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The Neighbor Effect in Bachelor and Breeding Groups of Western Lowland Gorillas (*Gorilla gorilla gorilla*)

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Behavioral monitoring is an essential tool for understanding how animal management decisions, including exhibit design choices, impact animal behavior and welfare. The purpose of this study was to use behavioral monitoring techniques to determine the interaction between 2 groups (bachelor and breeding groups) of western lowland gorillas that are housed in separate habitats that partially face one another. We performed simultaneous, 30-minute group observations on the breeding and bachelor groups and recorded all occurrences of agonistic and affiliative behavior, vocalizations, and visual monitoring of the adjacent group. At 5-minute intervals, we also recorded which gorillas in the observed group were potentially visible to the neighboring group. Our results indicated that there was considerable variation in the percentage of time each gorilla spent monitoring the neighboring group. We were also able to demonstrate that the visibility of individuals in the breeding group of gorillas was related to behavior of the gorillas in the bachelor group. Although non-contact aggression increased with the visual presence of the adult male of the breeding group, more severe aggression that could cause injury was not influenced by his presence. Results also showed an association between visual presence of a particular female in the breeding group and a decrease in contact aggression in the bachelor group. Since many zoological exhibits allow visual access to other animals, it is important to determine the impact that neighbors may have on each other. Our study investigating interactions between neighboring gorilla groups is an example of how behavioral monitoring can be used to assess the impact of a wide range of management decisions on animal behavior and welfare.

Behavioral research in zoos and aquariums provides a systematic and unbiased approach to address management questions related to the care and welfare of animals. For socially complex animals, such as gorillas, behavioral monitoring is an essential tool used to document interactions between individuals within a group and thus track changes in social relationships over time or in response to changes in their environment or group composition (e.g., Miller, Leighty, Maloney, Kuhar, & Bettinger, 2010; Pullen, 2005; Stoinski, Lukas, Kuhar, & Maple, 2004). Often when investigating the impact of environmental changes, the focus is on the animal's own habitat or group members; however, stimuli outside of the habitat, such as animals in neighboring exhibits also can have a significant influence on behavior.

The typical zoo environment differs from wild habitats in many ways including the presence of visitors, reduced space, and the management of social, nutritional and health needs. Although numerous studies have investigated how intragroup relationships, housing conditions, or husbandry routines influence captive primates (Hosey, 2005), few studies have focused on the impact of factors outside of the primate's immediate habitat, such as neighboring groups. Given that many zoo primates are housed in a way that allows them to see, smell, and/or hear animals outside of their group (often other primates), it is important to gain a better understanding of how neighboring groups influence one another. Intergroup interactions of wild populations of primates are well-documented (for primates: Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987; for

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western lowland gorillas: Bermejo, 2004; Gatti, Levréro, Ménard, & Gautier-Hion, 2004; Robbins et al., 2004), but only a handful of studies have investigated neighbor effects in managed primate populations. Studies of managed common marmosets (*Callithrix jacchus*) and chimpanzees (*Pan troglodytes*) have shown that neighbor vocalizations can have a negative impact on outside groups, such as increased intragroup agonistic behavior (Baker & Aureli, 1996; Watson & Caldwell, 2010) and increased stress-related behavior (Baker & Aureli, 1997). However, additional work with managed chimpanzees found that grooming vocalizations by neighboring groups increased intragroup grooming behavior, demonstrating the potential for positive as well as negative neighbor effects (Videan, Fritz, Schwant, & Howell, 2005). Although there are no known published studies of neighbor effects in zoo western lowland gorillas (*Gorilla g. gorilla*), intergroup encounters from wild observations of this subspecies are characterized as more tolerant compared to the more aggressive group encounters described in mountain gorillas (*Gorilla beringei beringei*) (Bermejo, 2004).

