, with low roost density associated with greater vocalisation distance from the centroid. Although *C. gouldii* is a widespread and highly successful species in urban landscapes, this thesis demonstrates that habitat modification associated with urbanisation affects vocal communication and social interactions beyond patterns of distribution and activity.

As an answer to the core question ‘Does *C. gouldii* adjust its vocal communication to cope with urban life?’, I found that *C. gouldii* may use different strategies depending on context: foraging versus roosting and in urban versus rural areas.

Social vocalisations are used in different contexts by *C. gouldii*. During foraging, social vocalisations may improve foraging efficiency by facilitating the sharing of information about prey locations or allowing the formation of foraging groups, particularly in urban areas with great canopy, as observed in other species (Wilkinson and Boughman 1998, Kohles et al. 2022). At roost areas, *C. gouldii* advertises the roost locations to assist roost mates finding roosts (Furmankiewicz et al. 2011, Chaverri et al 2012). In areas where roosts were common, *C. gouldii* not only congregates among conspecifics but also uses vocalisations that seem to encode group identity due to the existence of subgroups with spatial subdivision. Social interactions through vocal communication in *C. gouldii* may contribute, along with ecomorphology (edge-space forager) and presumably high physiological tolerance, to facilitate them to occupy diverse habitats throughout the Australian continent.



1. Conspecific and heterospecific social interactions may facilitate resource discovery, hence supporting diverse bat communities is important to enable heterospecific interactions
2. Canopy cover is important for urban bat social interactions, including potential impacts to foraging or roost location efficiency
3. Roost density affects social networks and potential bat population persistence

Figure 6.1 An overview of the effects of urbanisation on social communication, interaction patterns, and social networks in the Gould's wattled bat *Chalinolobus gouldii*. Black arrows indicated possible causal relationships, and red upward and down arrows indicate increase and decrease respectively.

6.2 Managing bat social interactions in urban areas

The negative effects of urbanisation on bat activity and social vocalisations, driven by habitat modification that directly alters behaviours and roost resources, pose a substantial threat to bat persistence in these ecosystems. A decline in *C. gouldii* echolocation activity is expected to limit conspecific encounter rates, thereby reducing opportunities for social interactions. In Chapter 4, I found that greater canopy cover played an important role in urban areas. In the urban areas, by increasing canopy cover, habitat quality can be improved, leading to increase *C. gouldii* social vocalisation rates. In Chapter 5, roost density is another issue for bats, as they cannot build their own roosts. Roost quantity and density of different roost types (e.g., bat boxes versus tree hollows) are key extrinsic factors affecting *C. gouldii* roosting social networks and variation in their social vocalisations. Because *C. gouldii* exhibits social roosting (Godinho et al. 2015, Eastick 2022), bats in areas with low roost density form a single colony with high network density, which could make colonies more vulnerable to local disturbance (Rhodes et al. 2006). Based on these findings, two recommendations are made regarding urban green spaces and compensatory roosts (see also Figure 6.1):

- Urban green spaces:

  Maintain or increase canopy cover to greater than 40% in urban areas to support bat social interactions. Continuous canopy and habitat connectivity provide more opportunities for bats to forage, encounter conspecifics, and find their roosts, thereby facilitating social interactions (Lumsden et al. 2002, Luck et al. 2013, Ancillotto et al. 2016, Silva de Araújo and Bernard 2016, Callas et al. 2024). Hence, these improvements enhance bat persistence in urban landscapes.

- Compensatory roosts:

  Providing diverse compensatory, or artificial, roosts may help bats meet different physiological requirements (Kerth et al. 2001b, Encarnaçao et al. 2005). For example, males often prefer to roost alone in tree hollows, while females require group roosts for rearing offspring (Evans and Lumsden 2011). Sufficient roosts can also allow colonies to split into subgroups, which may benefit colony health, such as reducing the risk of disease transmission and disturbance (Rhodes et al. 2006, Patterson and Ruckstuhl 2013).

