The behavioural costs of overcrowding for gregarious 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. Studying bat behaviour remains an underexplored aspect of bat ecology and conservation despite its ecological importance.
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 variations in the incident frequencies of various bat behavioural activities, particularly regarding aggression and movement, between these two groups. The increase in aggregation was closely related to negative social behaviour among bats.
4. In contrast, sexual behaviour was significantly related to the positive behaviour of individual bats and was headed in less crowded areas. The disparities in bat behaviour with an apparent decline in bat social behaviour because of overcrowding, with more aggressive behaviours emerging, align with the *'behavioural sink'* hypothesis.

5. Our study underscores the importance of considering habitat quality and availability of resources in the management and conservation of bat colonies, as these factors can reduce the occurrence of aggressive and negative 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 variety 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 bat species (679, 48%), probably 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). Many cave-dwelling bats are hypersocial, 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 relates 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).

Numerous animal species, including bats, exhibit aggregation (Philippe et al., 2016), wherein they are either attracted to a resource or socially drawn to other individuals, generally forming groups to reduce predation risk or improve access to resources and mates (Kerth, 2008; Safi, 2008). Interactions between individuals within these aggregates can subsequently alter the overall behaviour of the group

(Kerth, 2008). Most bat species have an optimal roost type and interindividual spacing, which varies based on aggression, body size, air temperature and other factors. Many species use darker spaces of the cave that are further from the entrance of 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 affect individual bat health (Allen et al., 2011; Zagmajster, 2019) and susceptibility to disease and parasitism (Hayman et al., 2013; Webber et al., 2015).

Research on cave-dwelling bat ecology is increasing (Tanalgo et al., 2022). Yet most studies have concentrated on their responses to ecological changes (Cajaiba et al., 2021), and very few on their behavioural responses to intrinsic and extrinsic factors. Empirical data on density-dependent responses remains scarce for many species (e.g., stress behaviour, overcrowding, and diseases) (Chaverri et al., 2018; Hoyt et al., 2021). A more precise understanding of the impacts of overcrowding is clearly needed, especially given that most mammals become more susceptible to pathogens when stressed (Horton et al., 2020; Webber et al., 2015).

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 cave 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 usually measure stress levels using hormones requiring blood or urine samples (Allen et al., 2011; Davy et al., 2017; Reeder et al., 2004), but this approach is costly and sometimes unreliable (Reeder et al., 2004). Therefore, less intrusive, and economically efficient techniques are required to understand how bats react to stress under natural conditions.

The loss of roost sites, such as due to mining, may displace bats from previous roost sites and increase density at remaining sites, potentially causing overcrowding, as well as forcing bats to roost in suboptimal conditions based on loss of more suitable sites (Pretorius et al., 2021). Overcrowding in bat colonies can increase negative interactions and even increase individual body temperature. The '*behavioural sink*' hypothesis, initially introduced by ethologist John B. Calhoun in his famous experiments with rodents in the mid-20th century (Calhoun, 1966, 1973), posits that when population density exceeds a specific threshold, there is a significant decline in behavioural and social patterns among individuals (Calhoun, 1966, 1973). Such behavioural changes may typically manifest as heightened aggression within the population (Calhoun, 1973). However, while the '*behavioural sink*' hypothesis has been demonstrated in laboratory experiments in other mammals (Ramsden, 2009), few natural conditions are likely to lead to comparable patterns of overcrowding, which could lead to such consequences under natural conditions; 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 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 (MBCS) 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). There is no prior study on the average population range of *R. amplexicaudatus* in Philippine caves. Previous surveys have an average estimate of more than 100 individuals in a single cave system (e.g., Sedlock et al., (2014) in Central Visayas and Tanalgo & Tabora (2015) in Southcentral Mindanao). However, more intensive population surveys in Panay showed that even the larger cave systems have a smaller population, ranging from 6,500 to 198,000 individuals, compared to the smaller cave of the MBCS (Mould, 2012). Previous field observations in MBCS further 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, suggesting individual overcrowding (Tanalgo et al., 2020).