In the wild, the most prevalent group structure for western lowland gorillas is the one-male/multiple female breeding group although solitary males and multiple male groups also are observed (Bermejo, 2004; Gatti et al., 2004; Levréro et al., 2006; Robbins et al., 2004). Over the years, zoos have adapted their gorilla breeding group composition from male-female pairs to the single-male, multiple-female breeding groups typically seen in the wild (Stoinski et al., 2004). To address the issue of surplus males resulting from the changes in breeding group composition, improvements in captive breeding, and an even sex ratio, zoos have developed ways to successfully form all-male groups (Coe, Scott, & Lukas, 2009; Stoinski et al., 2004). Although there are many factors to take into consideration when forming a bachelor group, one that is believed to have a destabilizing effect on bachelor groups is the nearby presence of breeding females (Stoinski et al., 2004).

In the present study, we sought to determine the influence of a nearby breeding group of gorillas on our well-established bachelor gorilla group at Disney's Animal Kingdom®. Here the breeding and bachelor groups of western lowland gorillas are in olfactory and auditory contact and are visible to each other from large portions of their habitats. This habitat design allowed us to investigate how the behavior of the bachelors was influenced when members of the breeding group were and were not visible to them. Specifically, we were able to address alterations in affiliation, contact and non-contact aggression as well as vocalizations and visual monitoring of the neighboring breeding group.

Method

Subjects and Housing

The subjects were 8 western lowland gorillas (*Gorilla gorilla gorilla*) housed in 2 groups at Disney's Animal Kingdom®, Bay Lake, Florida, USA. The breeding group consisted of an adult male (silverback), 3 adult females, and an infant and the bachelor group consisted of 4 silverbacks (see Table 1 for ages and historical information). The infant was not a subject of this study; however, from her birth until the completion of the study, she stayed in proximity to her mother and was therefore visible to the bachelor gorillas whenever her mother was visible.

Subjects have been housed in their groups at Animal Kingdom since 1997, with the exception of an adult female (Kashata) who was introduced to the breeding group in April 2008 and her infant, born February 2010. The breeding and bachelor groups are housed in large (1765.16 m^2 and 2601.29 m^2, respectively), outdoor naturalistic habitats containing dense vegetation, rocks, and waterfalls. The breeding and bachelor habitats are separate; however, there is a 60 m section where the habitats face one another, in which neighboring group members can be visible to each

other. Each habitat also has multiple areas where gorillas are unable to view and are out of sight of neighboring gorillas.

Table 1
Date of birth and group information for individual gorillas in the breeding and bachelor groups

	Date of Birth	Date of Arrival at Disney's Animal Kingdom®	Relationship to Other Gorillas
Family Group			
Gino	12/30/1980	06/29/1997	Sire of Lilly
Benga	04/21/1971	06/29/1997	Sibling is sire of Hope
Hope	09/07/1983	06/29/1997	Sire is sibling of Benga; Paternal half-sibling to Spike
Kashata	04/10/1993	03/20/2008	Dam of Lilly
Lilly	02/19/2010	02/19/2010	Offspring of Kashata and Gino
Bachelor Group			
Gus	08/09/1981	11/20/1997	Sire of Kejana
Kejana	05/10/1991	11/20/1997	Offspring of Gus
Zawadi	08/05/1991	06/08/1997	Maternal half-sibling to Spike
Spike/M'Bizi	08/14/1993	06/08/1997	Maternal half-sibling to Zawadi; Paternal half-sibling to Hope

Materials and Procedure

Data collection occurred between September 2009 and September 2010 and consisted of 30-min simultaneous behavioral observations of the breeding and bachelor habitats conducted by two separate observers. The observations were conducted from visitor areas 4 days per week (2 mornings and 2 afternoons). Morning observations were conducted at 0930 h, approximately 1 hr after gorillas were given access to their habitats from their night holding buildings; afternoon observations were conducted at 1530 h, approximately 1 hr prior to the gorillas going into the holding buildings for the night. Observations were conducted on days when weather and scheduling permitted (Monday-Sunday). It should be noted that husbandry and maintenance routines did not vary by day. In addition, the study period also included times of both relatively high and low visitor numbers. Gorillas were let into the outdoor habitats when temperatures were above 40° F, and observations were canceled in the event of moderate to heavy rainfall. All occurrences of aggressive and affiliative behavior, contact call and purr vocalizations, and visual monitoring of the neighboring habitat were recorded. Chest beats were analyzed separately since they are not exclusively an aggressive display (see Maple & Hoff, 1982; see Table 2 for ethogram).

