Too many men in the room? The cost of overcrowding for gregarious male cave-dwelling bats

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Abstract

1. Bats are known for their gregarious social behaviour, often congregating in caves and underground habitats, where they play a pivotal role in providing various ecosystem services. Despite their ecological importance, studying bat behaviour remains an underexplored aspect of bat conservation.
2. We explore the costs and impacts of overcrowding on bat social behaviour. This study examined variations in bat behavioural patterns between two distinct groups: aggregated and non-aggregated male *Rousettus amplexicaudatus*, within the Monfort Bat Cave Sanctuary on Mindanao Island, Philippines.
3. We found significant disparities in the frequencies of various bat behavioural activities, particularly in terms of aggression and movement, between these two groups. Increased aggregation was closely related to negative social behaviour among bats.
4. Conversely, positive social behaviours, such as sexual interactions and grooming, were more prevalent in less crowded conditions. The disparities in bat behaviour with an apparent decline in bat social behaviour as a consequence of overcrowding, with more aggressive behaviours emerging, aligns with the *'behavioural sink hypothesis'.*
5. Our study underscores the significance of considering the quality of habitat and the availability of resources in the management and conservation of bat colonies, as these factors may reduce the occurrence of detrimental social behaviours in colonies with high population density by providing alternative habitats.

Keywords: *Aggression, Antipredator behaviour, Caves, Ethology, Group size effects*

Introduction

Bats are one of the most widely distributed mammalian taxa worldwide, with a range of habitats and diverse roles within ecosystems. Given the high diversity of more than 1400 described species, bats may be specialists or generalists in diet, habitat, and roost sites (Simmons & Cirranello, 2020; Tanalgo et al., 2022). Caves are one of the most important roosting sites for roughly half of the species (679, 48%), which serve as sites for many bat species, likely because they reduce the risk of predation and provide thermally stable environments in which bats can safely shelter (Furey & Racey, 2016; Tanalgo et al., 2022). Large proportions of cave-dwelling bats are hyper-social, and their guano can form the basis of food webs in cave communities (Meierhofer et al., 2023). Colonies can host millions of individuals, and some species cluster in tight groups (Phelps et al., 2016; Barros et al. 2020). However, this reliance on caves means that loss of roost sites or high disturbance may lead to displacement or increased stress and crowding within cave sites. Furthermore, roost selection within cave environments not only relate to species-specific preferences but within a species may relate to reproductive modes and status, as well as dominance level (Ho & Lee, 2003; Lima & O'Keefe, 2013).

Most species have an optimal roost type and inter-individual spacing. Many species utilise darker spaces of the cave that are further from the entrance to the roost, and larger or more aggressive species may be more likely to have more space between individuals to reduce stress and the possibility of overheating (Medina-Bello et al., 2023; Rodrigues et al., 2003). Multiple variables can influence the well-being of roosting bats, including the structure of the roosts, surrounding ecological conditions, and anthropogenic interventions within cave ecosystems (Nagy & Postawa, 2011; Sedlock et al., 2014). Thus, factors that change interactions between individuals could increase stress and have consequences for individual bat health (Allen et al., 2011; Zagmajster, 2019) and susceptibility to disease and parasitism (Hayman et al., 2013; Webber et al., 2015).

However, while efforts to understand the ecology of cave-dwelling bats are growing (Tanalgo et al., 2022), most studies on bat cave responses to environmental change have focused on their responses to ecological conditions and changes (Cajaiba et al., 2021). However, there has been little research on their behavioural responses to intrinsic and extrinsic factors. However, although almost half of the bat activity cycle is spent roosting, our understanding based on empirical data of their density-dependent responses to conspecifics remains limited for many species (e.g., stress behaviour, overcrowding, and diseases) (Chaverri et al., 2018; Hoyt et al., 2021). These factors are interesting and important, given that most mammals become more susceptible to pathogens when stressed (Woolhouse et al., 2001); thus, understanding how bats react to suboptimal conditions presents a major challenge in ecology.

Most investigations have centred on non-cave bat species in their natural roosts or enclosures (Thomson et al. 1998; Hengjan et al. 2017; Garca-Rawlins et al. 2020). Thus, little work has been done to explore these phenomena in bats, likely due to the difficulty and expense of studying bats in the wild (Revilla-Martín et al. 2020; Reeder et al. 2004). Studies investigating bat responses to intrinsic and extrinsic factors typically involve measuring stress levels using hormones requiring blood or urine samples (Allen et al., 2011; Davy et al., 2017; Reeder et al., 2004). Therefore, less intrusive and economically efficient techniques are required to understand better how bats react to stress under natural conditions. Overcrowding can increase negative interaction rates body temperature and force some individuals to roost in suboptimal locations. However, whilst '*behavioural sink hypothesis*' effects have been known in lab experiments in other mammals (Ramsden, 2009), few natural conditions are likely to lead to comparable patterns of overcrowding which could lead to such consequences in natural conditions. The loss of roosts could force more than an optimal number of individuals to use a single cave, and thus the differing density in roosts within the cave provides the perfect arena to test these theories under natural conditions.

Tropical environments often host the most diverse bat assemblages; The Philippines is home to at least 78 bat species, and almost 40 species are cave dwellers (Lawrence et al., 2010; Tanalgo & Hughes, 2018). The world's largest colony of *Rousettus amplexicaudatus* is estimated to be approximately 1.8 million individuals in the Monfort Bat Cave Sanctuary in the Island Garden City of Samal in Davao del Norte, Philippines (Carpenter et al., 2014). The bat population at the roost can differ significantly between the walls and the ceiling. On average, the colony has a 427.9 9 bats/m^2 density, but the estimated density in the Monfort Bat Cave Sanctuary is predicted to be higher (Carpenter et al., 2014). Our previous field observations have led us to speculate that bats that roost in cave areas with a higher density of individual aggregations within their colonies exhibit more pronounced 'aggressive' and 'restless' behaviours throughout the day (Tanalgo et al., 2020).

