

ORIGINAL ARTICLES

Breeding and Post-Breeding Behavior of the Ghost Bat (*Macroderma gigas*) at Perth Zoo

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ABSTRACT

Understanding the behavior of wildlife in zoo environments is necessary to determine species' welfare states and minimize stress whilst optimizing social groupings, particularly where breeding programs are being undertaken. This observational study investigated the behavior and welfare of six groupings of ghost bats (*Macroderma gigas*) across the breeding and post-breeding seasons within Perth Zoo, Western Australia. Scan sampling was used to record behavioral states and interactions along with spatial preferences within enclosures for 198 hours of observations. A total of 11,895 interval observations were conducted during the study period. Exploratory behavior was correlated with enclosure size, with 18.7% of the total observations in the largest enclosure compared with only 7.1% of them in the smallest enclosure. Male ghost bats engaged in negative behaviors in 40.2% of observed male-male interactions, regardless of the season. Non-breeding females engaged in more female-female negative behaviors during the breeding season, while negative behaviors increased in the breeding female group after the end of the breeding season. This study highlights areas where management practice may be optimized in a zoo setting and provides evidence to consider revising standards of enclosure size for chiropteran species. An increase in heating structures and feeding platforms could also reduce the number of negative interactions between individuals. Given that ghost bats in the wild are listed as Vulnerable, zoo population management and breeding may form an integral part of conservation planning for this species in the near future. As the first published study of zoo-housed ghost bats, these findings help provide insight into the behaviors and interactions of ghost bats in different social groupings across the breeding and post-breeding seasons.

INTRODUCTION

The ghost bat (*Macroderma gigas*) is endemic to Australia, where it resides in genetically isolated populations (Hoyle et al. 2001). Anthropogenic disturbance, such as mining, combined with microclimate restrictions and resource competition from other species, is thought to affect the small and disjunct ghost bat populations (Armstrong & Anstee 2000). Permanent roosting sites for ghost bats tend to be natural caves or abandoned mines with moderate to high relative humidity and temperatures maintained between 23°-28° C (Toop 1985, Churchill 1998, Baudinette et al. 2000). The ghost bat has been poorly studied from a behavioral perspective in the wild due to its high sensitivity to disturbance. No recovery plan is currently in place for the ghost bat, despite being categorized as Vulnerable under the *Environment Protection and Biodiversity Conservation Act* (1999) (Woinarski et al. 2014). Given the ongoing nature of the specific threats faced by this species, as well as the recognized climate risks posed to chiropteran species globally (LaVal 2004), it is important to improve the captive management of this species in order to provide for future *ex*

situ conservation measures.

In the wild, ghost bats are polygynous and exhibit male-biased dispersal (Nagy et al. 2013, Nagy & Knörnschild 2016). Male-biased dispersal decreases the chances for kin competition and inbreeding (Rossiter et al. 2012). This also results in a higher percentage of females being related to other females in neighboring roosts, as seen in lesser flat-headed bats (*Tylonycteris pachypus*) (Hua et al. 2013).

Research of Indiana bat (*Myotis sodalis*) natal roosts also suggests non-random social assortment in chiropteran species (Silvis et al. 2014). Further evidence from this study suggests that reproductive condition plays an important role in mate selection among individuals, while social structure at the colony level may be related to spatio-temporal features, such as roost availability and quality (Silvis et al. 2014). Hence, behavior observed at roosting and feeding sites could play an integral role in understanding bat sociality and reproductive success. However, due to the nocturnal and cryptic nature of most bats, sociality, at least at the individual

level, can be challenging to observe in wild populations (Kerth et al. 2002). Additionally, data obtained from wild populations may not provide an accurate representation of animal behaviors expressed in a zoo setting.

Most literature relating to the captive management of ghost bats exists in the form of manuals, which describe husbandry, housing and welfare-related variables (e.g. enclosure size, heating structures and feeding platforms) that are likely to contribute to successful chiropteran breeding programs (e.g. Jones 2008). While such sources of information provide some useful recommendations, there is a need for further research to objectively quantify the relationship between specific behavioral variables and welfare states to confirm that neutral or positive welfare outcomes are being achieved.