Prior to the start of the study, researchers walked each gorilla habitat to determine the view of the neighboring habitat. At 5-min intervals in the observation period, the observers walked the portion of the visitor trail where gorillas could potentially view neighboring groups and noted if any of the group members that were being observed were in regions of their habitat which were in view of the neighboring group. With the exception of visual monitoring which was recorded as duration, all occurrence behaviors were recorded as frequency. Inter-rater reliability was greater than or equal to 90% for all behaviors. All data were recorded using Pocket Observer (v. 2.0, Noldus Information Technology) on a Hewlett-Packard iPAQ (#HX2495B). Data was summarized using Noldus Observer XT (v. 5.0, Noldus Information Technology).

Data Analysis

A total of 184, 30-min observations were conducted on each group, for a total of 92 hrs of data collection per group. There were 94 morning observations (47 hrs) and 90 afternoon observations (45 hrs) per group. We noted all occurrences of aggressive and affiliative behavior and purr and contact vocalizations in each group and recorded which individuals were visible in the neighboring group during the previous scan (1104 scans total). Due to the birth of an infant on 02/19/2010, Wilcoxon Signed Ranks tests were conducted to determine differences in bachelor group behavior before and after the birth of the infant and no significant differences were found. Therefore, behavioral data were analyzed across all observations. We conducted z-tests to determine significant differences between the number of times behavior occurred when a particular individual was visible (in proportion to the total number of scans when the individual was visible) vs. the number of times the behavior occurred when an individual was not visible (in proportion

to the total number of scans when the individual was not visible). Z-tests for determining the significant difference between proportions were performed using VassarStats (http://faculty.vassar.edu/lowry/VassarStats.html). Mann-Whitney U tests were conducted to determine differences between rates of visual monitoring. Mann-Whitney U and Wilcoxon Signed Rank Tests were conducted using PASW Statistics v. 18.0 (SPSS Inc). Alpha levels were set at 0.05 and *p* values were two-tailed. Some follow-up analyses and analyses for affiliative behavior in the bachelor group were precluded due to low occurrences. Low occurrences of behavior in the family group also precluded analyses to determine associations between bachelor group visibility and breeding group behavior.

Table 2
Ethogram for behavioral observations

Behavior	Definition
Non-Contact Aggression	
Posture	Rigid quadrupedal stance (legs wide and rigid, arms rigid often with elbows rotated outward, body stiff and erect), weight on fingertips or knuckles (not wrists); often accompanied by pursed lip
Displace	One gorilla walks within 5 m of another gorilla resulting in relocation of the 2nd gorilla within 3 s of the approach
Herd	Gorilla walks behind another gorilla, resulting in the gorilla in front moving at least 30 m from their original spot; movement is simultaneous within 5 s; gorilla in front often looks over shoulder at gorilla following
Contact Aggression	
Hit/Kick	Vigorous contact with hand or foot (recipient can be another gorilla or object)
Object Throw	Gorilla tosses object in the direction of another gorilla
Bite	Gorilla clenches teeth and closes jaws around another gorilla
Affiliation	
Contact	Gorilla touches another gorilla for at least 3 s and is not performing any of the following: bite, hit/kick, groom, social play, solicitation, mount/copulate
Groom	Gorilla strokes against the grain of the hair, picks or licks the body of another gorilla
Social Play	Frivolous, exaggerated movements or actions. Includes laughing, mouthing, and play face
Solicitation	Gorilla gives an over the shoulder gaze or stare, pinches, or tags the genital region, or presents rear to another gorilla
Mount/Copulate	Dorso-ventral or ventro-ventral mounting with or without pelvic thrusting
Other	
Chest Beat	Gorilla hits own chest/abdomen area creating a popping noise
Vocalization	Gorilla produces contact call or purr vocalization
Monitor	Visual gaze/stare of gorilla in other group lasting at least 3 s, includes repositioning of the actor's body and head for better/continual viewing
Visible	Gorilla is potentially in sight of neighboring gorilla