The Monfort cave is the least disturbed cave in the Philippines, leading to overcrowding. This condition forces bats to roost in open conditions, where the avoidance of predators provided inside caves is not possible thus these large groups may also need to remain active to explore any signs of imminent predator danger (Lima, 1995; Lima & O'Keefe, 2013). Interestingly, there are no published studies that assess bat social behaviour (i.e., negative and positive) in response to gregarious behaviour (e.g., overcrowding in colonies), and only a few caves considered to hold a hyper population, e.g., Bracken cave in the United States and Monfort cave in the Philippines.

However, it should be noted that establishing what constitutes overcrowding for specific species is challenging due to the lack of data. Testing how behaviours vary based on overcrowding remains an interesting topic which requires further research, especially as increased negative interactions which may increase as a consequence of overcrowding (sometimes described as a 'behavioural sink') can have major outcomes for health.

We investigated the patterns of diurnal behaviour of *Rousettus amplexicaudatus* in two different parts of the cave where there were different roosting densities (aggregated vs. non-aggregated). First, we assessed whether there was a notable disparity in incidents within bat behavioural units between aggregated roosting colonies and those that did not. Following this, we examined the correlations between the incident frequencies of these behavioural units. Lastly, we made predictions regarding the connection between the frequency of incidents within behavioural categories and aggregations and their impact on the occurrence of 'positive' and 'negative' social behaviours in roosting bats. We expect that greater colony aggregation is related to increased aggressive and negative behaviour in male cave-roosting bats. These interactions likely result from both over-heating due to increased density, and possibly even irritability due to repeated contact and disturbances. At the same time, other behavioural categories are associated with male social behaviour.

Materials and Methods

Study sites and species

Our observations were carried out within the Monfort Bat Cave Sanctuary (MBCS), situated on Samal Island in the Garden City of Samal, Davao del Norte, Philippines (7.050°N and 125.733°E) (Figure 2), and the data collection period spanned from August 2018 to March 2019. The Monfort family privately owns the cave sanctuary and has been responsible for its conservation for nearly a century. This cave has gained international acclaim and is documented in the Guinness Book of World Records for its estimated population of approximately 1.8 million individuals of *R. amplexicaudatus* (based on 2018 estimations). These bats are known to densely inhabit the walls and ceiling, with an average occupancy of approximately 60 bats per square foot. The cave is approximately 150 m long, 3 m high, and 5 m wide. In particular, the cave is open to ecotourism and scientific research, though visitors are not allowed to enter the cave **(Figure 1)**.

Geoffroy's Rousette fruit bat (*Rousettus amplexicaudatus*) is a colony-forming medium-sized fruit bat with a body size of approximately 128-154 millimetres and a forearm of roughly 80-92 millimetres. This species is widely distributed throughout Southeast Asia and is mainly found in caves in karstic environments. Unlike other fruit bats, *R. amplexicaudatus* has enhanced auditory acuity, an acute sense of smell, and relatively good eyesight. Collectively, these sensory attributes enhance aerial manoeuvrability, particularly during nocturnal flight.

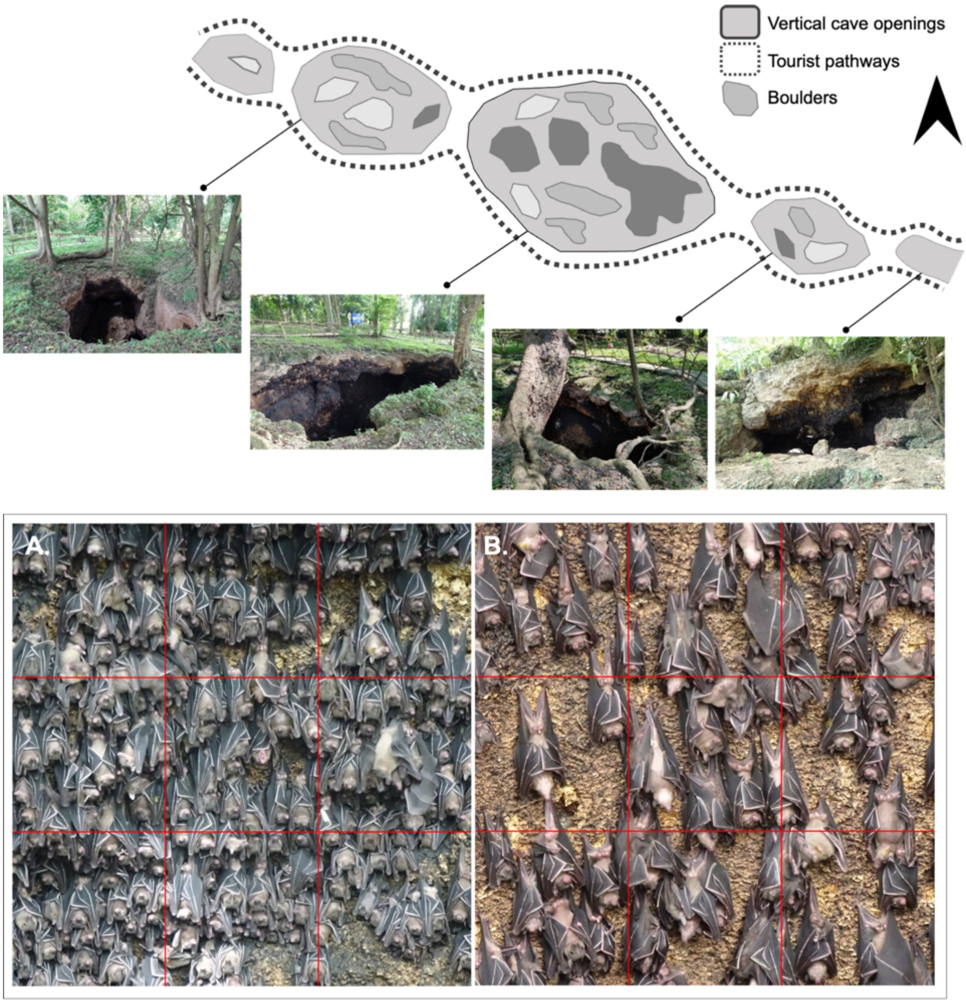

Figure 1. Cave map and entrances (upper photograph) showing two fruit bat colony aggregations in Monfort Bat Cave Sanctuary (MBCS): (a) aggregated and (b) non-aggregated roosting areas. The red grid lines indicate the sampling grid of the behavioural scan.