6.3 Opportunities for further research

*S*ome of the limitations identified in this study provide substantial opportunities for future research. The key opportunities are described briefly below:

Laboratory experiments and individual identification

Behavioural interactions and communication rely on who communicates with who and what the purpose of communication is. Individual recognition can affect how each signaller interacts with receivers (Beecher 1989, Kastein et al. 2013, Gokcekus et al. 2021). In my thesis, acoustic recordings, call playback experiments and video recordings were conducted in the field without individual identification. These have limitations, for example, social roosting bats respond to known individuals through the information encoded in the vocalisations, such as contact call differences between groups (Carter et al. 2009, Arnold and Wilkinson 2011, Furmankiewicz and Jones 2022), meaning potentially that the same individuals repeatedly visit experimental sites or individuals may respond differently to vocalisations from different groups. External factors, such as conspecific population density, prey abundance, microhabitats, and heterospecific interactions, affect individual responses, which could not control in the field (Lewanzik et al. 2019). Laboratory experiments can appropriately control these factors, including individual identification and external factors. However, the artefacts associated with artificial settings mean that observed behaviours in captive animals can potentially differ from the behaviours when bats are in the wild. Alternatively, microchips (Passive Integrated Transponder tags, PIT tags, for example) may be effectively deployed when recording bat behaviours around roosts via reading individual tags. Microchips can also assist in tracking *C. gouldii* associations and roosting behaviours (Godinho et al. 2015, 2019, Lumsden et al. 2020).

Acoustic lures for promoting bat box occupancy

Bat lures have been described as an effective method for increasing bat capture rates and improving sampling effectiveness. Broadcasting bat feeding calls or conspecific social calls has been shown to enhance netting success and detection rates as bats approach the sound source (Barclay 1982, Hill and Greenaway 2005, Gillam 2007, Goiti et al. 2007, Aylen et al. 2022, Hanrahan et al. 2024). Furthermore, some species respond to the vocalisations of sympatric heterospecifics occupying similar niches (Barclay 1982, Hill et al. 2015, Velasco 2018, Barclay and Jacobs 2022). In this thesis, playback experiments (Chapter 3) revealed that not only *M. orianae oceanensis* but also ecologically similar species to *C. gouldii* approached its vocalisations. These included cohabiting species with potentially similar foraging niches, such as *Scotorepens orion* (Velasco et al. 2023) (supplementary information Table S3.2), as well as *Nyctophilus* species that use the same bat boxes and tree hollows as *C. gouldii* at different times (Threlfall et al. 2013) (supplementary information Table S3.2).

These findings highlight an extended application of acoustic lures: the potential use in attracting bats to newly installed compensatory roosts.

To offset the loss of natural roosts associated with the removal of old and large trees in urban areas, bat boxes and artificial or carved hollows are commonly installed. However, bat occupancy of these structures is highly variable, with colonisation rates ranging from 7% to 100%, depending on species (Mering and Chambers 2014). Although roost microclimate is known to affect occupancy (Mering and Chambers 2014, Rueegger 2016), the role of social interactions and communication in driving roost use remains poorly understood. One study found that bat activity was higher at artificial roosts when social calls were broadcast compared to silent controls (Brokaw 2015), suggesting that acoustic lures may facilitate roost discovery and occupancy. Given that both conspecifics and heterospecifics were attracted to *C. gouldii* vocalisations in playback experiments (Chapter 3), broadcasting social calls around newly installed compensatory roosts could guide bats to these structures, but this requires explicit testing in Australia.

The effect of urban noise on social vocalisations

The effects of urban noise on bats’ social vocalisations is a further issue to investigate. In Australia, urban noise sources such as traffic noise produce frequencies that range up to 20 kHz (Bonsen et al. 2015), overlapping with the low-frequency components of *C. gouldii* social vocalisations (e.g., Syllable 1 median: 16.25 kHz in rural and 17.81 kHz in urban; Table 4.3). Previous studies have shown that echolocation calls in noisy environments generally shift toward higher frequencies to avoid masking and increase acoustic frequencies and rate to improve signal detectability (Bunkley et al. 2015, Bednarz 2020, Yantén et al. 2022).

Similarly, I found social vocalisations in *C. gouldii* shift toward higher frequencies, shorter durations, consistent with patterns in other species (Jiang et al. 2010, Starik and Göttert 2022). A previous study also demonstrated that bats have been shown to increase the amplitude of their social vocalisations in response to rising background noise level (Jiang et al. 2010), a response known as the Lombard effect (Lane and Tranel 1971, Hage et al. 2013), which was not explored in this thesis. Given the limited number of studies to date, there is an opportunity to assess the effect of noise pollution on bats' vocal communication.