Results

Visual Monitoring

The bachelor group spent more time visually monitoring the breeding group (M = 411.18 min, SE = 194.91) than the breeding group spent monitoring the bachelor group (M = 28.24 min, SE = 12.19; U = 5.33, p = 0.02). There was also a difference in visual monitoring between males (M = 341.47 min, SE = 166.30) and females (M = 16.77 min, SE = 5.85; U = 5.00, p = 0.03). However, there were no sex differences within the breeding group (male- M = 62.63 min, female- M = 16.77 min, SE = 5.85*;* U = 1.78 p = 0.18). On average, each member of the breeding group spent less than 1% of their time monitoring the bachelor group (see Table 3). In contrast, on average each member of the bachelor group spent nearly 8% of their time monitoring the breeding group. This was due to the large percentage of time two individuals spent monitoring the

breeding group (Zawadi: 10.30%; Spike: 16.12%). The other males in the bachelor group (Gus and Kejana) each spent less than 2% of their time observing the breeding group (see Table 3).

Table 3
Percentage of time each individual spent monitoring the neighboring group

Time spent monitoring bachelors	Gino	Benga	Hope	Kashata
	1.13%	0.47%	0.33%	0.11%
Time spent monitoring breeding group	Gus	Kejana	Zawadi	Spike
	1.53%	1.85%	10.30%	16.12%

Influence of Breeding Group Visibility

Non-contact aggression among the bachelors was higher when the silverback in the breeding group was visible to the bachelors than when he was not visible ($z = 2.57$, $p = 0.01$; see Figure 1). This was true when the silverback alone was visible to the bachelors ($z = 3.89$, $p < 0.01$) but not the case when he was visible with the adult females ($z = 1.79$, $p = 0.07$). There was no difference in non-contact aggression when the adult females, Hope, Benga, or Kashata were visible to the bachelors compared to when they were not visible ($z = 0.45$, $p = 0.96$; $z = -1.79$, $p = 0.07$; $z = 1.90$, $p = 0.06$, respectively; see Figure 1). Contact aggression did not increase with the presence of any members of the breeding group (Gino: $z = 0.98$, $p = 0.33$; Benga: $z = -1.72$, $p = 0.09$; Kashata: $z = -1.45$, $p = 0.46$); however, it did decrease when the adult female, Hope, was visible to them ($z = -2.31$, $p = 0.02$) (see Figure 2).

Chest beats by the bachelors increased when the breeding group silverback or the newest female (Kashata) were visible to the bachelors ($z = 3.06$, $p < 0.01$; $z = 2.11$, $p = 0.03$, respectively; see Figure 3). Rates of chest beats by the bachelors were not influenced by the visibility of the more established and familiar females (Hope and Benga) to the bachelors ($z = 1.04$, $p = 0.30$; $z = -0.25$, $p = 0.80$, respectively; see Figure 3). Bachelor males made more contact calls and purr vocalizations when any member of the breeding group was visible to them compared to when they were not visible (Gino: $z = 6.30$, $p < 0.01$; Hope: $z = 6.80$, $p < 0.01$; Benga: $z = 8.73$, $p < 0.001$; Kashata: $z = 5.52$, $p < 0.01$; see Figure 4). However, there was no difference between occurrences of vocalizations when the breeding group silverback was visible to the bachelors alone and when he was not visible ($z = 1.00$, $p = 0.32$).