Video recordings

Based on the density of individuals within the observed area, we classified bat aggregations into two distinct categories ‘aggregated’ and ‘non-aggregated’. Aggregated colonies are described when bat individuals cluster together to form a sizable colony. Conversely, non-aggregated groups were characterized by evenly spaced individuals (at least 1-meter from each other) within their roosting area, lacking significant clustering (Figure 2AB). We filmed the diurnal behaviour of *R. amplexicaudatus* using a Sony™ DSC-WX500 digital camera (maximum 30× optical zoom) on the two aggregations.

Within each colony aggregation, our filming sessions covered an approximate area of 1 × 1.5 metres within the roosting site. We filmed colonies once every hour and each filming session lasted for 10 min every hour from 07:00 to 17:00 (for example, Connell et al. 2006). To minimise the influence of observers on bat behaviour, the observer wore neutral clothing and was located at least 5 to 10 metres from the roosting colonies.

Behavioural ethograms

Cave bat videography was observed and timed using Behavioural Observation Research Interactive Software (BORIS) (Friard & Gamba, 2016). Behaviour was recorded from the recordings in each observation dataset. Behaviour observation was replicated by dividing the observed colony into 3 × 3 plane grids in the BORIS interface (http://www.boris.unito.it/). We then randomly selected a single individual from the three grids, designating them as focal subjects for behavioural observation. Although it is challenging to confirm that we tracked the same specific individual within the same grid all day, our initial observations indicated that bats tend to remain within the same colony throughout the day.

The behaviours recorded included sexual activity, self-maintenance, thermoregulation, positive social behaviour, negative social behaviour, territorial behaviour, and non-categorised behaviour following Friard & Gamba (2016) and Hengjan et al. (2017) (Table 1). We only included and analysed complete diurnal observations in the colonies and excluded recordings disturbed by crow and varanid predators (e.g., Tanalgo et al. 2020) or weather conditions.

We exported and cleaned the data from BORIS and quantified the frequency (count) of incidents of each behavioural unit and category by tallying the number of times a specific behaviour occurred within the designated time frame of observation. Similarly, we determined the duration of each behavioural category and unit by calculating the ratio of the observed time (t, seconds) for each behavioural unit to the total observation period (T, seconds) (Connell et al., 2006; Hengjan et al., 2017). In our final analysis, we only analysed the frequency of incidents because we found a strong correlation between frequency and the duration of the behaviour (Supplementary Data S1).

Table 1. Ethogram of the diurnal behaviour observed in colonies of *R. amplexicaudatus.*

Behaviour Category	**Behavioural Unit**	**Description**
Sexual activities	Courtship/Fellatio	The male approaches the male and licks the genital area of the conspecifics.
	Masturbation	The male starts to lick his penis, leading to an erection, continuously licking the erect penis

		for more than one minute without urination and ejaculation.
Self-maintenance	Self-grooming	Licking wing membranes or occasional bouts of the genitals, including the head.
Thermoregulation	Wing flapping	Fanning body on the wing membrane.
Positive social behaviour	Mutual grooming	Licking the body of the conspecifics.
	Play	Mock biting or mock wrestling with an absence of vocalisation.
Negative social behaviour	Aggression	Aggressive vocalisations, wing shaking, chasing, biting, and/or fighting between individuals.
	Hang alert	They are hanging bipedally or monopedally with eyes open and ears moving.
Relaxed behaviour	Sleeping	Immobile, eyes closed, wings wrapped around the body.
	Hanging relax	Hanging bipedally or monopedally with wings folded or wings open and eyes open, looking around.
	Movement	Moving along a cave wall without flying.
	Excretion	Turning the body upright to urinate and/or defecate.

Data analysis

We found that none of our datasets conformed to the normal distribution assumption. We used the Mann-Whitney U test to compare whether there was a significant difference in the frequency of incidents of behavioural units between the aggregated and non-aggregated groups. A separate Kruskal-Wallis test was then performed to test the difference in the frequency of incidents between behavioural units between the aggregations. Subsequently, we used Kendall's τ-B correlation analysis to examine the correlation of incident frequency in behavioural categories. Furthermore, we constructed a complete Poisson generalized linear regression (GLM) to predict the relationship between the frequency of incidence of positive and negative social behaviour of bats. We included bat colony aggregation, frequency of incidence of sexual behaviour, self-maintenance, thermoregulation, and relaxed behaviour.

All data and statistical analyses were performed using the open software Jamovi2.3.22 (The Jamovi Project, 2023). Data visualisations were performed with GraphPad Prism 9 (GraphPad Prism, 2022). Statistical significance was set at $p \leq 0.05$. Data were presented as mean ± standard deviation (SD) or 95% CI.

Ethical Considerations

We adhered to all relevant international, national, and institutional regulations that govern the ethical treatment and use of animals. Under the Philippine and Chinese law, no specific approval was required for this non-invasive study. We strictly adhered to the protocols and guidelines established by the Animal Behaviour Society (ABS) and the

Association for the Study of Animal Behaviour (ASAB) recommendations for animal handling in behavioural research and teaching (ASAB Ethical Committee & ABS Animal Care Committee, 2022).