Zoo-based behavioral studies for poorly studied species in the wild allow for a greater understanding of species-specific behaviors, whilst also informing practices that reduce stress-related behaviors in zoos, therefore improving animal welfare (Olive & Jansen 2017). Pilot studies can be a useful way to provide preliminary benchmarks and refine hypotheses (Thabane et al. 2010) as well as contribute to captive breeding programs of threatened species. Captive collections can provide valuable insight into their wild counterparts and help maintain a genetic safety net for endangered species worldwide (Olive & Jansen 2017).

All modern models for assessing captive animal welfare (Kagan et al. 2015, Mellor 2016, Brando & Buchanan-Smith 2018) have as one of their requirements a need to derive measurable, objective, specific, and enduring measures of welfare states. This can be challenging yet critical to providing robust conclusions when the aim of a study is to optimize welfare in captivity or otherwise. Welfare can be assessed at an individual and group level, as members of the same species may possess specific and different needs within a given environment based on their individual characteristics (Hill & Broom 2009).

The Perth Zoo has maintained a colony of ghost bats since the late 1970s, providing an opportunity to observe breeding behaviors exhibited by this species in captivity. In this study, we employed scan sampling to collect behavioral data and compare the frequency of different observations of male and female ghost bats established in breeding, non-breeding and male-only bachelor groups across the breeding and post-breeding season. The study's final goal was to better understand the captive management of this species, optimize welfare and breeding outcomes, and provide a baseline methodology to compare future management interventions.

METHODS

Enclosures

Observations took place inside the Perth Zoo nocturnal house in 2017, equipped with a reverse light cycle. Three groups of ghost bats were observed in three separate enclosures (A, B and C) during the breeding (early June to mid-July) and post-breeding (late July to early September)

seasons (totalling six separate animal groups). The enclosure descriptions are outlined in Table 1.

Design features and furnishings within the three enclosures included wire mesh, mock rock, timber, branches, corners and a designated general area. Numerical area codes were assigned to specific areas inside each enclosure, including feeding and heated basking areas, to assist with determining individual and group spatial usage (Table 1).

Study Groups

Individual ghost bats were selected and introduced into the breeding and post-breeding season groups by Perth Zoo staff according to management needs (SM 1). This study was conducted with Perth Zoo Animal Ethics Committee approval (AEC No.2017-9).

The individuals composing each study group, as well as the enclosure each group occupied during the breeding season and post-breeding season (Table 2) are described below.

Although individual ghost bat subjects were previously marked with a colored visible implantable elastomer (VIE), not all subjects were identifiable during the study. Due to this study's commitment to non-invasive, minimal-disturbance sampling techniques, a black light was not used to enhance ghost bat identification. VIEs could be seen without the use of a black light for certain individuals. Some ghost bat subjects were identifiable through physical characteristics at an individual level by the observer. Two ghost bats (Male 1 and Female 3) were held in an off-display enclosure during the breeding season and were not observed during that period of the study, but both bats were integrated into post-breeding groups and subsequently observed.

Behavioral surveys

Behavioral data were recorded at one-minute intervals via scan sampling (Lehner 1992) during thirty-minute observation periods. During the sampling minute, the current individual behavioral state or social interaction performed by each individually identifiable member in the group was recorded along with the location (i.e., area code, elevation and furnishing) of that individual within the enclosure.

Behavioral states (at the group level) and social interactions were coded with the use of an ethogram of events and states (Table 3). The categories used to describe specific group-level states were resting (R), exploratory (E), stereotypic (S) and other (O); with each state comprising one or more specific individual-level behavioral events that were considered characteristic of that state. Social interactions were categorized as: positive/neutral (P), which included proximity, huddling, copulating and suckling. Negative (N) social interactions were categorized as: displace, chase, stationary wing flap, aggression and stare (Table 3). Feeding behavior for ghost bats are placed into the 'exploratory' category, as foraging for food is assumed to be an activity that requires exploration. Drinking events were not recorded, as water bowls were out of sight to the observer.