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), yet there are no clear studies that assess bat social behaviour (i.e., negative and positive) in response to gregarious behaviour (e.g., overcrowding in colonies). The interest in the behavioural investigation of cave-dwelling bats and their social interactions (Cardiff et al., 2012; Ramanantsalama et al., 2019) is increasing, but only a few caves are 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, as well as potentially confounding factors which may alter density. Testing how behaviours vary based on overcrowding remains an interesting topic that requires further research, especially as increased negative interactions that may increase because of overcrowding can have major health outcomes.

Here, we investigate whether the patterns of diurnal behaviour among cave-dwelling bats are influenced by their roosting density (aggregated vs. non-aggregated) in their cave colony. To do this, we observed two aggregations of male *Rousettus amplexicaudatus* in Monfort Bat Cave Sanctuary and assessed notable disparities in frequency incidents within various bat behavioural categories and units between aggregated roosting colonies and those that did not. Specifically, we estimate the effects of density on the occurrence of ‘positive’ and ‘negative’ behaviours. We then test if there are correlations between the incident frequencies of these behavioural units. We made predictions on the association between the frequency of incidents within behavioural categories and aggregations and their effects on the occurrence of ‘positive’ and ‘negative’ actions and interactions in roosting bats. We predict that (1) aggregated colonies sleep less than non-aggregated colonies and (2) increased colony aggregation increases aggressiveness and negative behaviours. We posit that increased negative interactions in aggregated colonies likely result from overheating due to increased density and possibly even irritability due to repeated contact and disturbances.

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 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 estimates). These bats are known to inhabit the walls and ceiling, with an average occupancy of approximately 403 bats/m^2 and 452 bats/m^2, respectively. 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, although visitors are not allowed to enter the cave **(Figure 1)**.

The Geoffroy’s Rousette fruit bat (*Rousettus amplexicaudatus*) is a medium-sized colony-forming fruit bat with a body size of approximately 128-154 millimetres and a forearm of approximately 80-92 millimetres. This species is widely distributed throughout Southeast Asia and is mainly found in caves in karstic environments. Unlike other Old-World 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.