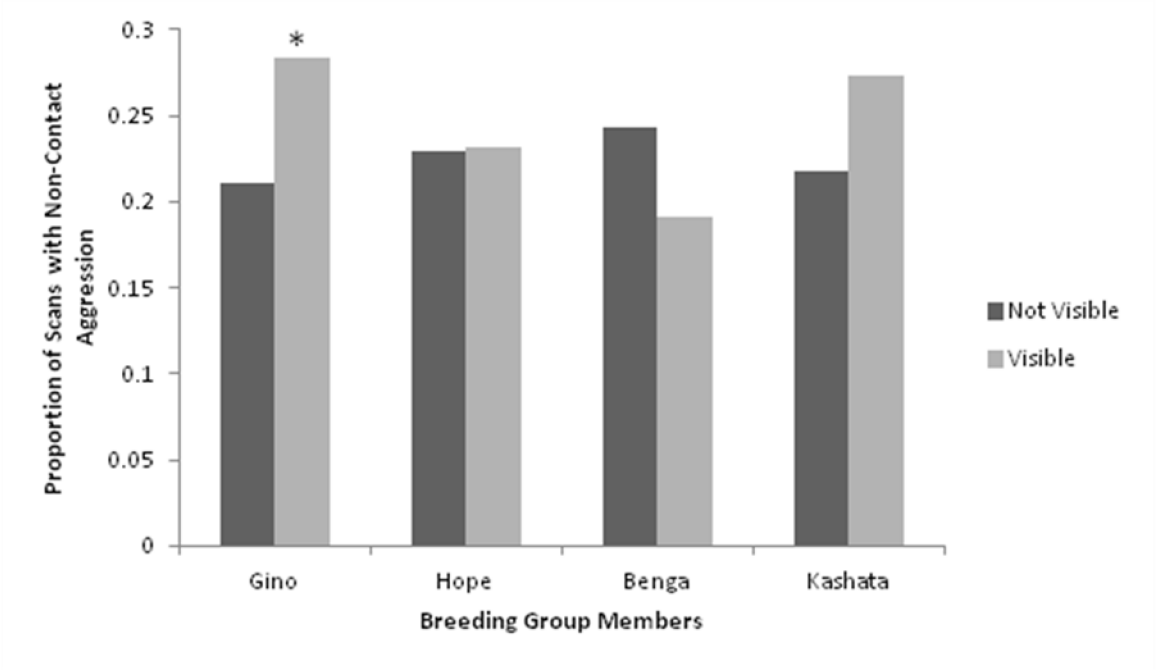

Figure 1. Proportion of scans when there was non-contact aggression in the bachelor group when individuals of the breeding group were visible and not visible. Asterisks indicate significant effects. Gino: silverback; Hope and Benga: established adult females; Kashata: newly introduced adult female.