Table 1 - Summary of ghost bat enclosures where observations were conducted for this study.

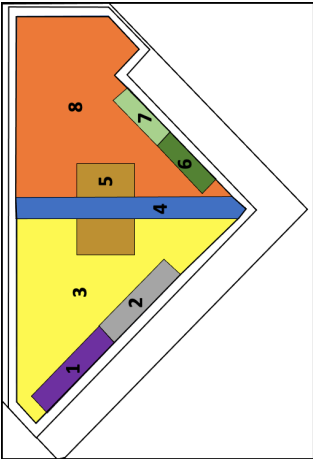
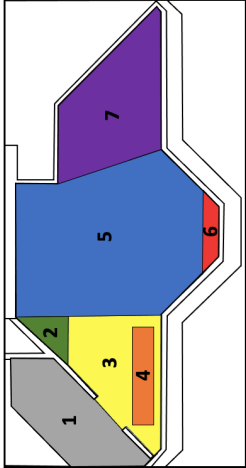
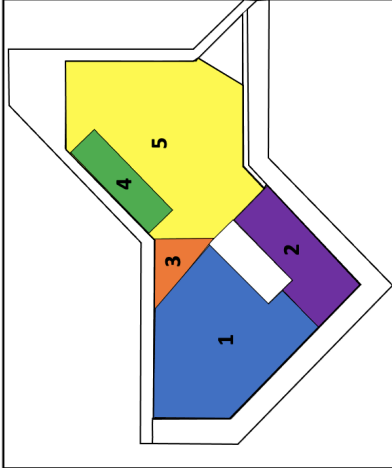
Enclosure ID	Height Range	Area	Vertices	Shape	Number of Heat Sources	Number of Feeding Platforms	Mixed Species Enclosure
A	2,06 m	12,12 m ²	7		2 (area 6 & 7)	1 (area 5)	No
B	3,28-3,77 m	47,37 m ²	15		3 (area 1, 4 & 6)	2 (area 2 & 7)	Yes, shared enclosure space with terrestrial marsupials
C	1,50 m-3,10 m	32 m ²	9		1 (area 4)	1 (area 3)	Yes, shared enclosure space with terrestrial marsupials

Table 2 - Study groups and enclosures and individual history of the combined breeding and post-breeding season ghost bat subjects.

	Breeding season	Post-breeding season
Enclosure A (12.12m²)	Breeding group (Male 2 / Female 1 / Female 2)	Female group (Female 1 / Female 2 / Female 3)
Enclosure B (47.37m²)	Non-breeding female group (4 unidentifiable ♀)	Bachelor group (3 unidentifiable ♂ / Male 1 / Male 2)
Enclosure C (32 m²)	Bachelor group (3 unidentifiable ♂)	Non-breeding female group (4 unidentifiable ♀)
Off Display Enclosure (not studied)	Male 1 & Female 3	N/A (empty enclosure)

Table 3 - Ethogram of behavioral events used to document ghost bat group-level states and social interactions.

Group-level behavioral states				Social interactions	
Resting	Exploratory	Stereotypic	Other	Positive/Neutral Social Behaviors	Negative Social Behaviors
Group: R	Group: E	Group: S	Group: O	Group: P	Group: N
Hanging (stationary while gripping surface with feet)	Flying (Airborne and not engaged negative behaviors such as chase or displace)	Pacing (same pathway is repeated two or more times)	Out of sight	Proximity (within 20 cm of each other)	Displace (Take another individual's place)
Self-grooming (Individual grooming itself)	Walking (locomotion using feet only)	Turning in circles (two or more times)	Urinating	Huddle (within 2 cm of each other)	Chase (Drive another individual away from a specific location)
Lying on ground (wings and feet fully on ground)	Climbing (locomotion using feet and wing hooks)		Defecating	Copulating	Stationary wing flap Wings flapping while body is stationary (not airborne))
	Eating food (whenever food is in mouth)			Suckling	Aggression (foot-grab or biting)
	Vocalizing			Nil (did not occur)	Stare (head oriented towards another >5 seconds within 30 cm)
					Nil (did not occur)

Proximity was assessed through direct observation (Table 3). Time intervals were recorded using a stopwatch timer

For the groups which contained unidentifiable individuals, a majority behavior and an outlier behavior were recorded at each interval. The majority behavior was considered the one exhibited by the greatest number of bats at one time, while the outlier behavior was the one exhibited by the least number of bats (Table 3).