The applications of social vocalisation on habitat conservation

Exploring social vocalisations in bats provides new insights into their social behaviours and helps identify key habitats for social interactions. Methods for identifying bat species through their echolocation calls are already well-developed, and acoustic recordings are widely used to estimate species richness and relative abundance (Luck et al. 2013, Ancillotto et al. 2016, Silva de Araújo and Bernard 2016, Callas et al. 2024). Expanding the application of acoustic data, I found that bats frequently produce social vocalisations in roost areas (Chapter 2) and in urban areas with greater canopy cover (Chapter 4). This suggests that areas with high levels of social vocalisation may represent key habitats for bats, consistent with previous studies (Velasco et al. 2023). Other researchers also found that bats produce more social vocalisations during autumn swarming near hibernacula, reflecting important mating and hibernation locations (e.g., Furmankiewicz et al. 2013, van Schaik et al. 2015, Bergmann et al. 2022a, Bergmann et al. 2022b) It is valuable to quantify the occurrence of social vocalisations and assign them to species in acoustic databases where possible, even though the functions of social vocalisations in many species remain unknown (Appendix 1). Areas with frequent social vocalisations are likely to play an important role in both bat social interactions and habitat use, indicating these areas be a priority for conservation.

6.4 Conclusion

Recording changes in animal vocal communication in response to urbanisation has focused on species within the human audible range, while communication in ultrasonic range remains comparatively overlooked. In this thesis, I used *C. gouldii* as a model species because it is widely distributed across different habitats and is well adapted to urban areas. To understand how *C. gouldii* persists in urban areas, I focused on its social communication. By analysing their call measurements and call playback experiments, I found that *C. gouldii* has at least five types of social vocalisations, and that both conspecifics and heterospecifics were attracted to *C. gouldii* vocalisations. Social vocalisation rates increased in areas with substantial canopy cover, particularly when canopy exceeded 40% in urban areas. In addition, *C. gouldii* adjusted its social vocalisations toward higher frequencies and shorter durations in urban areas. Moreover, in areas with limited roost density, *C. gouldii* colonies displayed a high network density, and individuals exhibited greater variation in their social vocalisations. These findings suggest that bat social vocalisations play an important role in enabling persistence and communication across diverse environments, including urban areas. They also provide preliminary guidance for habitat management, such as retaining and improving canopy cover and installing compensatory roosts in urban green spaces, extending insights beyond well-studied, human audible vocal communication of other animals. Further research should validate the specific functions of these social vocalisations, assess the potential use of acoustic lures for attracting bats to new installed compensatory roost in key habitats, and evaluate how urban noise influences bat communication.

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Appendix 1. Social vocalisations of common echolocating bats in the Great Sydney region

These social vocalisations of common echolocating bats in the Great Sydney region were recorded during autumn 2023 (March and May), using the same acoustic files as in Chapter 4. In this appendix, signalling species were identified by the surrounding echolocation calls, as social vocalisations in flight typically occur within echolocation sequences. Vocalisations were then manually annotated based on spectrogram differences. At least eight species (excluding *Chalinolobus gouldii*) were recorded, ranging from common and urban-tolerant species such as *Miniopterus orianae oceanensis*, *Myotis macropus*, and *Scotorepens orion*, to more urban-sensitive species including *Chalinolobus morio*, *Falsistrellus tasmaniensis*, *Mormopterus norfolkensis*, *Ozimops ridei*, and *Vespadelus vulturnus*. In addition, a *Nyctophilus* species complex (*N. geoffroyi* and *N. gouldi*) was detected, although species-level identification could not be made from their echolocation sequences.