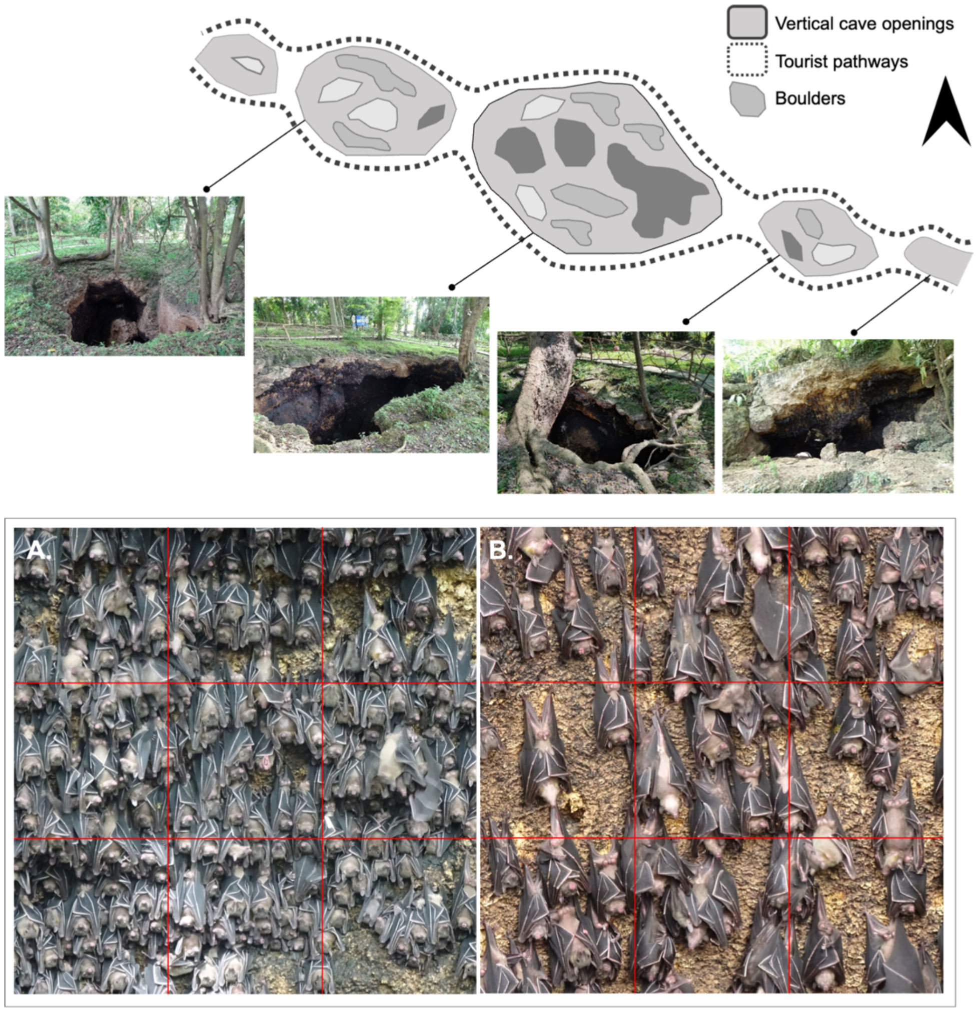

Figure 1. Cave map and entrances (upper photograph) showing two fruit bat colony aggregations in Monfort Bat Cave Sanctuary (MBCS): (a) aggregated and (b) non-aggregated roosting areas. The red grid lines indicate the sampling grid of the behavioural scan.

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 0.305 metre (1 foot) 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, for 10 minutes every hour from 07:00 to 17:00 (for example, Connell et al. 2006). To minimize 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 assessed 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 stay 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-categorized behaviour following Friard & Gamba (2016) and Hengjan et al. (2017) **(Table 1).** The two openings of the cave are vertical, and bats roosting in these areas are prone to predation, and some colonies move in the inner part during heavy rains. We only included and analyzed complete diurnal observations in the colonies to reduce bias and excluded recordings disturbed by predators 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 analyzed the frequency of incidents because we found a strong correlation between frequency and duration of behaviour.

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 vocalization.
Negative social behaviour	Aggression	Aggressive vocalizations, 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 assumption of normal distribution. 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 separate complete Poisson generalized linear regression (GLM) to predict the effects of aggregation and behavioural categories on 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 as explanatory variables.

All data and statistical analyses were performed using the open software Jamovi 2.3.22 (The Jamovi Project, 2023). Data visualizations 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 Philippine and Chinese law. We conformed 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 analyzed 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 a significant variation in the allocation of bat behavioural units in the time budget 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 frequent behaviour observed in non-aggregated colonies (24.73%). We found the highest difference between the aggregation in behavioural incidents in wing flapping (93.57%) and aggression behaviour (89.32%) (**Figure 2A**).

We compared the differences in behavioural units between aggregated and non-aggregated groups. We found that the five behavioural units differed significantly between the aggregations (**Figure 3**). Aggregated groups (mean = 3.18 ± 2.63) had a higher frequency of individual movement behaviour compared to the 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).