The study period covered the breeding season and post-breeding season, with an approximate twelve-week rolling schedule of observation days to ensure approximately equal representation across all study groups. An adaptation period of one week was implemented in-between the breeding and post-breeding seasons. Observation days included both weekdays and weekends to ensure sampling occurred across

parts of the week with both lower and higher zoo visitor numbers, which might have influenced the bats' behavioral states and interactions.

Observations either took place during hours of light or hours of dark, for three time periods, with reverse light cycling operating within the enclosures. Data were collected during three study periods: 7:15am- 8:45am (Time period 1 – a time period consisting of both dark and light hours) and 9:30am- 12:30pm (Time period 2 – a time period consisting of only dark hours) on Tuesdays and Saturdays, and 12:30pm- 5pm (Time period 3 – a time period consisting of only dark hours) on Thursdays and Sundays (SM 2). A total of 198.25 hours of observations were recorded across these three time periods. The exhibits were displayed to Zoo visitors, with observations conducted both before and

during Zoo opening hours. All observations were recorded by the same observer.

RESULTS

A total of 11,895 interval observations were recorded during the entire study period. During the breeding season (Early-June–Mid-July), a total of 5,985 interval observations were recorded across the three study groups (breeding group 2,010 observations, non-breeding female group 1,980 observations, and bachelor group 1,995 observations). During the post-breeding season (Mid-July–Early-September), a total of 5,910 observations were recorded across the three study groups (breeding female group 1,980 observations, non-breeding female group 1,950 observations, and bachelor group 1,980 observations).

The three most commonly observed behaviors (not accounting for out of sight observations) were huddling (27,0%), hanging (24,9%), and proximity (18,8%), which together accounted for 90,8% of the total observed behaviors. Less frequently observed behaviors included flying (3,2%), eating (2,5%) and vocalizing (2,8%). The remaining observations accounted for approximately 0,5% of grooming, climbing, copulating, urinating, lying on the ground and walking.

Behavioral states within enclosures

A total of 2,917 exploratory behaviors were observed during the study period, which accounted for 8.7% of total observed behaviors. Of the total exploratory behaviors, flying accounted for 37.5%, vocalizing (32.3%), eating (29.4%), and walking/climbing (0.8%). The amount of exploratory behaviors observed for identifiable individuals (Female 1, Female 2, Female 3, Male 2, Male 1) and groups of unidentifiable individuals (non-breeding females and bachelor group) varied between different enclosures (Table 4).

Male 2 exhibited the most variance in exploratory behaviors between enclosures. While residing in enclosure A, 15% of Male 2's total observed behaviors were exploratory, and when relocated to enclosure B, 40,6% of them were exploratory. The non-breeding females, as a group, exhibited 13,7% exploratory behaviors while residing in enclosure B, and only 2,3% while residing in enclosure C. Similarly, the bachelor group exhibited 13,7% exploratory behaviors whilst in enclosure C, and 22,7% while in enclosure B (Note: Male 2 and Male 1 were both integrated into the bachelor group enclosure B at the start of the post-breeding season). Female 1 and Female 2 were the only study subjects to remain in the same enclosure (A) across both the breeding and post-breeding seasons. There was no difference in the

Table 4 - Exploratory behavior as a proportion of total behavioral observations by enclosure during the breeding and post-breeding seasons.

	Enclosure					
	A (Breeding)	A (Post-Breeding)	C (Breeding)	C (Post-Breeding)	B (Breeding)	B (Post-Breeding)
Male 2	15%	-	-	-	-	40,6%
Female 1	7,5%	7,2%	-	-	-	-
Female 2	4,1%	4,6%	-	-	-	-
Non-breeding Female Group	-	-	-	2,3%	13,7%	-
Bachelor Group	-	-	13,7%	-	-	22,7%

Table 5 - Relative proportions of negative and positive/neutral social interactions for each of the three study groups, during breeding and post-breeding seasons.