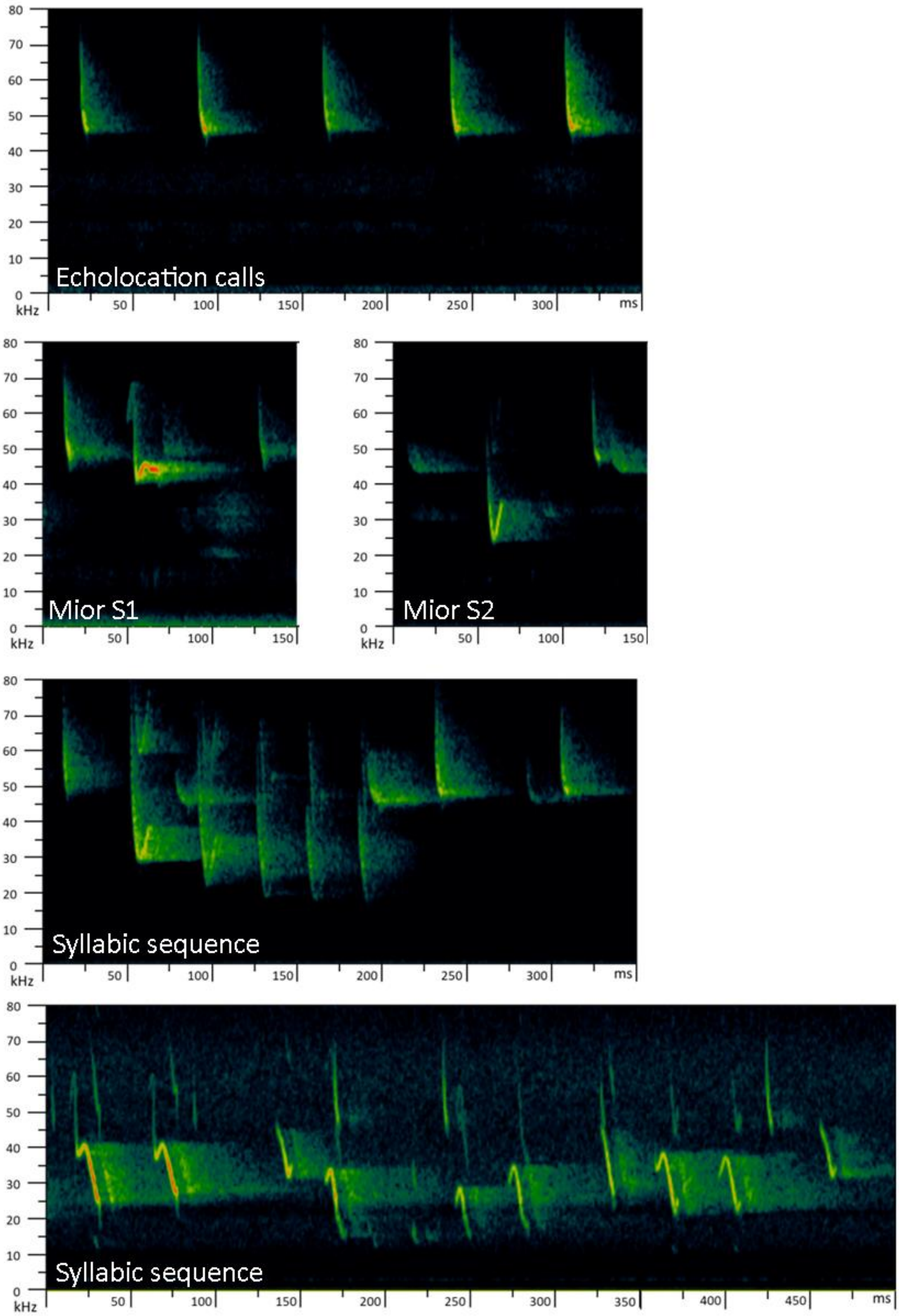

Figure A1. Echolocation sequences and social vocalisations of the large bent-winged bat *Miniopterus orianae oceanensis*.