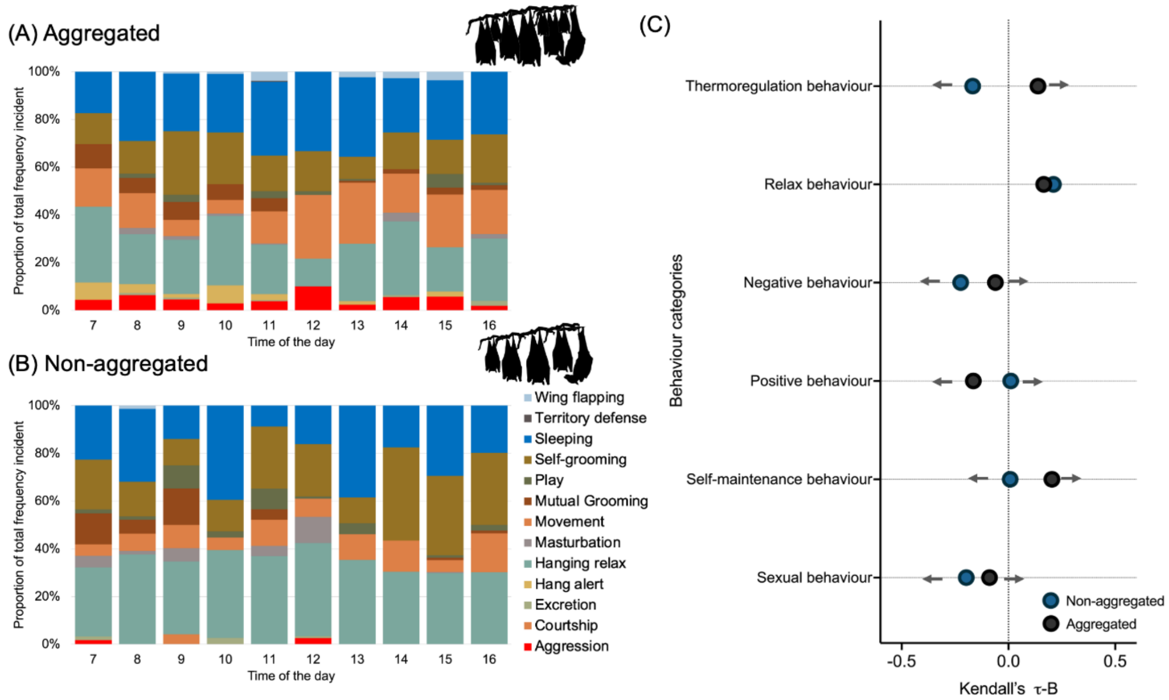

Figure 2. Comparison of the proportion of incident frequency of behavioural units (A and B) and the correlation plot of behavioural categories throughout the day. Each dot represents the correlation coefficient values.