	Breeding Group		Female Group		Bachelor Group	
	Breeding	Post-breeding	Breeding	Post-breeding	Breeding	Post-breeding
Negative	86 (29.6%)	102 (51.0%)	26 (14.6%)	6 (4.2%)	229 (60.9%)	101 (56.4%)
Positive/Neutral	205 (70.4%)	98 (49.0%)	152 (85.4%)	137 (95.8%)	147 (39.1%)	78 (43.6%)
Total	291	200	178	143	376	179

amount of exploratory behaviors exhibited by Female 1 and Female 2 during the breeding and post-breeding seasons.

Social Interactions by Season

A total of 1,367 social interactions occurred across the breeding and post-breeding seasons (Table 5). Of these interactions, 550 (40,2 %) were classed as negative, and 817 (59,8 %) were classed as positive/neutral. There was a notable difference between the study groups in the number of negative social interactions during the breeding and post-breeding season (Table 5). While the bachelor group had the highest occurrence of negative interactions during both breeding and post-breeding seasons, there was no substantial difference in the level of negative interactions between seasons (60.9%, 56.4%). The non-breeding female group showed a difference in negative interactions between the seasons, with a reduction (14.6%, 4.2%) in negative interactions once the breeding season ended. The breeding group also showed a difference in the number of negative interactions but with an increase (29.6%, 51.0%) in negative interactions once the breeding season ended (Table 5). All groups showed a decrease in the overall number of interactions (positive/neutral or negative), ranging from 20%-53%, during the post-breeding season.

Social Interactions and Enclosure Area

For both the bachelor and non-breeding female groups, a decrease in negative interactions was observed from breeding to post-breeding seasons (Fig. 1). In enclosure C, both the non-breeding female and the bachelor groups (excluding Male 2 and Male 1) were observed to have higher proportions of negative interactions in Areas 3 and 5 than in other areas (Fig. 1). Area 3 contained the feeding platform, and area 5 was designated as a general area, in close proximity to a feeding platform and a heating source (Table 1). This likely contributed to the high proportion of negative interactions observed in these areas for both study groups. Similarly, in enclosure B, both the non-breeding female and the bachelor groups (excluding Male 2 and Male 1) were observed to have their highest proportion of negative interactions in Areas 3 and 5 (including Area 7 for the non-breeding females) (Fig. 1).

DISCUSSION

Behavioral states within enclosures

Zoo environments can produce a wide range of behavioral differences between captive and wild populations (Hill & Broom 2009). For bats, there is a requirement for sufficient roosting sites and associated space for shelter, resting, mating, rearing of young and social interactions (Günther et al. 2016). A lack of sufficient space can facilitate aggression (Günther et al. 2016) although this was not observed for all groups in the present study. However, a positive relationship was found between enclosure size and the amount of exploratory behaviors exhibited by the ghost bat groups. For the three unidentifiable (and subordinate) males in the bachelor group, their exploratory behaviors were reduced during the post-breeding season compared to the breeding season. This may have been related to the introduction during the post-breeding season, of the dominant males