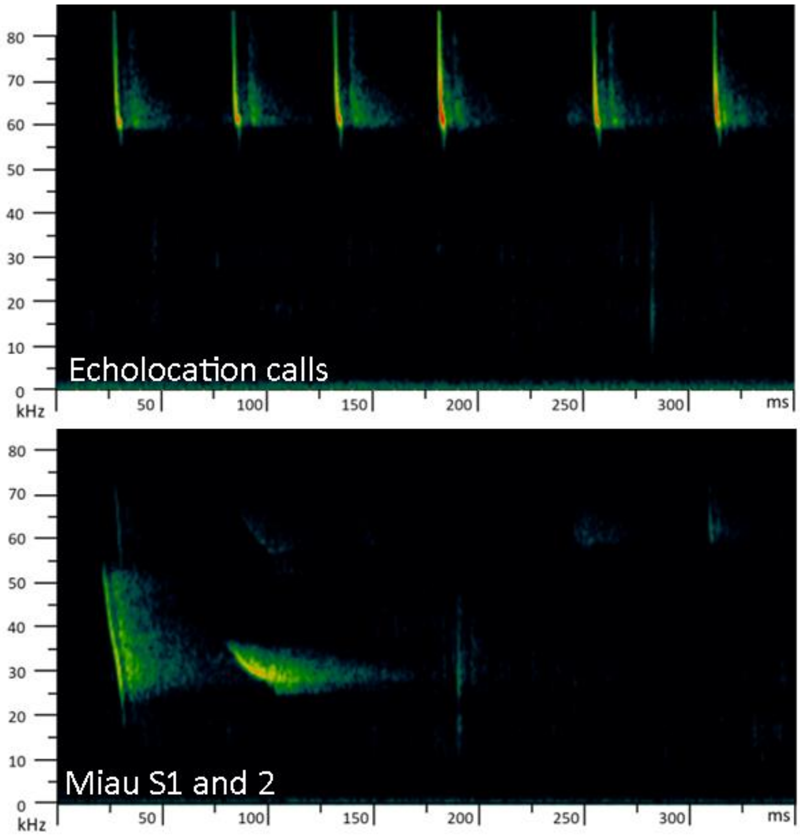

Figure A2. Echolocation sequences and social vocalisations of of the little bent-winged bat *Miniopterus australis.*

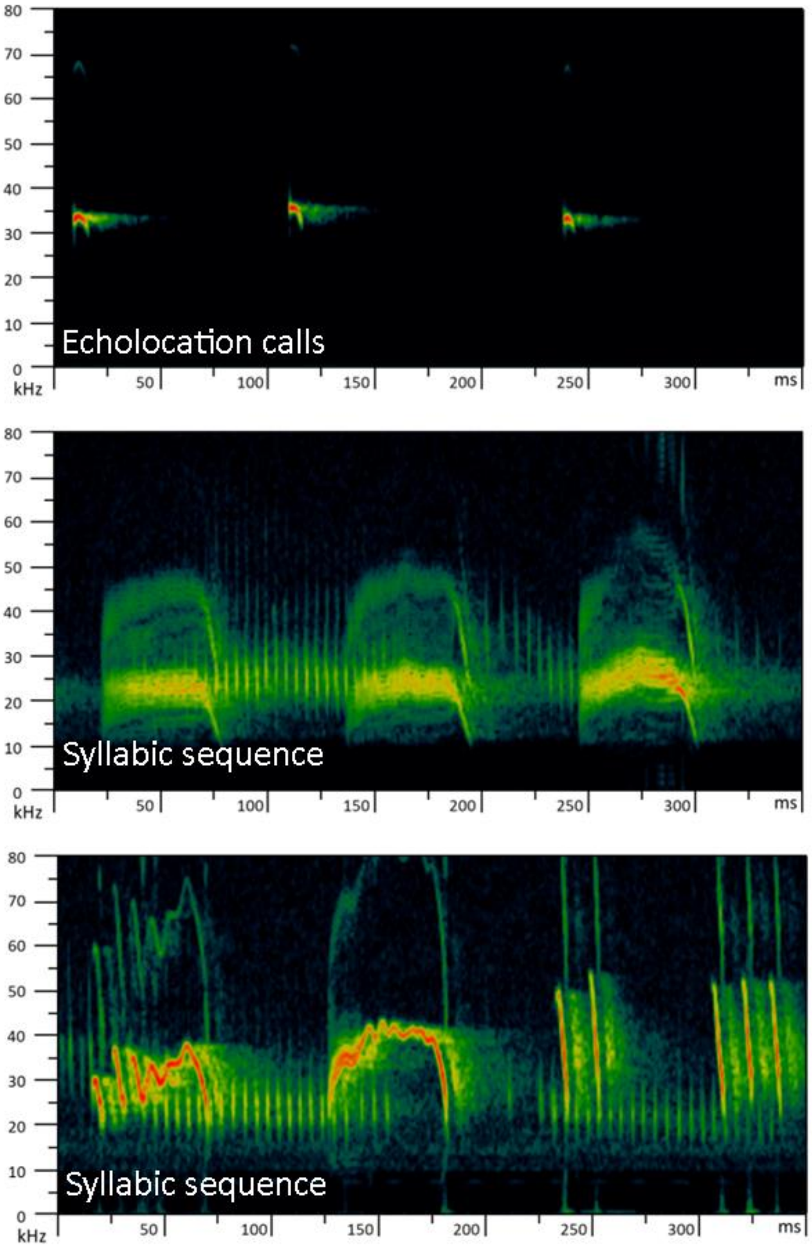

Figure A3. Echolocation sequences and social vocalisations of the eastern coastal free-tailed Bat *Mormopterus norfolkensis*.