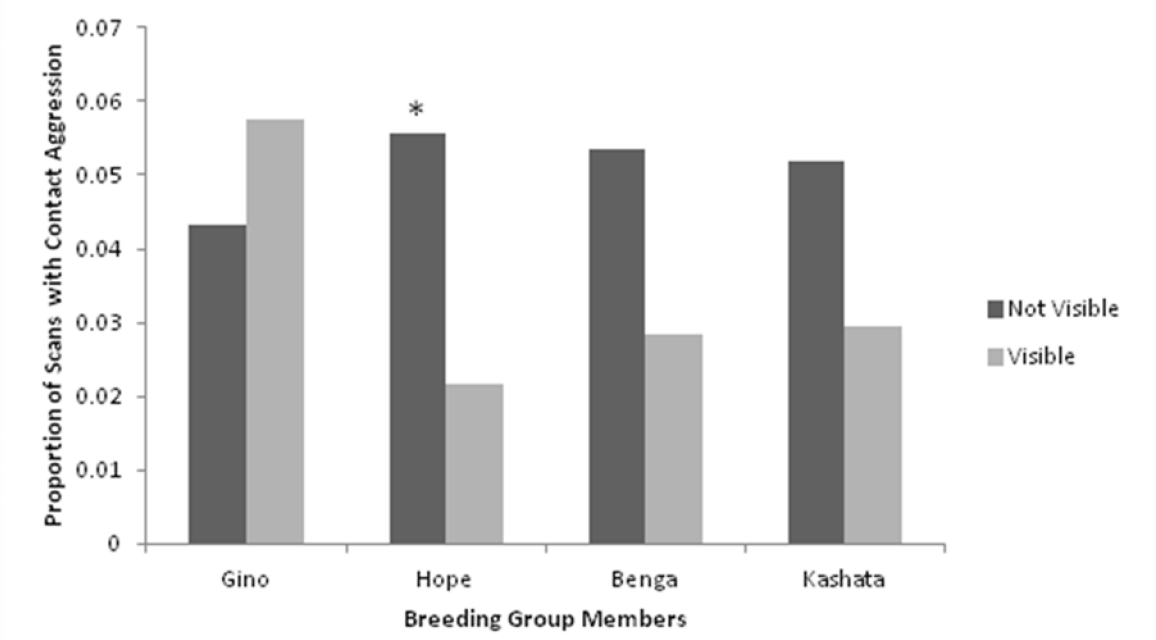

Figure 2. Proportion of scans when there was contact aggression in the bachelor group when individuals of the breeding group were visible and not visible. Asterisks indicate significant effects. Gino: silverback; Hope and Benga: established adult females; Kashata: newly introduced adult female.

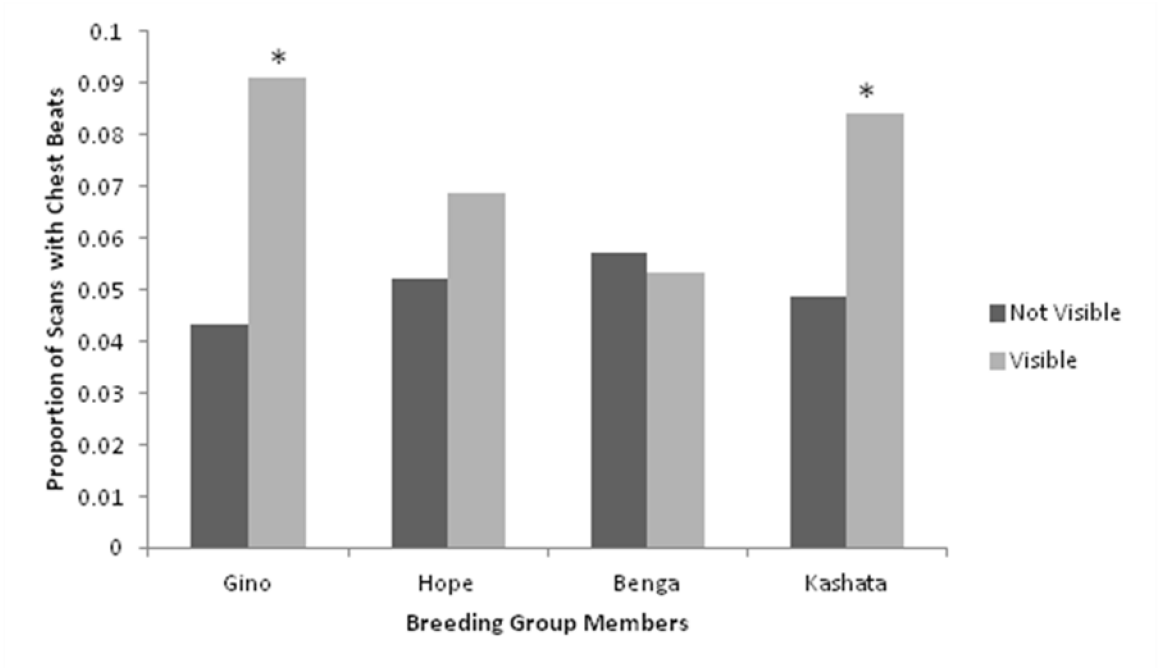

Figure 3. Proportion of scans when there was chest beating in the bachelor group when individuals of the breeding group were visible and not visible. Asterisks indicate significant effects. Gino: silverback; Hope and Benga: established adult females; Kashata: newly introduced adult female.