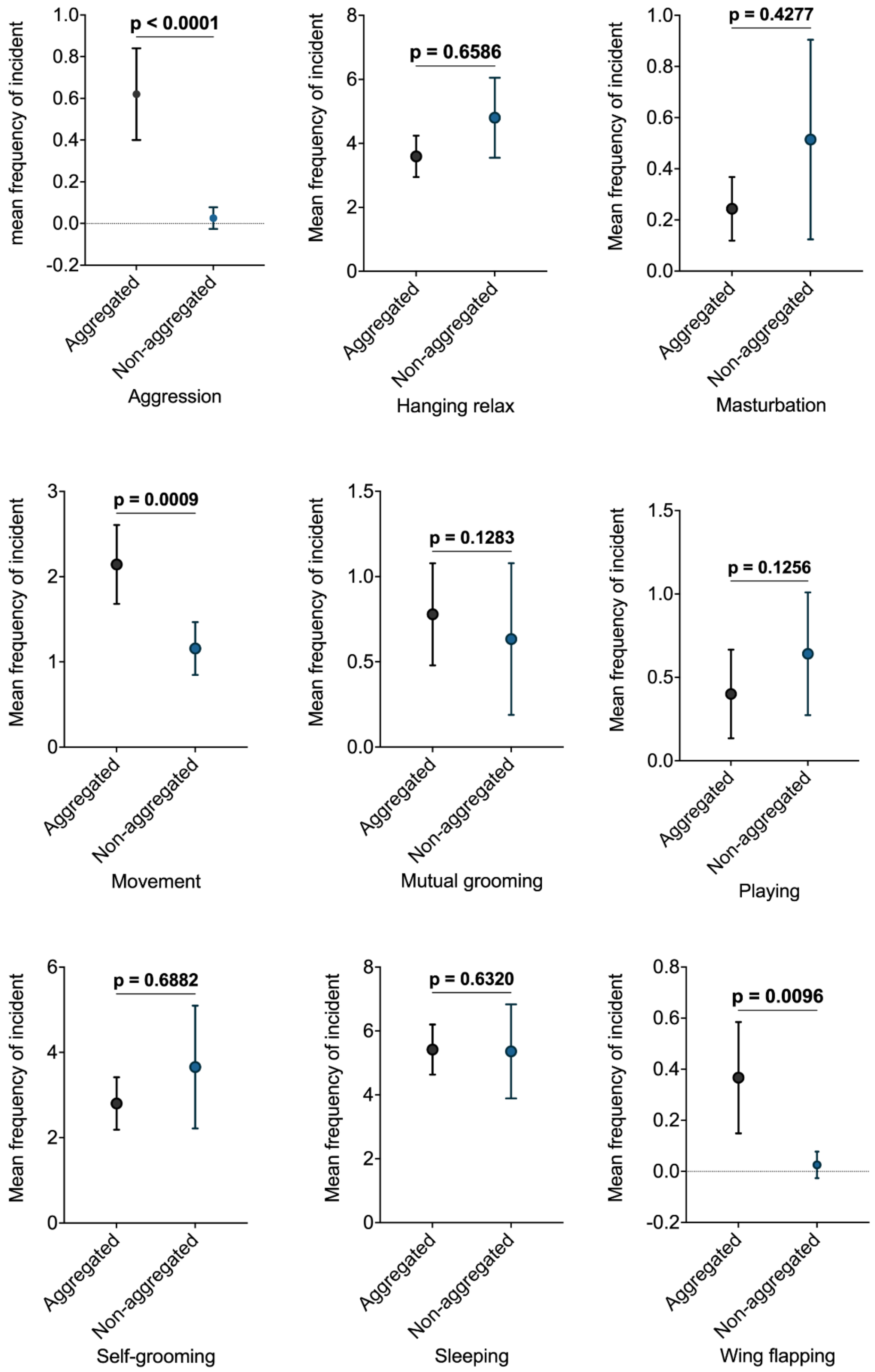

Figure 3. A graph shows the differences in the mean incident frequency between colony aggregations (A) and behavioural units (B). Whiskers represent the 95% CI.

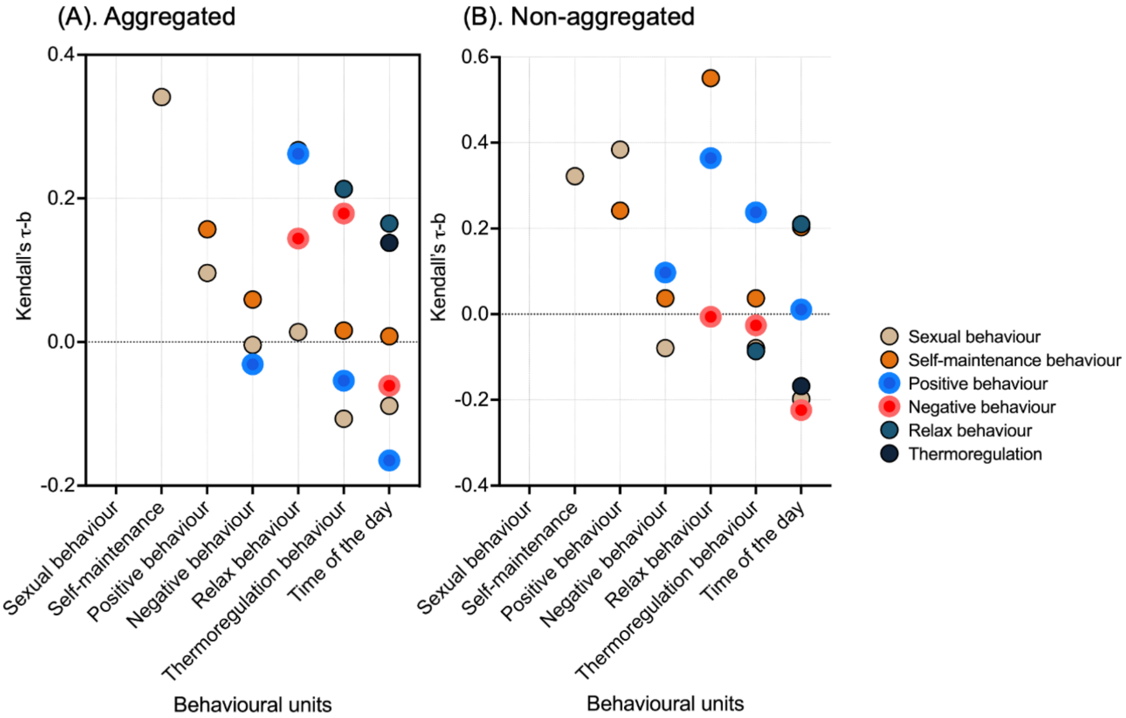

Figure 4. Correlation dot plot (Kendall's τ-B) showing the relationship among behavioural units and time of the day in (a) aggregated and (b) non-aggregated colonies of *R. amplexicaudatus*. Each dot represents the correlation coefficient values.