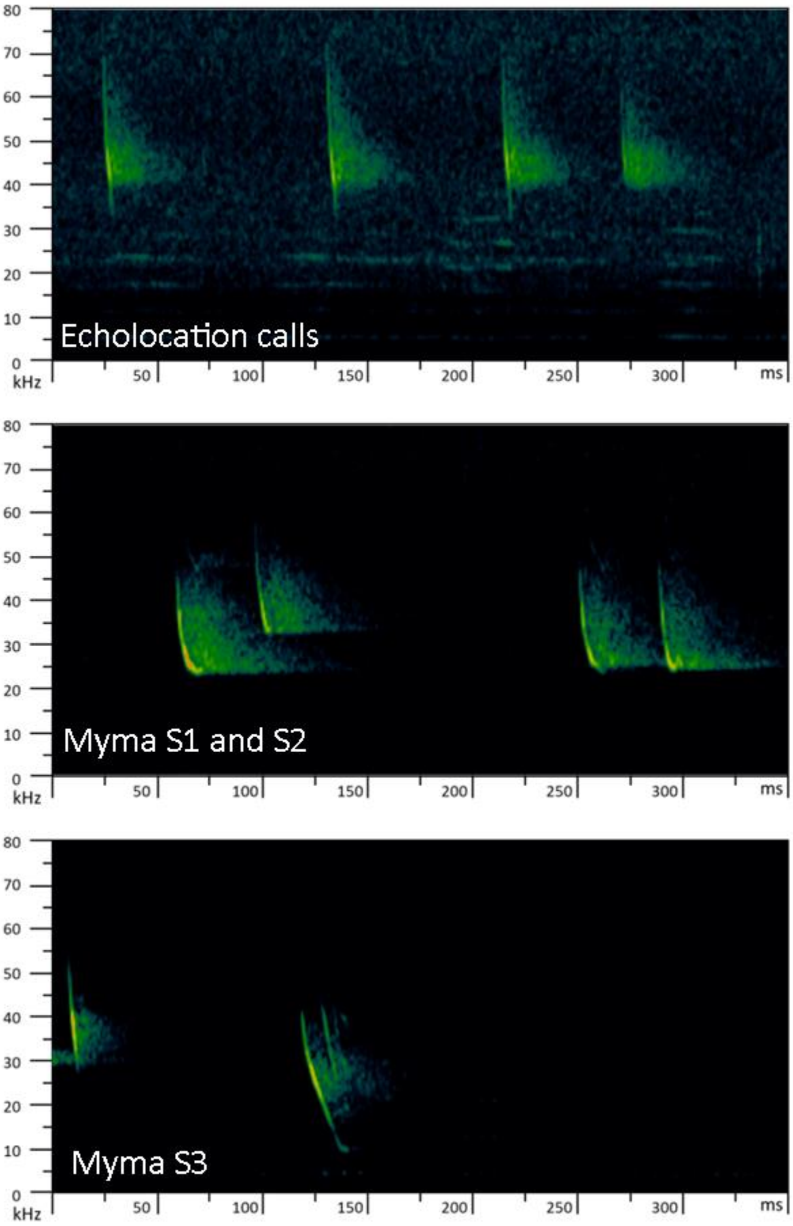

Figure A4. Echolocation sequences and social vocalisations of the southern myotis *Myotis Macropus*.