Results

We analysed a total of 59,400 seconds of observations from 99 male focal individuals in Monfort bat cave (aggregated = 60; non-aggregated = 39). Our study found significant variation in the time budget allocation of bat behavioural units between aggregations (**Figure 2**). Among aggregated colonies, sleeping was the most frequent behaviour throughout the day (27.20%), while hanging relax was more dominant among non-aggregated colonies (33.73%). Sleeping was the second most dominant behaviour observed in non-aggregated colonies (24.73%). We found the highest difference between aggregation in behavioural incidents in wing flapping (93.57%) and aggression behaviour (89.32%) (**Figure 2A**).

We compared the difference in behavioural units between aggregated and non-aggregated groups. We found that the five behavioural units differed significantly between aggregations (**Figure 3**). Aggregated groups (mean = 3.18 ± 2.63) had a higher frequency of individual movement behaviour compared to non-aggregated groups mean = 1.85 ± 1.65) (MWU test = 827.50, $p = 0.01$). Aggregated bats (mean = 0.88 ± 1.15) were also more aggressive compared to those in non-aggregated groups (mean = 0.03 ± 0.16) (MWU test = 626.50, $p < .0001$). Aggregated colonies (mean = 0.37 ± 0.84) also had a higher incidence of dominant wing flapping behaviour compared to non-aggregated colonies (mean = 0.03 ± 0.16) (MWU test = 963, $p = .01$). Furthermore, the incident frequency of the behavioural units differed significantly between the aggregated and non-aggregated colonies (KW test, H = 460.5, $p < 0.0001$ and KW test, H = 327.4, $p < 0.0001$, respectively).

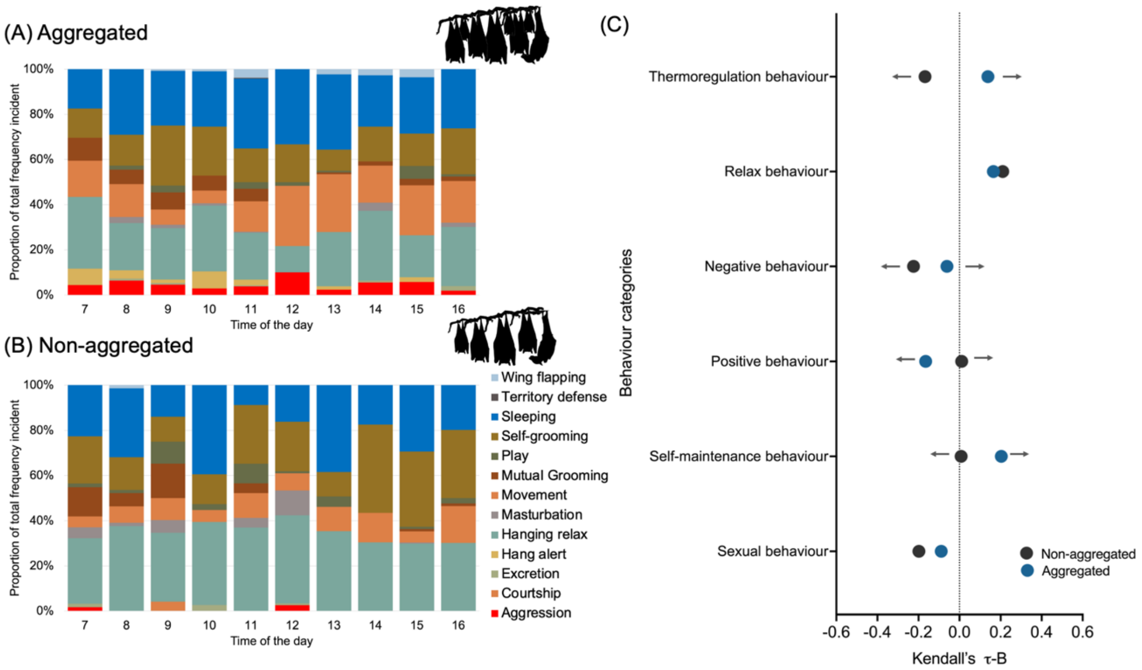

Figure 2. Comparison of the proportion of the incident frequency of behavioural units (A and B) and the correlation of behavioural categories over the day.