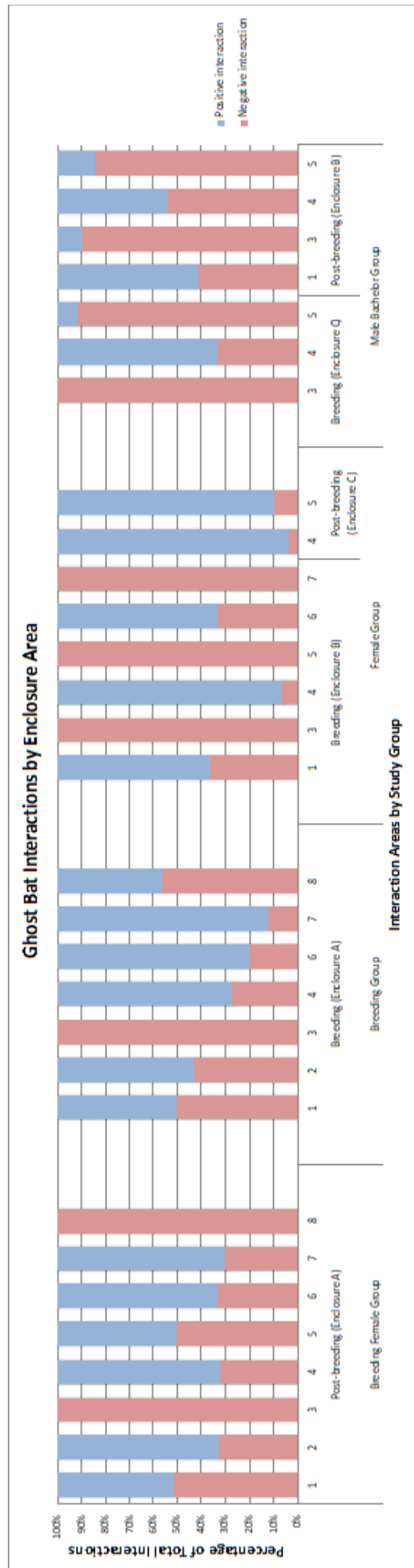


Fig. 1 - Proportions of positive/neutral (P) and negative (N) social ghost bat interactions by study group (breeding group, female group, male bachelor group), enclosure (A, B & C) and area code (1-7) during the breeding and post-breeding seasons. Both negative and positive/neutral social interactions showed differences across different areas within each exhibit.

(male 1 and male 2), who were territory holders after being moved from the breeding groups into the bachelor group for the non-breeding season.

Exploratory behavior, negative social interactions and enclosure area

We found that enclosure size had a positive relationship with exploratory behaviors. Specific areas and resources within enclosures also appeared to influence bat behavior, with negative interactions being recorded in higher proportions in regions of the enclosure in proximity to valued resources, such as feeding platforms and heating lamps. These results underscore the importance of considering enclosure design and size to maximize welfare for captive individuals and potentially, breeding opportunities.

In the bachelor group, during the post-breeding season, Male 2 spent more time in Areas 4 and 7 whilst Male 1 spent more time in Area 1. The subordinate males spent the majority of the time together in an out-of-sight cave Area 5 (Table 1). Although aggression is a recognized part of the natural social dynamics for many bat species (Fernandez et al. 2014), a study conducted on behavior and communication in male Seba's short-tailed fruit bats (*Carollia perspicillata*) provides further insight into how aggressive behaviors impact upon the social structure of that species (Fernandez et al. 2014). In that study, aggressive interactions between territory holders indicated that social hierarchy played a role in preferred spatial distribution. In the current study, the presence of the two dominant males potentially caused the subordinate males to roost together to avoid negative interactions.

Optimal enclosure size can facilitate exploratory behaviors and breeding success for many species (Marshall et al. 2016). Standards of practice for animal welfare, including housing standards for particular species, have not yet been agreed across many zoos (Marshall et al. 2016). However, for ghost bats it has been recommended that they should be housed in no less than a 12 m² area (Jackson 2003). Whilst all enclosures at Perth Zoo are >12 m², a significant increase in the amount of exploratory behaviours was observed in the larger enclosures. Therefore, these minimum standards may not reflect optimal conditions for ghost bats.

Many questions remain regarding appropriate enclosure sizes for chiropteran species, including whether enclosure size is reflected in reproductive success. Future research aimed at identifying aspects of enclosure design and related husbandry, which represent best practices for welfare and breeding, would be valuable for optimizing captive breeding programs.