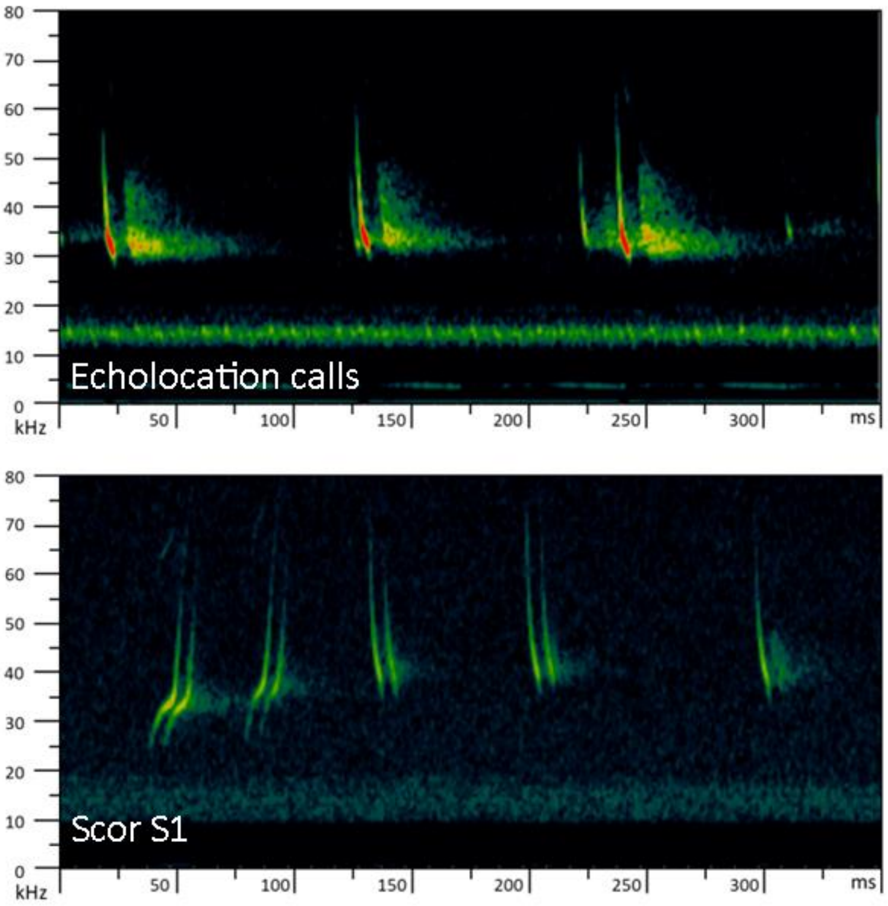

Figure A5. Echolocation sequences and social vocalisations of the eastern broad-nosed bat *Scotorepens orion*.