Although we did not find statistical significance in the correlation between time of day and 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**). In the non-aggregated group 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 Poisson generalized linear models (GLMs) to predict the frequency of occurrence of positive and negative social behaviour **(Table 2).** There was a significantly higher incidence of negative social behaviour in the aggregated colony ($\beta = 3.997$, $p < 0.0001$). Interestingly, we found that the increased frequency of incidents of sexual behaviour positively influenced positive social behaviour among bats ($\beta = 0.114$, $p = 0.0097$).

Table 2. Results of the generalized linear model (GLM) predicting the effects of the frequency of (A) positive social behaviour and (B) negative social behaviour with colony aggregation and other behavioural categories. Values in bold are significant.

A. Positive social behaviour	**β**	**SE**	**Lower**	**Upper**	***p***
(Intercept)	0.106	0.103	-0.104	0.3	0.303
Aggregated (Non-aggregated)	0.278	0.204	-0.685	0.116	0.172
Sexual behaviour	**0.114**	**0.044**	**0.025**	**0.198**	**0.010**
Self-maintenance behaviour	-0.012	0.022	-0.057	0.030	0.590
Relaxation behaviour	**0.084**	**0.020**	**0.044**	**0.124**	**< .0001**
Thermoregulation behaviour	-0.211	0.149	-0.529	0.059	0.156

B. Negative social behaviour	**β**	**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
Relaxation 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 effects of overcrowding on animal social behaviour are not well established, especially in natural situations. Our study is the first attempt to understand the differences and costs in behaviours between aggregated and non-aggregated groups of bats. Here, we demonstrate that individual bats showed increased aggression, movement, and negative interactions within high-density aggregations compared to those in non-aggregated groups. At the same time, increased sexual behaviour was related to more positive interactions and increased in less aggregated colonies. The variation we observed in bat diurnal activities in the two groups suggests that animal social dynamics may shape the behaviour of these male bats, with possible implications for individual health (Hengjan et al., 2017; Manandhar et al., 2018).

Differences in behaviour

Sleeping was the most frequently observed behaviour, comprising over a quarter of the total observed behaviour, and the frequency between the two groups and throughout the day was not significantly different, as this is a universally important activity for bats (Harding et al., 2022; Roy et al., 2020). The most key difference between the two aggregations can be indicated by the significant increased observation of negative behaviour including aggression, movement, and wing flapping in aggregated colonies compared to non-aggregated ones.

Hanging relax was more dominant in the non-aggregated than the aggregated group, indicating that solitary or loosely associated bats may exhibit a different energy allocation strategy, possibly involving increased vigilance to defend against potential threats (Harten et al., 2018; Kelm et al., 2021; Markus & Blackshaw, 2002). Sleep was the second most frequently observed behaviour in non-aggregated bat colonies (25% of their activities) (Harding et al., 2022; Lewis, 1996; Roy et al., 2020). Generally, the observed alertness in both aggregations can be associated with the presence of aggressive predators in the bat cave, which prey on bats irrespective of roosting density (Tanalgo et al., 2020). In a behavioural study of gulls, Beauchamp (2009) observed that individuals even within a smaller group (i.e., less crowded) were more likely to have interrupted sleeping bouts to scan their surroundings when their neighbours were alert. This proposes that animals perceive threats similarly and would 'copy' the vigilance of their neighbours, which can help them better assess the risk of predation (Beauchamp, 2009).

The incidence of other active behaviours differed between aggregated and non-aggregated colonies, particularly in wing flapping and aggressive behaviour. Wing flapping in aggregated colonies showed a 94% difference versus non-aggregated. This difference in behaviour is likely associated with increased temperatures due to heightened physical activity levels within large groups attributed to individual proximity, 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 (Reher & Dausmann, 2021). Aggregated colonies exhibited a significantly higher incidence of wing-flapping behaviour, which is also used to assert dominance within a group and may be more prevalent in densely populated aggregations with limited space (Beauchamp, 2007; Kerth, 2008). Furthermore, aggregated groups exhibited a higher frequency of individual movement than their non-aggregated counterparts, possibly due to disturbing each other and being hotter and, therefore, uncomfortable (Hengjan et al., 2017; Ramanantsalama et al., 2019).