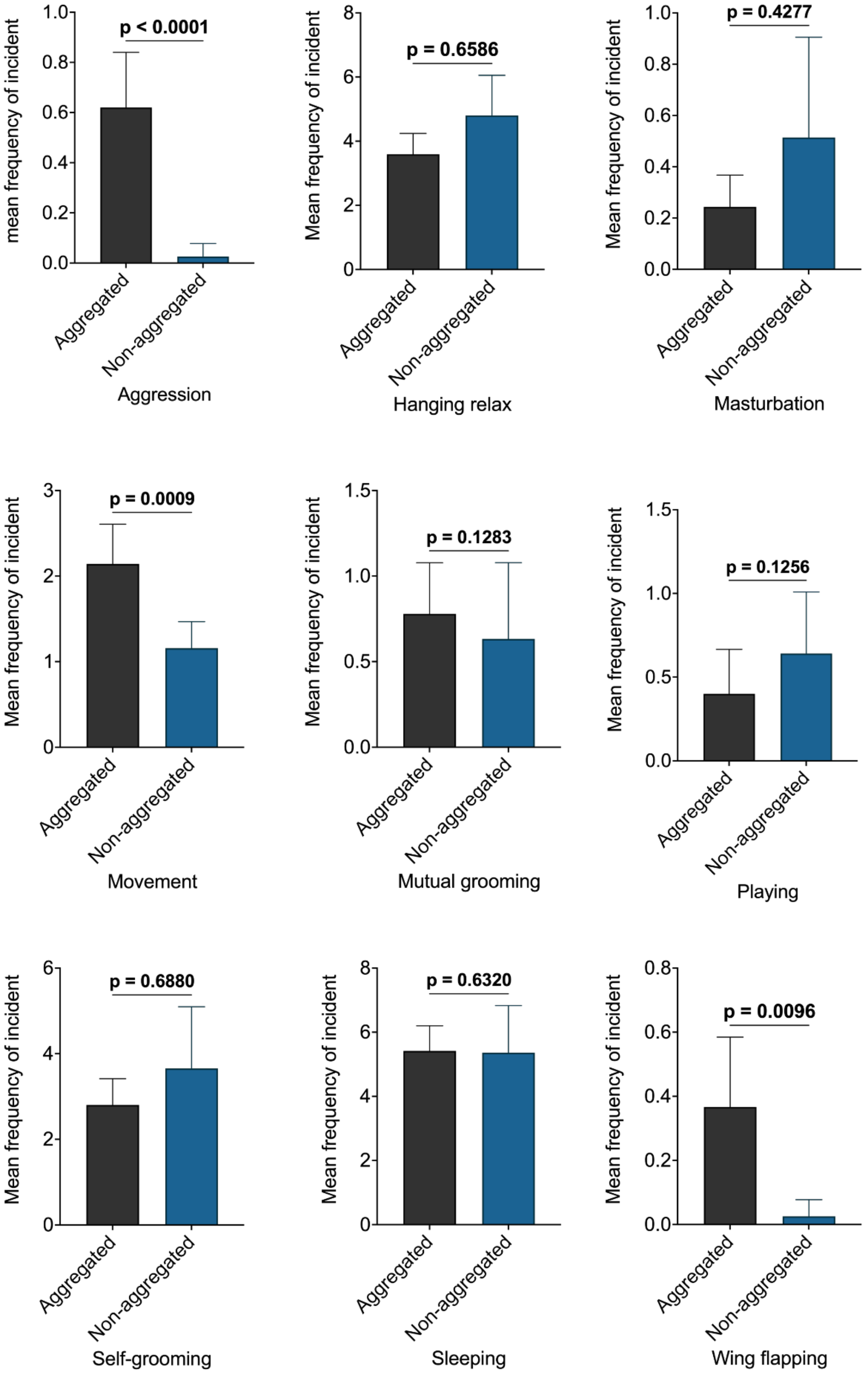

Figure 3. A bar graph shows the differences in the mean incident frequency between colony aggregations (A) and behavioural units (B).

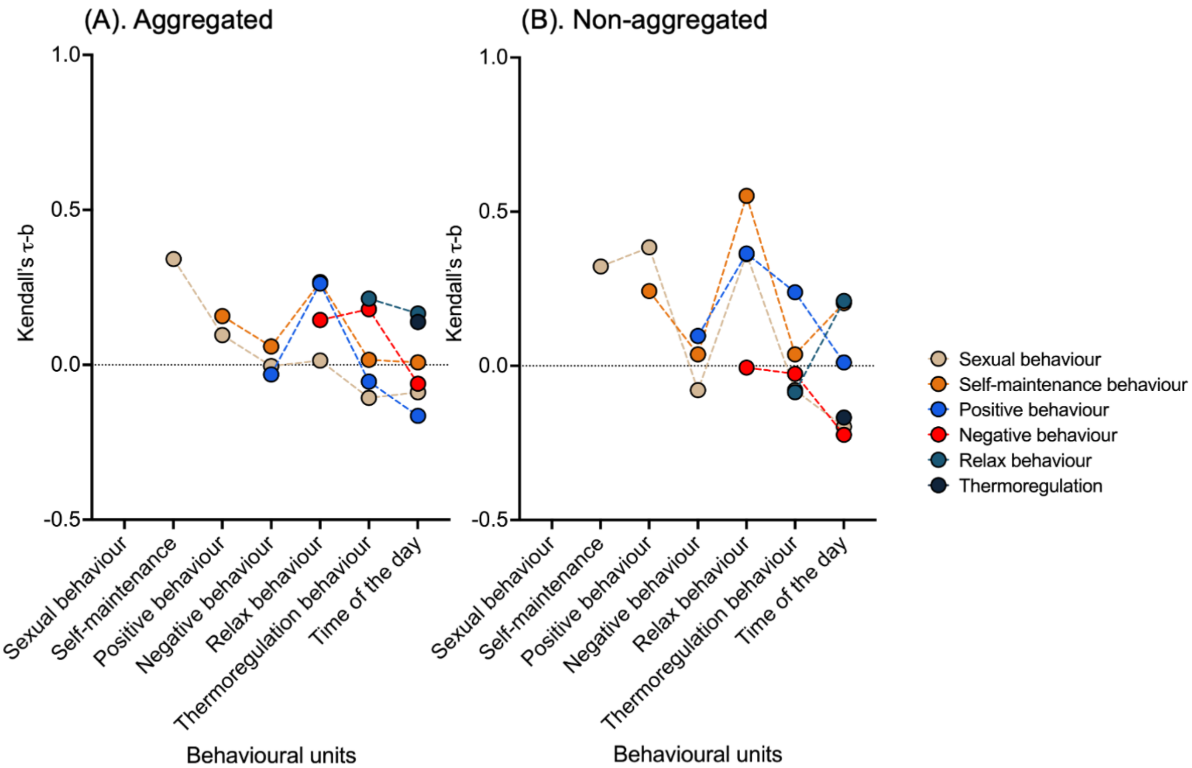

Figure 4. Visualised correlation (Kendall's τ-B) plot of behavioural units in (a) aggregated and (b) non-aggregated colonies of *R. amplexicaudatus*.