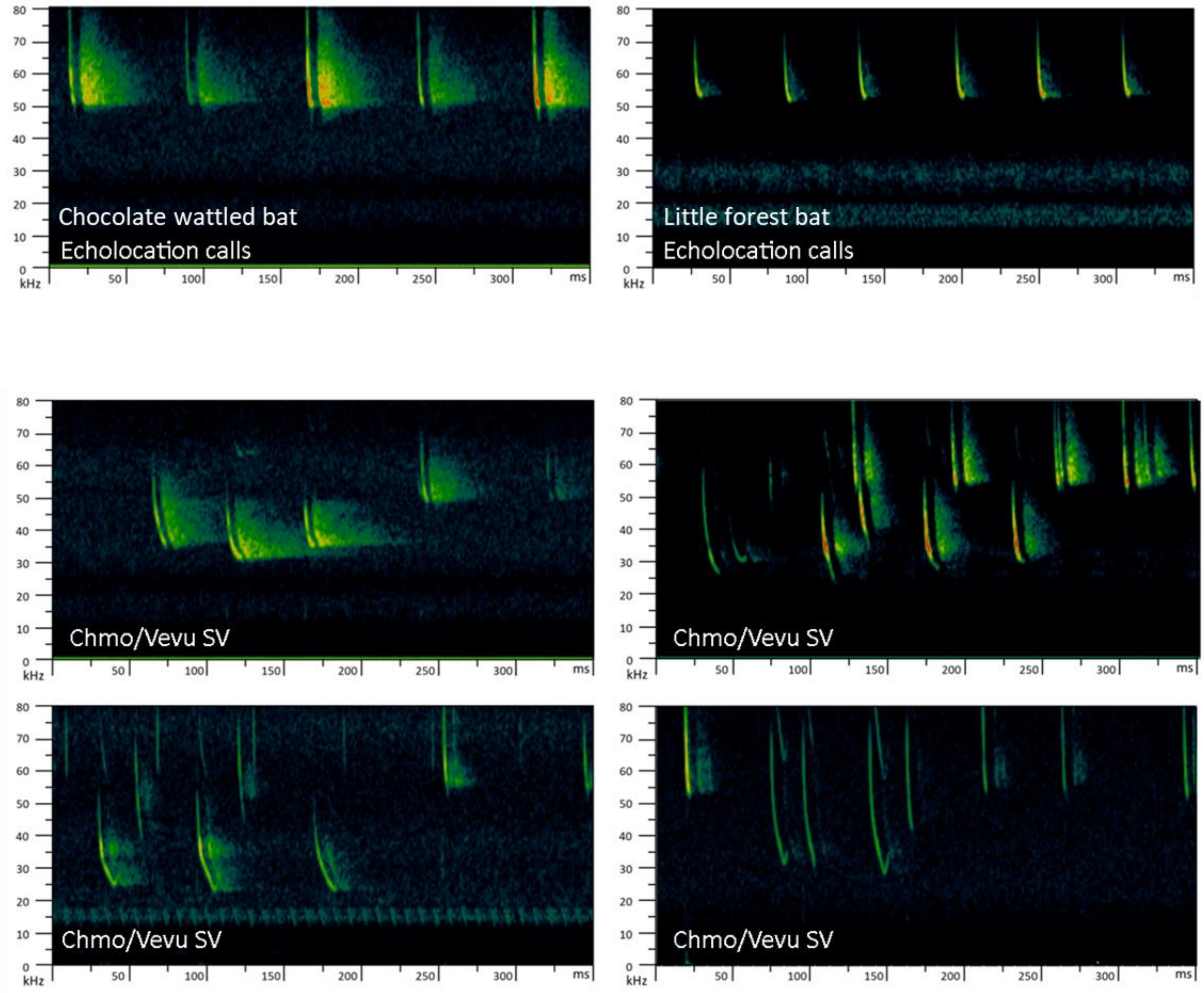

Figure A6. Echolocation sequences of the chocolate wattled bat *Chalinolobus morio* and the little forest bat *Vespadelus vulturnus*, along with similar unidentified social vocalisations (SV).

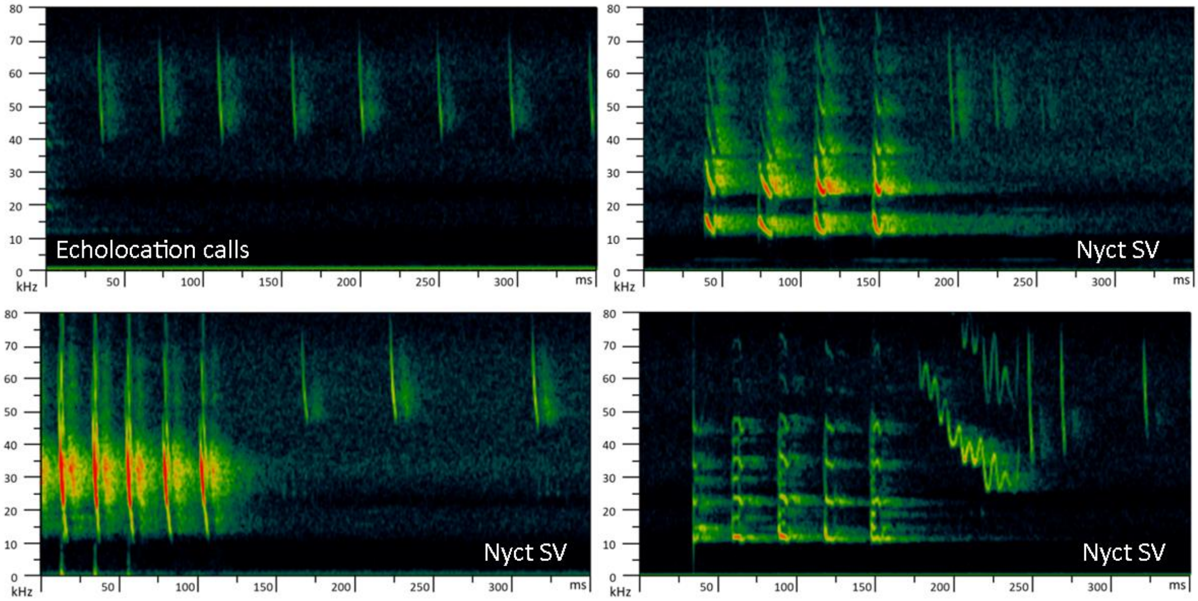

Figure A7. Unidentified echolocation sequences of Nyctophilus species (*N. geoffroyi* and *N. gouldi*) and their associated social vocalisation (SV) sequences.