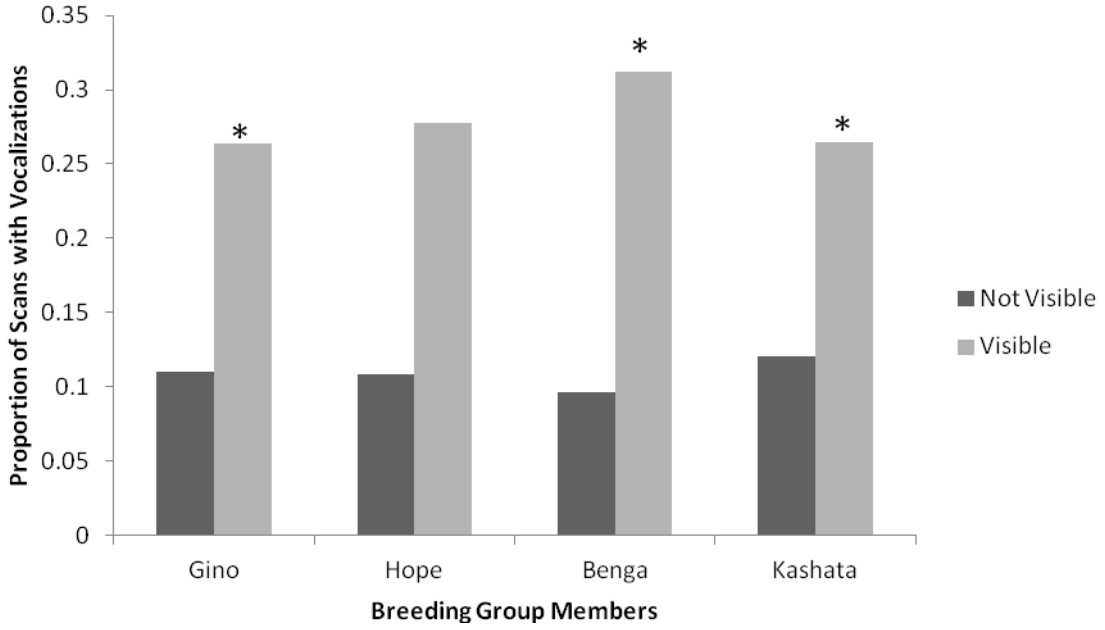

Figure 4. Proportion of scans when there was contact calls and purr vocalizations in the bachelor group when individuals of the breeding group were visible and not visible. Asterisks indicate significant effects. Gino: silverback; Hope and Benga: established adult females; Kashata: newly introduced adult female.

Discussion

The results of our study demonstrated that the behavior of animals housed in zoos can be influenced by neighboring groups. We found that our neighboring bachelor and breeding groups of gorillas did invest time visually monitoring each other and that aggression, vocalizations, and chest beats in the bachelor group were associated with the visual presence of individuals in the breeding group.

The percentage of time individual gorillas spent monitoring the neighboring group varied by group and individual. While on average individuals in the breeding group spent less than 1% of their time monitoring the bachelor group, bachelor males spent on average nearly 8% of their time monitoring the breeding group. Although we found that males monitored more than females, the effect was primarily driven by group (bachelor vs. breeding) differences since there were no sex differences within the breeding group. Two bachelor males in particular (Zawadi and Spike) spent a large percentage of time monitoring the breeding group. Although the motivation for their heightened monitoring is unknown, we do know that one of the individuals (Spike) is related to the established females (Hope and Benga). Also, prior to their transfer to Disney's Animal Kingdom®, Zawadi and Spike were housed at the same zoological institution (in a separate group) as the established members of the breeding group (Gino, Hope, and Benga). Therefore, familiarity early in life may play a role in visual monitoring of neighbors. Interestingly, in a previous study with these bachelor gorillas on their reactions to videos, these same individuals also spent more time than other gorillas watching videos portraying male and female gorillas, which included clips of the breeding group (Maloney, Leighty, Kuhar, & Bettinger, 2011).