Although we did not find statistical significance in the correlation between time of day and the frequency of behavioural categories, we observed a contrasting relationship in all behavioural categories except relaxation behaviour (**Figure 4**). For example, aggregated colonies have increased thermoregulation, negative behaviour, and less self-maintenance throughout the day. When comparing each colony group, bats in the aggregated groups showed a positive and significant correlation between self-maintenance and sexual behaviour (Kendall's τ-B = 0.341, *p* = 0.0022), while a similar correlation pattern was observed in relaxation behaviour with self-maintenance (Kendall's τ-B = 0.267, *p* = 0.005), and positive social behaviour (Kendall's τ-B = 0.262, *p* = 0.01) (**Figure 4A**). Conversely, we found a different correlation pattern within the non-aggregated group. We observed that sexual behaviour was positively correlated with self-maintenance (Kendall's τ-B = 0.322, *p* = 0.0164), positive social behaviour (Kendall's τ-B = 0.384, *p* = 0.0082), and relaxation behaviour (Kendall's τ-B = 0.362, *p* = 0.0063). Furthermore, relaxation behaviour was significantly and positively correlated with self-maintenance behaviour (Kendall's τ-B = 0.551, *p* < 0.0001) and positive social behaviour (Kendall's τ-B = 0.364, *p* = 0.0045) (**Figure 4B**).

We constructed two separate generalised linear models to predict the frequency of occurrence of the behaviour (Table 2). Aggregation was significantly associated with an increase in the incidence of negative social behaviour ($\beta = 3.997$, $p < 0.0001$). Interestingly, we found that increased incidents of sexual behaviour were positively associated with positive social behaviour among bats ($\beta = 0.114$, $p = 0.0097$). Although not statistically significant, we found a contrasting relationship between sexual behaviour and negative social behaviour ($\beta = -0.126$, $p = 0.5775$).

Table 2. Results of the generalised linear model (GLM) predicting the association of the frequency of (A) positive social behaviour and (B) negative social behaviour with colony aggregation and other behavioural categories.

A. Positive social behaviour	**Estimate**	**SE**	**Lower**	**Upper**	***p***
(Intercept)	0.106	0.103	-0.104	0.3	0.303
Aggregated (Non-aggregated)	0.278	0.204	-0.116	0.685	0.172
Sexual behaviour	**0.114**	**0.044**	**0.025**	**0.198**	**0.010**
Self-maintenance behaviour	-0.012	0.022	-0.057	0.03	0.590
Relaxation behaviour	**0.084**	**0.02**	**0.044**	**0.124**	**< .0001**
Thermoregulation behaviour	-0.211	0.149	-0.529	0.059	0.156

B. Negative social behaviour	**Estimate**	**SE**	**Lower**	**Upper**	***p***
(Intercept)	-1.694	0.505	-3.131	-0.938	0.0008
Aggregated (Non-aggregated)	**3.997**	**1.012**	**2.476**	**6.873**	**< .0001**
Sexual behaviour	-0.126	0.226	-0.612	0.27	0.578
Self-maintenance behaviour	0.018	0.041	-0.065	0.096	0.657
Relax behaviour	0.031	0.025	-0.018	0.078	0.204
Thermoregulation behaviour	0.032	0.129	-0.238	0.272	0.807

Discussion

The diurnal activities of bats have been investigated in a number of species, with a particular focus on *Pteropus* species, both in their natural habitats and in captivity (Hengjan et al., 2017; Manandhar et al., 2018; Ramanantsalama et al., 2019; Roy et al., 2020; Thomson et al., 1998). There is also a growing interest in the behavioural investigation of cave-dwelling bats and their social interactions (Cardiff et al., 2012; Ramanantsalama et al., 2019). However, there is limited information on how bats respond to intrinsic factors such as overcrowding. Our study aimed to understand the differences in behaviours between aggregated and non-aggregated groups of bats. Variation in various activities in the two groups suggests that social dynamics and environmental factors may play a crucial role in shaping the behaviour of these male bats, with possible implications for individual health (Hengjan et al., 2017; Manandhar et al., 2018).

Sleeping was observed to be a common behaviour in both aggregated and non-aggregated colonies. In aggregated colonies, sleeping was the most frequently observed behaviour throughout the day, comprising more than a quarter of the total observed behaviour, though was not significantly different in frequency between the two groups. Various connections have been proposed between sleep duration and social behaviour (Harding et al., 2022). The frequency of sleep that occurs consistently throughout the day is consistent with the natural circadian rhythms of bats, as they are primarily nocturnal animals. This dominance of sleeping behaviour among colonies may indicate the importance of rest and energy conservation within these groups after a night of activity (Harding et al., 2022; Roy et al., 2020). Bats in aggregated colonies can prioritise sleep to prepare for nocturnal activities, such as foraging and mating (Amichai et al., 2013; Harding et al., 2022; Lewis, 1996; Muñoz-Romo, 2006) and to conserve and recover energy spent on increased movement and interactions within the aggregated colony. One primary advantage of forming groups is to reduce the risk of predation (Beauchamp, 2001, 2007; Wang et al., 2015), and this reduction in predation risk is believed to affect sleep duration (Lendrem, 1983; Lima et al., 2005; McBlain et al., 2020). However, it is worth noting that in our study, we did not observe a significant difference in sleep frequency between different aggregations. But this can be associated to the presence of aggressive predators in the bat cave, including crows entering the caves and varanids that predate resting bats. In a behavioural study of gulls (Beauchamp, 2009) observed that individuals even within a smaller group size (i.e., less crowded) were more likely to have interrupted sleeping bouts to scan their surroundings when their larger group neighbours were alert. This proposes that animals perceive threats similarly and would ‘copy’ the vigilance of their neighbours, which may help them to assess the risk of predation better (Beauchamp, 2009).