Intrinsic Correlations of Gregarious Bat Social Behaviour

In contrast to aggregated colonies, non-aggregated groups exhibited different correlation patterns between times of day. Thermoregulation, negative behaviours, 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 optimize thermoregulation and self-maintenance, and given increased heat in larger-bodied bats, they may need to work harder to stay cool as temperature increases (Czenze et al., 2020; Stones & Wiebers, 1965). We observe a positive correlation between sexual, self-maintenance, positive social, and relaxation behaviour, hinting that the animals in non-aggregated colonies may prioritize positive activities throughout the day (Byerly et al., 2021). This could be related to less crowded conditions in non-aggregated settings, allowing bats to engage in social interactions.

We found that there is a positive and significant correlation between self-maintenance and sexual behaviour within aggregated groups. 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 and thermoregulation behaviour indicates that bats in aggregated colonies may alternate between cooling down and resting (Becker et al., 2012; Komar et al., 2022). 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 (Hengjan et al., 2017).

The increased aggression and negative behaviour pattern in overcrowded bat populations is consistent with the ‘behavioural sink’ hypothesis concept in social animals such as bats. Overcrowding leads 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). The high population density and proximity can increase competition for resources, such as roosting sites and foraging opportunities, which may escalate social conflicts within bat colonies (O'Connor et al., 2015), and drive negative interactions among individuals (Dai et al., 2018; Fernandez et al., 2014; Holekamp & Strauss, 2016; O'Connor et al., 2015). Previous observations of 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). 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 but does not account for the impacts of over-population which may result from a loss of key resources, such as roosts. Furthermore, when a group becomes overcrowded, individuals often face challenges related to resource competition, increased stress, and restricted access to potential mates. Such stressors can substantially affect bat immune systems and overall health, potentially making them more susceptible to pathogen transmission (Hing et al., 2016). 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).

Another particularly interesting finding was the contrasting relationship between the incidence of sexual behaviour and positive social behaviour. Positive social behaviour could include grooming, affiliative interactions, or cooperative behaviours. Sexual behaviour can be regulated within the colony to minimize conflict and maintain overall social harmony (Alves et al., 2013). Additionally, 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 bats *Cynopterus sphinx* facilitates a longer copulation time during sexual activities. Similar behaviours were observed among colonies of the Indian flying fox *Pteropus giganteus,* showing that oral sex increases positive sexual behaviour; however, the 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). Maintaining sexual behaviour within an overcrowded group of bats may have implications for maintaining reproductive success within the population (Maruthupandian & Marimuthu, 2013; 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.

Limitations and Conclusions

This is the first study to compare bat behaviour with different roost densities in their natural roosting habitat. Bats in aggregated colonies displayed a higher aggression level than those in non-aggregated groups. These findings highlight the importance of understanding social interactions within bat colonies, as increased movement and increased aggressive behaviour could be attributed to resource acquisition, space competition, or territorial disputes within the confines of the aggregation (Hengjan et al., 2017; Kilgour & Brigham, 2013a; Ramanantsalama et al., 2019). For example, Big brown bats (*Eptesicus fuscus*) exhibited higher levels of aggression within groups, which were associated with improved competitive abilities for resources (Kilgour & Brigham, 2013b).

However, our current methods present limitations, including a greater understanding of the role of hormones and the influences of predator presence and other ecological factors in predicting social behaviour (Allen et al., 2011; Reeder et al., 2004). In addition, 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, individual health, resource utilization, and overall colony dynamics can provide valuable insights into bat ecology and conservation.

In conclusion, our work highlights the nuanced impacts of overcrowding in shaping the interplay of bat behaviour. The observed differences in behavioural units and incident frequencies between aggregated and non-aggregated groups emphasize the need for a holistic understanding of bat behaviour that considers individual and group dynamics. Recognizing the connection between bat social behaviour and roosting site conservation has several implications for conservation efforts. First, it emphasizes 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 prioritize 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 recognizing 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 overcrowding 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. 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. Based on our findings, we also propose exploration in future studies, particularly of the drivers of bat aggregations in caves. The absence of apparent anthropogenic disturbance surrounding the cave has potentially increased the population of bats (i.e., spillover effects), consequently increasing predator recruitment (Tanalgo et al., 2020). To deter predators, we hypothesize that bats adopt a 'many-eye' behavioural strategy to collectively survey and monitor their environment for any signs of imminent danger from predators, and this may be particularly important on the edges of roosts when exposed to additional predators (such as crows) (Lima, 1995; Lima & O'Keefe, 2013). Future research can build on 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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