Several behaviors in the bachelor group were associated with visibility of individuals in the breeding group. Consistent with anecdotal observations of higher levels of aggression in bachelor groups housed at institutions that also maintained breeding groups (Stoinski et al., 2004), we found increases in non-contact aggression in the bachelor group when a member of the breeding group was visible to them. In our study, non-contact aggression and chest beats in the bachelor group were more likely to occur when the silverback in the breeding group was visible; the presence of females and the presence of the breeding group silverback with females were not related to non-contact aggression. This suggests that it is the presence of the breeding group silverback that increases tensions in the bachelor group, expressed through an increase in posturing, charges, displacements, herding, and chest beats within the group. Visibility of the breeding group was not associated with an increase in more extreme forms of aggression (i.e., bites, hits, and throwing objects) in the bachelor group, and our data suggest that the presence of females may even help reduce contact aggression. Although the difference was modest, there was a significant reduction in contact aggression when one of the established and familiar females in the breeding group (Hope) was visible. Therefore, the influence of females on bachelor male behavior may depend on the history between neighbors and the amount of time the female has been part of the neighboring breeding group. Alternatively, it is also possible that the female preferred to spend time in view of the bachelor males when they were not involved in contact aggression.

The bachelors increased their contact calls and purr vocalizations when members of the breeding group were visible, which is similar to findings in wild populations of western lowland gorillas. This is an interesting finding given that these vocalizations have been interpreted as a means to maintain group cohesion or coordinate group activities (Harcourt & Stewart, 1996). However, the bachelor males did not vocalize more when the breeding group silverback was visible without females, suggesting that they were possibly vocalizing specifically to get the attention of the females. Chest beats, which have been proposed to demonstrate excitement in

addition to aggression, (see Maple & Hoff, 1982), also increased in the presence of the newly introduced female. From observations in the wild, it is believed that the strategy of males in bachelor groups or lone males is to remain in the periphery of breeding groups and attempt to attract females to establish a new breeding group (Levréro et al., 2006). Thus, bachelor males may be using chest beats, contact calls and purr vocalizations as part of a strategy to solicit females from the breeding group to transfer to their group.

Compared to mountain gorillas, western lowland gorillas are reported to have more frequent intergroup encounters and show greater tolerance to other groups, including outside males (Bermejo, 2004; Doran-Sheehy, Greer, Mongo, & Schwindt, 2004; Sicotte, 2001). Although there are no published data on the interactions between neighboring gorilla groups in zoos, previous literature has suggested that the presence of nearby breeding female gorillas may lead to instability in bachelor groups housed in zoos (Stoinksi et al., 2004). However, under our specific conditions, our bachelor group appeared to tolerate the presence of nearby breeding females. In addition to our institution, there are several zoological institutions that house multiple gorilla groups, which are sometimes housed in a way that allows for visual, auditory, and/or olfactory contact between groups. According to the 2011 AZA Population Analysis and Breeding Plan for western lowland gorillas, there are 73 bachelor males in 29 bachelor groups in 24 AZA institutions. Of the 29 institutions that house bachelor males, 13 institutions also house females (Lukas, Elsner, Long, & Groome, 2011). With continued breeding success and an increase in knowledge with regards to the establishment of bachelor groups, additional zoos could potentially expand their gorilla programs to include multiple breeding and/or bachelor groups. For this reason, it is important to determine the influence of neighboring gorilla groups housed in zoological parks.

In our study, we demonstrated that the visual presence of the silverback male of the breeding group was associated with increased aggressive threats and displays in the bachelor group. However, more extreme forms of aggression (i.e., aggression with the potential to cause injury) did not increase with the presence of the breeding group and actually decreased when a particular female (Hope) was in view. The amount of time bachelor males spent monitoring the breeding group coupled with the associations between female visibility and chest beats, purr vocalizations and contact calls, suggests that females do attract considerable attention from bachelor males. Our observations also suggest that familiarity early in life may be an important factor in these intergroup interactions. Therefore, zoos with bachelor and breeding groups in view should expect bachelor males to invest much time visually monitoring and trying to attract the attention of neighboring females.

Although our study investigated the influence of breeding group visibility on bachelor group behavior at our institution, future work should focus on documenting intergroup gorilla interactions at additional institutions with a wide range of housing conditions and social dynamics. Collecting systematic data on the influence of outside factors, such as neighboring groups, could greatly enhance an institution’s understanding of their gorillas. This information could provide gorilla managers and caregivers with a more complete view of the factors associated with gorilla behavior, allowing them to better understand and predict the behavior of the gorillas under their care.

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