In contrast, hanging relax was more dominant in non-aggregated colonies, comprising 33.73% of the observed behaviours. This indicates that solitary or loosely associated bats may exhibit a different energy allocation strategy, possibly involving increased vigilance while at rest to defend against potential threats (Harten et al., 2018; Kelm et al., 2021; Markus & Blackshaw, 2002). Moreover, it is notable that sleeping was the second most dominant behaviour observed in non-aggregated colonies (24.73%). This denotes that even in more solitary settings, sleep remains a crucial aspect of a bat diurnal routine (Harding et al., 2022; Lewis, 1996; Roy et al., 2020).

We found a stark difference in behavioural incidence between aggregated and non-aggregated colonies, particularly in wing flapping and aggressive behaviour. Wing flapping showed a 93.57% difference in behavioural incidents within the aggregated colonies versus non-aggregated, which exhibited a strikingly lower incidence of wing flapping (6.43%), likely due to both increased temperatures due to the proximity of individuals and possibly aggressive posturing in aggregated settings. This difference in behaviour suggests a heightened level of physical activity within large-sized groups that is attributed to the proximity of individuals, potentially leading to increased interaction and movement. Overcrowding increases colony temperature (Arends et al., 1995), and the dominance of wing-flapping behaviour among bat individuals in more aggregated colonies facilitates thermoregulation. Bats have several mechanisms to help dissipate heat and prevent their body temperature from rising to lethal levels (Reher & Dausmann, 2021). These mechanisms include the special membrane structure of their wings and the increased airflow created by flapping their wings (Stones & Wiebers, 1965). In addition, aggregated colonies exhibited a significantly higher incidence of wing-flapping behaviour, which is often associated with communication or asserting dominance within a group and may be more prevalent in densely populated aggregations where hierarchy and social status are essential for resource allocation and mating opportunities (Beauchamp, 2007; Kerth, 2008).

Aggregated groups exhibited a higher frequency of individual movement compared to their non-aggregated counterparts, possibly due to disturbing each other and being hotter and, therefore possibly uncomfortable (Hengjan et al., 2017; Ramanantsalama et al., 2019). Our study also revealed that bats in aggregated colonies (89.32%) displayed a higher level of aggression compared to those in non-aggregated groups. Our findings highlight the importance of understanding social interactions within bat colonies, as such heightened movement and increased aggressive behaviour could be attributed to the need to navigate within densely populated aggregations, potentially related to resource acquisition, space competition, or territorial disputes within the close confines of the aggregation (Hengjan et al., 2017; Kilgour & Brigham, 2013a; Ramanantsalama et al., 2019). For example, large brown bats (*Eptesicus fuscus*) exhibited higher levels of aggression within groups, which were associated with improved competitive abilities for resources (Kilgour & Brigham, 2013b).

Intrinsic correlates of gregarious bat social behaviour

The lack of a strong correlation between time of day and behavioural categories suggests that bats in our study system did not show clear diurnal patterns in their behaviour. This indicates that factors beyond time, social interactions, and physiological needs are crucial in shaping their behaviour. In the aggregated colonies, we observed a noticeable pattern between time of day and various behavioural categories. For example, thermoregulation, negative behaviour, and self-maintenance exhibited an increasing trend throughout the day. This may be because bats in aggregated colonies may adjust their behaviour in response to a change in daily ambient temperature, possibly to optimise thermoregulation and self-maintenance, and given increased heat in larger bodied bats, they may need to work harder to stay cool as temperature increases (Stones & Wiebers, 1965). The positive and significant correlation between self-maintenance and sexual behaviour within aggregated groups is interesting. It may imply that bats in these colonies allocate their energy resources strategically, as self-maintenance behaviour is crucial for individual health and reproductive success. A similar correlation pattern was also observed in relaxation behaviour, suggesting a potential connection between relaxation and energy conservation strategies (Luo et al., 2021). Furthermore, the positive correlation between relaxation behaviour and thermoregulation behaviour indicates that bats in aggregated colonies may alternate between cooling down and resting, whilst non-aggregated bats are able to sleep longer (Becker et al., 2012; Komar et al., 2022).

In contrast to aggregated colonies, non-aggregated groups exhibited different correlation patterns between time of day. For example, the positive correlation between sexual behaviour and self-maintenance, positive social behaviour, and relaxation behaviour hints that the animals in non-aggregated colonies may prioritise reproductive activities throughout the day (Byerly et al., 2021). This could be related to the increased autonomy and less crowded conditions in non-aggregated settings, allowing bats to engage in mating and other social interactions as needed. Additionally, the positive correlation between relaxation behaviour and self-maintenance, as well as positive social behaviour, implies that bats in non-aggregated colonies might use relaxation to recharge and engage in social interactions during their active hours, which could enhance their overall fitness and well-being.

The current study provides valuable insights into the complex dynamics of social behaviour within overcrowded bat colonies. Two key behavioural findings shed light on the interplay between aggregation, social behaviour, and the potential factors influencing these relationships. One of the notable findings is that aggregation was significantly associated with increased negative social behaviour among bats, which evidently has costs, including increased risk of injury and even pathogen spread. Negative social behaviours may include competition for resources, territorial disputes, or conflicts within the group (O’Connor et al., 2015). This finding aligns with previous research on social animals, where increased individual proximity and interaction can lead to heightened aggression or conflict over limited resources (Dai et al., 2018; Fernandez et al., 2014; Holekamp & Strauss, 2016; O’Connor et al., 2015).

Our observation aligns with previous research suggesting that high population density and proximity can lead to heightened competition for resources, such as roosting sites and foraging opportunities, which may consequently escalate social conflicts within bat colonies. The crowded conditions within these more densely aggregated colonies may intensify intra-specific competition, potentially driving negative interactions among individuals. Previous observations on pigs showed that reducing the space allotted per individual increases the frequency of aggressive interactions, except during feeding, where the decrease in space primarily influenced the quality of interactions (Ewbank & Bryant, 1972). This implies that densely populated zones, particularly around the feeding area, might disrupt communication patterns and potentially undermine dominance-subordination relationships.