Intra-group social interactions by season

There were clear differences in how each of the three groupings of ghost bats responded at the end of the breeding season. The breeding group was restructured in-between the breeding and post-breeding season with the removal of the breeding male (which was relocated to the bachelor group) and the addition of one new female to the group. While the enclosure (A) and stocking rate both remained unchanged, there was an increase in negative interactions between

members of this new grouping. Possible explanations for this could be that the addition of the third female to an established group was not accepted, that the one female that became pregnant during the breeding season exerted some influence over the other two females, or that both changes jointly affected the new female grouping. The non-breeding female group displayed a reduced level of negative interactions after the end of the breeding season despite being moved to a smaller enclosure. Although the bachelor group had the highest level of negative interactions, there was only a small reduction in the amount of negative interactions observed during the post-breeding season, despite being moved to a larger enclosure thereby reducing stocking density. For the bachelor group (excluding Male 2 and Male 1), one explanation for the observed reduction in negative social behaviors during the post-breeding season may be the integration of two dominant males (Male 2 and Male 1).

Our results provide some insights into negative social interactions within the breeding group. This group was observed to have a higher proportion of negative social interactions during the post-breeding season than during the breeding season. With respect to areas of the enclosure, the highest proportion of negative interactions was observed in Area 3 during the breeding season. During the post-breeding season, the highest proportion of negative interactions were observed in Areas 3 and 8 for this group. Both of these areas were designated general areas. It was noted that once an individual moved to within close proximity of another individual in areas containing heat sources, a negative social interaction frequently followed. This increase in negative social interactions may be integration-related; given that some individuals were moved between enclosures seasonally. Bats *in situ* live in temporary subgroups of multi-level societies, where individuals typically maintain a level of companionship if the population remains stable (Baigger et al. 2013). Identifying and monitoring the bonds between individuals within a group could aid in the management of aggressive interactions between individuals. In the wild, female ghost bats exhibit natal philopatry and form harems during the breeding season, and later disperse into separate colonies comprising mainly mothers and young (Armstrong & Anstee 2000). In captivity, although the separation of breeding females from other bats during the post-breeding season could aid in the reduction of negative social interactions, this may be impractical, as more enclosures would need to be available. Additionally, this separation may not facilitate the specific social requirements of females post-breeding season or when raising young.

Huddling Followed by a Negative Social Interaction

Although this study demonstrated an observed decrease in negative social interactions for the bachelor group during the post-breeding season, a review of the findings of this study highlights that what constitutes positive/neutral interactions and negative interactions may require further consideration. Specifically, huddling is often considered to be a positive/neutral social interaction (Liwanağ et al. 2014), and indeed, is categorized as such in this present study. However, during the post-breeding season the dominant male 1 was often observed huddling a subordinate male,

which was always followed by an aggressive behavioral event, such as foot grabbing, biting, chasing or displacing. In a study of Jamaican fruit bats (*Artibeus jamaicensis*), dominant males tolerated the presence of a subordinate male in the breeding roost site to deter aggressive attempts made from males of other roosts (Ortega et al. 2003). However, another potential explanation for the observed behavior in our present study was that the dominant male was engaging in mis-directed mate guarding of the subordinate male in the absence of any females in the enclosure.

Limitations

A number of confounding variables were present during this study, and it is important to note the following limitations of this research. The use of a black light to facilitate the identification of individuals was not permitted, meaning not all subjects could be identified. Further, the movement of individuals into different enclosures between the seasons, which was undertaken for management purposes, impacted the study and its analyses (in particular, one group was out of sight to the observer throughout the breeding season, but was later integrated into the post-breeding study groups). In addition, the afternoon observation period often concluded before 5pm due to unforeseen management reasons. Although hours of observation were added on later occasions, this may have affected the consistency of sampling. Finally, although scan sampling is a preferred method for collecting behavioral data on all individuals within groups, it often necessitates sampling only a limited (pre-determined) number of behaviors; and under challenging observation conditions such as the low light levels in bat enclosures, which may lead to inaccuracies.

CONCLUSION

This observational study provides valuable insight for future hypothesis-based studies whilst also providing some evidence to consider revising standards of enclosure size for chiropteran species. It also highlights areas where management practice may be optimized in a zoo setting. An increase in heating structures and feeding platforms could reduce the number of negative interactions between individuals. Future studies focused on ghost bats' hormonal and behavioral responses along with the introduction or separation of group members among roosting sites could also provide information to help interpret observations of negative interactions. Determining whether and to what extent social hierarchy may play a role in mate selection could provide insight for pairing individuals during the breeding seasons.

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