We propose that our findings linked to the ‘behavioural sink’ hypothesis, initially introduced by ethologist John B. Calhoun in his famous experiments with rodents in the mid-20th century (Calhoun, 1973). This suggests that when population density exceeds a certain threshold, behavioural and social patterns among the individuals can deteriorate dramatically. These behavioural changes often involve increased aggression within the population. Our findings reveal a similar pattern of increased negative behaviour in overcrowded bat populations, which offer substantial support for the link to the ‘behavioural sink’ hypothesis concept in the context of social animals such as bats. In situations of overcrowding, it appears that the natural social dynamics of bats are disrupted, leading to higher levels of aggression and stress. Such negative behaviours may not only impact individual well-being but can also have far-reaching consequences for the overall health of the bat colony, and could perpetuate the spread of pathogens (Eby et al., 2023; Ruiz-Aravena et al., 2022).

Understanding the ‘behavioural sink’ hypothesis in the context of bats and other social species is useful for conservation efforts and population management, which highlights the importance of considering habitat quality and resource availability in the context of bat colony management and conservation efforts, as these factors could mitigate the prevalence of negative social behaviours in densely populated colonies.

Another particularly intriguing finding was the contrasting relationship between the incidence of sexual behaviour and positive social behaviour among *Rousettus amplexicaudatus*. Positive social behaviour could encompass grooming, affiliative interactions, or cooperative behaviours. Sexual behaviour can be regulated within the colony to minimise conflict and maintain overall social harmony (Alves et al., 2013). In addition, sexual behaviour may act as a bonding mechanism, fostering cooperation and coordination among individuals (Díaz-Muñoz et al., 2014; King et al., 2021). For example, Tan et al. (2017) found that fellatio among short-nosed fruit bat *Cynopterus sphinx* facilitate longer copulation time during sexual activities. A similar behaviour was also observed among colonies of Indian flying fox *Pteropus gigateus,* showing that oral sex increases positive sexual behaviour, however same sex-interactions have not been well explored in bats, but play roles in bonding in other social mammals (Vasey et al., 2007; Archie et al., 2014). Furthermore, when a group becomes overcrowded, individuals often face challenges related to resource competition, increased stress, and restricted access to potential mates. Hence, sustaining sexual behaviour within an overcrowded group of bats holds significant implications for maintaining reproductive success within the population (Maruthupandian & Marimuthu, 2013; M. Tan et al., 2009). Understanding the mechanisms by which sexual behaviour influences positive social behaviour could have important implications for our comprehension of the evolution of social behaviours in bats and other social animals. Yet, more research with a larger sample size or a more focused investigation of specific aspects of sexual and negative social behaviours is needed to draw definitive conclusions.

Another useful idea for future studies on overcrowding could involve investigating the potential connection between physiological stress levels within bat colonies and the heightened risk of pathogen transmission and its consequent impact on the population (Hing et al., 2016). As bats face overcrowding, they may experience elevated stress levels due to the proximity of their peers, potential resource competition, and changes in their social structures. Such stressors can substantially impact the bat immune systems and overall health, potentially making them more susceptible to pathogen transmission. Understanding the link between physiological stress and pathogen spread is crucial because it provides insight into the health of bat populations and has implications for human health (Moreno et al., 2021).

Caveats and conclusions

This is the first study to compare bat behaviour within different groups in their natural roosting habitat. Our study highlights the adaptability of bats in response to overcrowding within the cave system. Yet, our current methods present limitations, including a greater understanding of the role of hormones, social interactions, predator presence, and other ecological factors (Allen et al., 2011; Reeder et al., 2004). Moreover, a deeper exploration of the ecological and evolutionary consequences of these behavioural differences is also essential. For example, understanding how increased aggression in aggregated colonies affects mating success, resource utilisation, and overall colony dynamics can provide valuable insights into bat ecology and conservation.

In conclusion, highlights the nuanced impacts of overcrowding in shaping the interplay of male bat behaviour. The observed differences in behavioural units and incident frequencies between aggregated and non-aggregated groups highlight the need for a holistic understanding of bat behaviour that considers individual and group dynamics. Recognising the connection between bat social behaviour and roosting site conservation has several implications for conservation efforts. First, it emphasises the importance of preserving roosting sites, not just as physical locations but as social hubs for bat communities; furthermore, it underscores that overcrowding has negative implications for bat colonies. Bats usually choose particular roosting locations and conditions influenced by various ecological factors, with safety being one of them (Lima et al., 2005; Lima & O'Keefe, 2013). Conservationists can prioritise the protection of these sites to ensure the continued well-being of bat populations (Meierhofer et al., 2023; Tanalgo et al., 2022). More importantly, we highlight the importance of recognising the link between understanding bat social behaviour and the conservation of roosting sites, underscoring the need to consider roost behaviour and a nuanced approach to bat conservation, significantly as loss or disturbance of roosts may drive over-crowding at remaining sites.

Furthermore, our findings raise the question of how these patterns may be influenced by environmental factors or social structure within bat colonies. Further work is needed to provide a more comprehensive understanding of the dynamics of social behaviour in bat populations. In conclusion, our study highlights the intricate relationship between bat aggregation, social behaviour, and the role of sexual behaviour in shaping these interactions, and the positive and negative impacts that may occur as a result of overcrowding. By shedding light on these complexities, our research contributes to the broader understanding of social dynamics within bat colonies and may offer insights that can inform conservation and management strategies. Future research can build upon these findings to explore the underlying mechanisms and external factors influencing these observed associations, providing a more comprehensive understanding of social behaviour in bat populations.

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